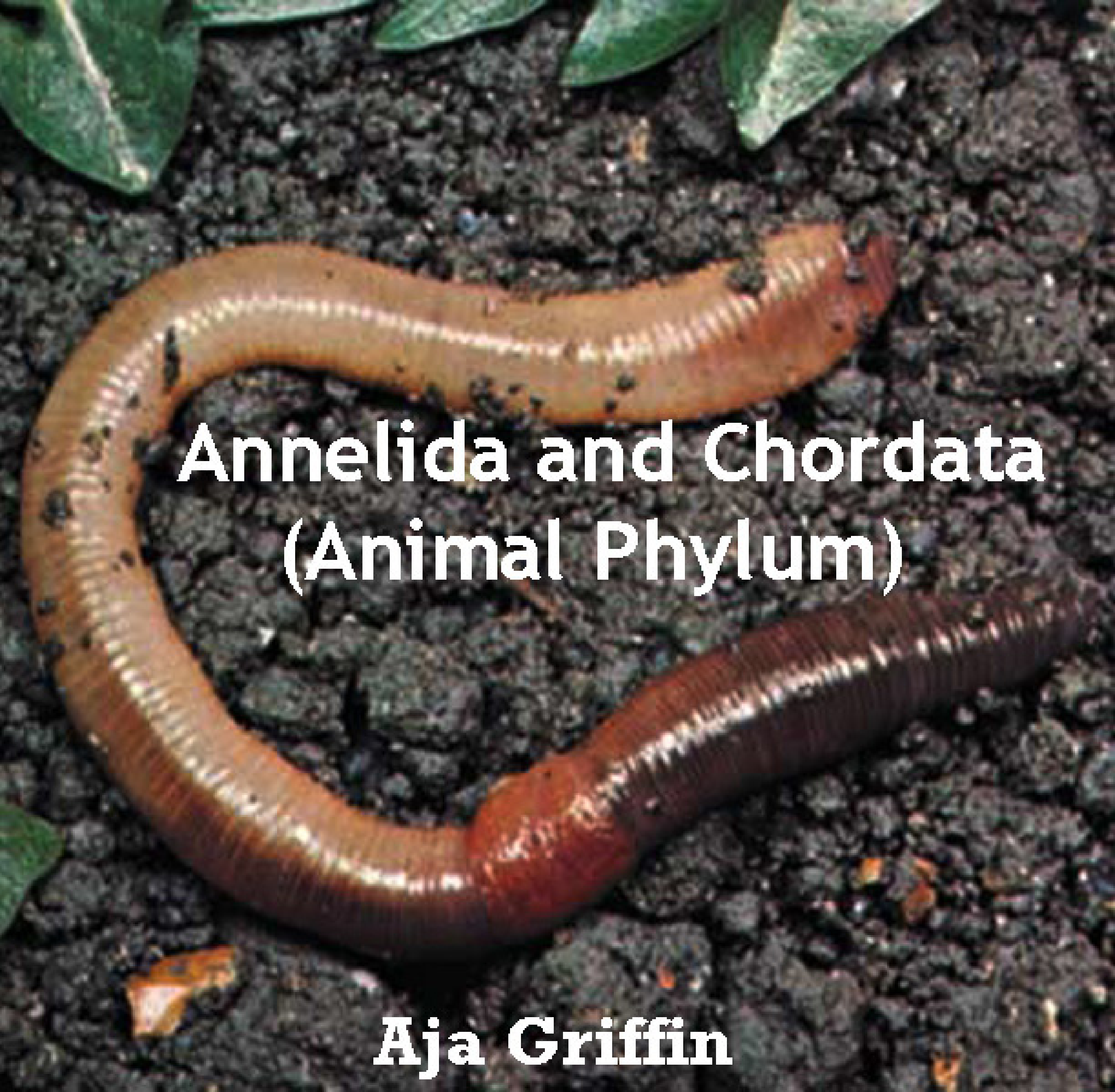

Annelida and Chordata (Animal Phylum)

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First Edition, 2012

ISBN 978-81-323-4084-3

Published by:
White Word Publications
4735/22 Prakashdeep Bldg,
Ansari Road, Darya Ganj,
Delhi - 110002
Email: info@wtbooks.com

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Annelid

Annelid
Temporal range: Early Ordovician–Recent

Glycera sp.

Scientific classification

Kingdom:	Animalia
Superphylum:	Lophotrochozoa
Phylum:	**Annelida** Lamarck, 1809

Classes and subclasses

Class Polychaeta (paraphyletic?)
Class Clitellata

Oligochaeta – earthworms, etc.
Branchiobdellida
Hirudinea – leeches
Class Myzostomida
Class Archiannelida
(polyphyletic)

The **annelids** (also called "ringed worms"), formally called **Annelida** (from French *annelés* "ringed ones", ultimately from Latin *anellus* "little ring"), are a large phylum of segmented worms, with over 17,000 modern species including ragworms, earthworms and leeches. They are found in marine environments from tidal zones to hydrothermal vents, in freshwater, and in moist terrestrial environments. Although most textbooks still use the traditional division into polychaetes (almost all marine), oligochaetes (which include earthworms) and leech-like species, research since 1997 has radically changed this scheme, viewing leeches as a sub-group of oligochaetes and oligochaetes as a sub-group of polychaetes. In addition, the Pogonophora, Echiura and Sipuncula, previously regarded as separate phyla, are now regarded as sub-groups of polychaetes. Annelids are considered members of the Lophotrochozoa, a "super-phylum" of protostomes that also includes molluscs, brachiopods, flatworms and nemerteans.

The basic annelid form consists of multiple segments, each of which has the same sets of organs and, in most polychaetes, a pair of parapodia that many species use for locomotion. Septa separate the segments of many species, but are poorly-defined or absent in some, and Echiura and Sipuncula show no obvious signs of segmentation. In species with well-developed septa, the blood circulates entirely within blood vessels, and the vessels in segments near the front ends of these species are often built up with muscles to act as hearts. The septa of these species also enable them to change the shapes of individual segments, which facilitates movement by peristalsis ("ripples" that pass along the body) or by undulations that improve the effectiveness of the parapodia. In species with incomplete septa or none, the blood circulates through the main body cavity without any kind of pump, and there is a wide range of locomotory techniques – some burrowing species turn their pharynges inside out to drag themselves through the sediment.

Although many species can reproduce asexually and use similar mechanisms to regenerate after severe injuries, sexual reproduction is the normal method in species whose reproduction has been studied. The minority of living polychaetes whose reproduction and lifecycles are known produce trochophore larvae, which live as plankton and then sink and metamorphose into miniature adults. Oligochaetes are full hermaphrodites and produce a ring-like cocoon round their bodies, in which the eggs and hatchlings are nourished until they are ready to emerge.

Earthworms support terrestrial food chains both as prey and by aerating and enriching soil. The burrowing of marine polychaetes, which may constitute up to a third of all species in near-shore environments, encourages the development of ecosystems by enabling water and oxygen to penetrate the sea floor. In addition to improving soil fertility, annelids serve humans as food and as bait. Scientists observe annelids to monitor the quality of marine and fresh water. Although blood-letting is no longer in favor with doctors, some leech species are regarded as endangered species because they have been over-harvested for this purpose in the last few centuries. Ragworms' jaws are now being studied by engineers as they offer an exceptional combination of lightness and strength.

Since annelids are soft-bodied, their fossils are rare – mostly jaws and the mineralized tubes that some of the species secreted. Although some late Ediacaran fossils may represent annelids, the oldest known fossil that is identified with confidence comes from about 518 million years ago in the early Cambrian period. Fossils of most modern mobile polychaete groups appeared by the end of the Carboniferous, about 299 million years ago. Scientists disagree about whether some body fossils from the mid Ordovician, about 472 to 461 million years ago, are the remains of oligochaetes, and the earliest certain fossils of the group appear in the Tertiary period, which began 65 million years ago.

Classification and diversity

There are over 17,000 living annelid species, ranging in size from microscopic to the Australian giant Gippsland earthworm, which can grow up to 3 metres (9.8 ft) long. Although research since 1997 has radically changed scientists' views about the evolutionary family tree of the annelids, most textbooks use the traditional classification into the following sub-groups:

- **Polychaetes** (about 12,000 species). As their name suggests, they have multiple chetae ("hairs") per segment. Polychaetes have parapodia that function as limbs, and nuchal organs ("nuchal" means "on the neck") that are thought to be chemosensors. Most are marine animals, although a few species live in fresh water and even fewer on land.

An earthworm's clitellum

- **Clitellates** (about 5,000 species). These have few or no chetae per segment, and no nuchal organs or parapodia. However, they have a unique reproductive organ, the ring-shaped clitellum ("pack saddle") round their bodies, which produces a cocoon that stores and nourishes fertilized eggs until they hatch. The clitellates are sub-divided into:
    - **Oligochaetes** ("with few hairs"), which includes earthworms. Oligochaetes have a sticky pad in the roof of the mouth. Most are burrowers that feed on wholly or partly decomposed organic materials.
    - **Hirudinea**, whose name means "leech-shaped" and whose best known members are leeches. Marine species are mostly blood-sucking parasites, mainly on fish, while most freshwater species are predators. They have suckers at both ends of their bodies, and use these to move rather like inchworms.

The Archiannelida, minute annelids that live in the spaces between grains of sediment, were treated as a separate class because of their simple body structure, but are now regarded as polychaetes. Some other groups of animals have been classified in various ways, but are now widely regarded as annelids:

- Pogonophora / Siboglinidae were first discovered in 1914, and their lack of a recognizable gut made it difficult to classify them. They have been classified as a separate phylum, Pogonophora, or as two phyla, Pogonophora and Vestimentifera. More recently they have been re-classified as a family, Siboglinidae, within the polychaetes.
- The Echiura have a checkered taxonomic history: in the 19th century they were assigned to the phylum "Gephyrea", which is now empty as its members have been assigned to other phyla; the Echiura were next regarded as annelids until the 1940s, when they were classified as a phylum in their own right; but a molecular phylogenetics analysis in 1997 concluded that Echiurans are annelids.
- Myzostomida live on crinoids and other echinoderms, mainly as parasites. In the past they have been regarded as close relatives of the trematode flatworms or of the tardigrades, but in 1998 it was suggested that they are a sub-group of polychaetes. However, another analysis in 2002 suggested that myzostomids are more closely related to flatworms or to rotifers and acanthocephales.

Distinguishing features

No single feature distinguishes Annelids from other invertebrate phyla, but they have a distinctive combination of features. Their bodies are long, with segments that are divided externally by shallow ring-like constrictions called annuli and internally by septa ("partitions") at the same points, although in some species the septa are incomplete and in a few cases missing. Most of the segments contain the same sets of organs, although sharing a common gut, circulatory system and nervous system makes them inter-dependent. Their bodies are covered by a cuticle (outer covering) that does not contain cells but is secreted by cells in the skin underneath, is made of tough but flexible collagen and does not molt – on the other hand arthropods' cuticles are made of the more rigid α-chitin, and molt until the arthropods reach their full size. Most annelids have closed circulatory systems, where the blood makes its entire circuit via blood vessels.

Summary of distinguishing features

	Annelida	**Recently merged into Annelida**		**Closely-related**	**Similar-looking phyla**	
		Echiura	**Sipuncula**	**Nemertea**	**Arthropoda**	**Onychophora**
External segmentation	Yes	no	no	Only in a few species	Yes, except in mites	no
Repetition of internal organs	Yes	no	no	Yes	In primitive forms	Yes
Septa between segments	In most species	no	no	No	No	No
Cuticle material	collagen	collagen	collagen	none	α-chitin	α-chitin
Molting	Generally no; but some polychaetes molt their jaws, and leeches molt their skins	no	no	no	Yes	Yes
Body cavity	Coelom; but this is reduced or missing in many leeches and some small polychaetes	2 coeloms, main and in proboscis	2 coeloms, main and in tentacles	Coelom only in proboscis	Hemocoel	Hemocoel
Circulatory system	Closed in most species	Open outflow, return via branched vein	Open	Closed	Open	Open

Description

Most of an annelid's body consists of segments that are practically identical, having the same sets of internal organs and external chaetae (Greek χαιτη, meaning "hair") and, in some species, appendages. However, the frontmost and rearmost sections are not regarded as true segments as they do not contain the standard sets of organs and do not develop in the same way as the true segments. The frontmost section, called the prostomium (Greek προ- meaning "in front of" and στομα meaning "mouth") contains the brain and sense organs, while the rearmost, called the pygidium (Greek πυγιδιον, meaning "little tail") contains the anus, generally on the underside. The first section behind the prostomium, called the peristomium (Greek περι- meaning "around" and στομα meaning "mouth"), is regarded by some zoologists as not a true segment, but in some polychaetes the peristomium has chetae and appendages like those of other segments.

The segments develop one at a time from a growth zone just ahead of the pygidium, so that an annelid's youngest segment is just in front of the growth zone while the peristomium is the oldest. This pattern is called teloblastic growth. Some groups of annelids, including all leeches, have fixed maximum numbers of segments, while others add segments throughout their lives.

The phylum's name is derived from the Latin word *annelus*, meaning "little ring".

Body wall, chetae and parapodia

Annelids' cuticles are made of collagen fibers, usually in layers that spiral in alternating directions so that the fibers cross each other. These are secreted by the one-cell deep epidermis (outermost skin layer). A few marine annelids that live in tubes lack cuticles, but their tubes have a similar structure, and mucus-secreting glands in the epidermis protect their skins. Under the epidermis is the dermis, which is made of connective tissue, in other words a combination of cells and non-cellular materials such as collagen. Below this are two layers of muscles, which develop from the lining of the coelom (body cavity): circular muscles make a segment longer and slimmer when they contract, while under them are longitudinal muscles, usually four distinct strips, whose contractions make the segment shorter and fatter. Some annelids also have oblique internal muscles that connect the underside of the body to each side.

The chetae ("hairs") of annelids project out from the epidermis to provide traction and other capabilities. The simplest are unjointed and form paired bundles near the top and bottom of each side of each segment. The parapodia ("limbs") of annelids that have them often bear more complex chetae at their tips – for example jointed, comb-like or hooked. Chetae are made of moderately flexible β-chitin and are formed by follicles, each of which has a chaetoblast ("hair-forming") cell at the bottom and muscles that can extend or retract the cheta. The chetoblasts produce chetae by forming microvilli, fine hair-like extensions that increase the area available for secreting the cheta. When the cheta is complete, the microvilli withdraw into the chetoblast, leaving parallel tunnels that run almost the full length of the cheta. Hence annelids' chetae are structurally different from the setae ("bristles") of arthropods, which are made of the more rigid α-chitin, have a single internal cavity, and are mounted on flexible joints in shallow pits in the cuticle.

Nearly all polychaetes have parapodia that function as limbs, while other major annelid groups lack them. Parapodia are unjointed paired extensions of the body wall, and their muscles are derived from the circular muscles of the body. They are often supported internally by one or more large, thick chetae. The parapodia of burrowing and tube-dwelling polychaetes are often just ridges whose tips bear hooked chetae. In active crawlers and swimmers the parapodia are often divided into large upper and lower paddles on a very short trunk, and the paddles are generally fringed with chetae and sometimes with cirri (fused bundles of cilia) and gills.

Nervous system and senses

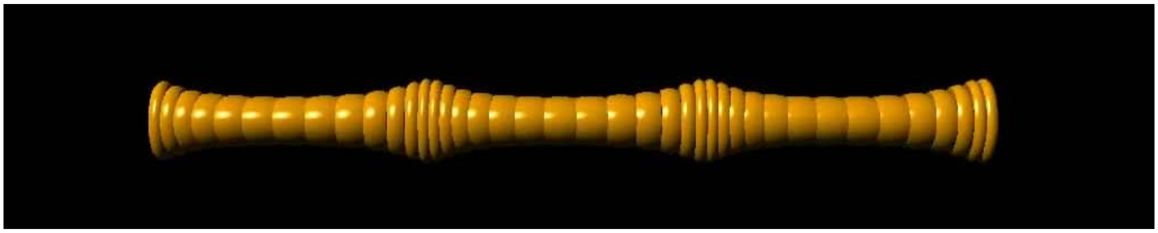
The brain generally forms a ring round the pharynx (throat), consisting of a pair of ganglia (local control centers) above and in front of the pharynx, linked by nerve cords either side of the pharynx to another pair of ganglia just below and behind it. The brains of polychaetes are generally in the prostomium, while those of clitellates are in the peristomium or sometimes the first segment behind the peristomium. In some very mobile and active polychaetes the brain is enlarged and more complex, with visible hindbrain, midbrain and forebrain sections. The rest of the central nervous system is generally "ladder-like", consisting of a pair of nerve cords that run through the bottom part of the body and have in each segment paired ganglia linked by a transverse connection. From each segmental ganglion a branching system of local nerves runs into the body wall and then encircles the body. However, in most polychaetes the two main nerve cords are fused, and in the tube-dwelling genus *Owenia* the single nerve chord has no ganglia and is located in the epidermis.

As in arthropods, each muscle fiber (cell) is controlled by more than one neuron, and the speed and power of the fiber's contractions depends on the combined effects of all its neurons. Vertebrates have a different system, in which one neuron controls a group of muscle fibers. Most annelids' longitudinal nerve trunks include giant axons (the output signal lines of nerve cells). Their large diameter decreases their resistance, which allows them to transmit signals exceptionally fast. This enables these worms to withdraw rapidly from danger by shortening their bodies. Experiments have shown that cutting the giant axons prevents this escape response but does not affect normal movement.

The sensors are primarily single cells that detect light, chemicals, pressure waves and contact, and are present on the head, appendages (if any) and other parts of the body. Nuchal ("on the neck") organs are paired, ciliated structures found only in polychaetes, and are thought to be chemosensors. Some polychaetes also have various combinations of ocelli ("little eyes") that detect the direction from which light is coming and camera eyes or compound eyes that can probably form images. The compound eyes probably evolved independently of arthropods' eyes. Some tube-worms use ocelli widely spread over their bodies to detect the shadows of fish, so that they can quickly withraw into their tubes. Some burrowing and tube-dwelling polychaetes have statocysts (tilt and balance sensors) that tell them which way is down. A few polychaete genera have on the undersides of their heads palps that are used both in feeding and as "feelers", and some of these also have antennae that are structurally similar but probably are used mainly as "feelers".

Coelom, locomotion and circulatory system

Most annelids have a pair of coeloms (body cavities) in each segment, separated from other segments by septa and from each other by vertical mesenteries. Each septum forms a sandwich with connective tissue in the middle and mesothelium (membrane that serves as a lining) from the preceding and following segments on either side. Each mesentery is similar except that the mesothelium is the lining of each of the pair of coeloms, and the blood vessels and, in polychaetes, the main nerve cords are embedded in it. The mesothelium is made of modified epitheliomuscular cells, in other words their bodies form part of the epithelium but their bases extend to form muscle fibers in the body wall. The mesothelium may also form radial and circular muscles on the septa, and circular muscles around the blood vessels and gut. Parts of the mesothelium, especially on the outside of the gut, may also form chloragogen cells that perform similar functions to the livers of vertebrates: producing and storing glycogen and fat; producing the oxygen-carrier hemoglobin; breaking down proteins; and turning nitrogenous waste products into ammonia and urea to be excreted.



Peristalsis moves this "worm" to the right

Many annelids move by peristalsis (waves of contraction and expansion that sweep along the body), or flex the body while using parapodia to crawl or swim. In these animals the septa enable the circular and longitudinal muscles to change the shape of individual segments, by making each segment a separate fluid-filled "balloon". However, the septa are often incomplete in annelids that are semi-sessile or that do not move by peristalsis or by movements of parapodia – for example some move by whipping movements of the body, some small marine species move by means of cilia (fine muscle-powered hairs) and some burrowers turn their pharynges (throats) inside out to penetrate the sea-floor and drag themselves into it.

The fluid in the coeloms contains coelomocyte cells that defend the animals against parasites and infections. In some species coelomocytes may also contain a respiratory pigment – red hemoglobin in some species, green chlorocruorin in others – and provide oxygen transport within their segments. Respiratory pigment is also dissolved in the blood plasma. Species with well-developed septa generally also have blood vessels running all long their bodies above and below the gut, the upper one carrying blood forwards while the lower one carries it backwards. Networks of capillaries (fine blood vessels) in the body wall and around the gut transfer blood between the main blood vessels and to parts of the segment that need oxygen and nutrients. Both of the major vessels, especially the upper one, can pump blood by contracting. In some annelids the forward end of the upper blood vessel is enlarged with muscles to form a heart, while in the forward ends of many earthworms some of the vessels that connect the upper and lower main vessels function as hearts. Species with poorly-developed or no septa generally have no blood vessels and rely on the circulation within the coelom for delivering nutrients and oxygen.

However, leeches and their closest relatives have a body structure that is very uniform within the group but significantly different from that of other annelids, including other members of the Clitellata. In leeches there are no septa, the connective tissue layer of the body wall is so thick that it occupies much of the body, and the two coeloms are widely separated and run the length of the body. They function as the main blood vessels, although they are side-by-side rather than upper and lower. However, they are lined with mesothelium, like the coeloms and unlike the blood vessels of other annelids. Leeches generally use suckers at their front and rear ends to move like inchworms. The anus is on the upper surface of the pygidium.

Respiration

In some annelids, including earthworms, all respiration is via the skin. However, many polychaetes and some clitellates (the group to which earthworms belong) have gills associated with most segments, often as extensions of the parapodia in polychaetes. The gills of tube-dwellers and burrowers usually cluster around whichever end has the stronger water flow.

Feeding and excretion

Feeding structures in the mouth region vary widely, and have little correlation with the animals' diets. Many polychaetes have a muscular pharynx that can be everted (turned inside out to extend it). In these animals the foremost few segments often lack septa so that, when the muscles in these segments contract, the sharp increase in fluid pressure from all these segments everts the pharynx very quickly. Two families, the Eunicidae and Phyllodocidae, have evolved jaws, which can be used for seizing prey, biting off pieces of vegetation, or grasping dead and decaying matter. On the other hand some predatory polychaetes have neither jaws nor eversible pharynges. Selective deposit feeders generally live in tubes on the sea-floor and use palps to find food particles in the sediment and then wipe them into their mouths. Filter feeders use "crowns" of palps covered in cilia that wash food particles towards their mouths. Non-selective deposit feeders ingest soil or marine sediments via mouths that are generally unspecialized. Some clitellates have sticky pads in the roofs of their mouths, and some of these can evert the pads to capture prey. Leeches often have an eversible proboscis, or a muscular pharynx with two or three teeth.

The gut is generally an almost straight tube supported by the mesenteries (vertical partitions within segments), and ends with the anus on the underside of the pygidium. However, in members of the tube-dwelling family Siboglinidae the gut is blocked by a swollen lining that houses symbiotic bacteria, which can make up 15% of the worms' total weight. The bacteria convert inorganic matter – such as hydrogen sulfide and carbon dioxide from hydrothermal vents, or methane from seeps – to organic matter that feeds themselves and their hosts, while the worms extend their palps into the gas flows to absorb the gases needed by the bacteria.

Annelids with blood vessels use metanephridia to remove soluble waste products, while those without use protonephridia. Both of these systems use a two-stage filtration process, in which fluid and waste products are first extracted and these are filtered again to re-absorb any re-usable materials while dumping toxic and spent materials as urine. The difference is that protonephridia combine both filtration stages in the same organ, while metanephridia perform only the second filtration and rely on other mechanisms for the first – in annelids special filter cells in the walls of the blood vessels let fluids and other small molecules pass into the coelomic fluid, where it circulates to the metanephridia. In annelids the points at which fluid enters the protonephridia or metanephridia are on the forward side of a septum while the second-stage filter and the nephridiopore (exit opening in the body wall) are in the following segment. As a result the hindmost segment (before the growth zone and pygidium) has no structure that extracts its wastes, as there is no following segment to filter and discharge them, while the first segment contains an extraction structure that passes wastes to the second, but does not contain the structures that re-filter and discharge urine.

Reproduction and life cycle

Asexual reproduction

This sabellid tubeworm is budding

Polychaetes can reproduce asexually, by dividing into two or more pieces or by budding off a new individual while the parent remains a complete organism. Some oligochaetes, such as *Aulophorus furcatus*, seem to reproduce entirely asexually, while others reproduce asexually in summer and sexually in autumn. Asexual reproduction in oligochaetes is always by dividing into two or more pieces, rather than by budding. However, leeches have never been seen reproducing asexually.

Most polychaetes and oligochaetes also use similar mechanisms to regenerate after suffering damage. Two polychaete genera, *Chaetopterus* and *Dodecaceria*, can regenerate from a single segment, and others can regenerate even if their heads are removed. Annelids are the most complex animals that can regenerate after such severe damage. On the other hand leeches cannot regenerate.

Sexual reproduction

It is thought that annelids were originally animals with two separate sexes, which released ova and sperm into the water via their nephridia. The fertilized eggs develop into trochophore larvae, which live as plankton. Later they sink to the sea-floor and metamorphose into miniature adults: the part of the trochophore between the apical tuft and the prototroch becomes the prostomium (head); a small area round the trochophore's anus becomes the pygidium (tail-piece); a narrow band immediately in front of that becomes the growth zone that produces new segments; and the rest of the trochophore becomes the peristomium (the segment that contains the mouth).

However, the lifecycles of most living polychaetes, which are almost all marine animals, are unknown, and only about 25% of the 300+ species whose lifecycles are known follow this pattern. About 14% use a similar external fertilization but produce yolk-rich eggs, which reduce the time the larva needs to spend among the plankton, or eggs from which miniature adults emerge rather than larvae. The rest care for the fertilized eggs until they hatch – some by producing jelly-covered masses of eggs which they tend, some by attaching the eggs to their bodies and a few species by keeping the eggs within their bodies until they hatch. These species use a variety of methods for sperm transfer; for example, in some the females collect sperm released into the water, while in others the males have penes that inject sperm into the female. There is no guarantee that this is a representative sample of polychaetes' reproductive patterns, and it simply reflects scientists' current knowledge.

Some polychaetes breed only once in their lives, while others breed almost continuously or through several breeding seasons. While most polychaetes remain of one sex all their lives, a significant percentage of species are full hermaphrodites or change sex during their lives. Most polychaetes whose reproduction has been studied lack permanent gonads, and it is uncertain how they produce ova and sperm. In a few species the rear of the body splits off and becomes a separate individual that lives just long enough to swim to a suitable environment, usually near the surface, and spawn.

Most mature clitellates (the group that includes earthworms and leeches) are full hermaphrodites, although in a few leech species younger adults function as males and become female at maturity. All have well-developed gonads, and all copulate. Earthworms store their partners' sperm in spermathecae ("sperm stores") and then the clitellum produces a cocoon that collects ova from the ovaries and then sperm from the spermathecae. Fertilization and development of earthworm eggs takes place in the cocoon. Leeches' eggs are fertilized in the ovaries, and then transferred to the cocoon. In all clitellates the cocoon also either produces yolk when the eggs are fertilized or nutrients while they are developing. All clitellates hatch as miniature adults rather than larvae.

Ecological significance

Charles Darwin's book *The Formation of Vegetable Mould through the Action of Worms* (1881) presented the first scientific analysis of earthworms' contributions to soil fertility. Some burrow while others live entirely on the surface, generally in moist leaf litter. The burrowers loosen the soil so that oxygen and water can penetrate it, and both surface and burrowing worms help to produce soil by mixing organic and mineral matter, by accelerating the decomposition of organic matter and thus making it more quickly available to other organisms, and by concentrating minerals and converting them to forms that plants can use more easily. Earthworms are also important prey for birds ranging in size from robins to storks, and for mammals ranging from shrews to badgers, and in some cases conserving earthworms may be essential for conserving endangered birds.

Marine annelids may account for over one-third of bottom-dwelling animal species round coral reefs and in tidal zones. Burrowing species increase the penetration of water and oxygen and water into the sea-floor sediment, which encourages the growth of populations of bacteria and small animals alongside their burrows.

Although blood-sucking leeches do little direct harm to their victims, some transmit flagellates that can be very dangerous to their hosts. Some small tube-dwelling oligochaetes transmit myxosporean parasites that cause whirling disease in fish.

Interaction with humans

Earthworms make a significant contribution to soil fertility. The rear end of the Palolo worm, a marine polychaete that tunnels through coral, detaches in order to spawn at the surface, and the people of Samoa regard these spawning modules as a delicacy. Anglers sometimes find that worms are more effective bait than artificial flies, and worms can be kept for several days in a tin lined with damp moss. Ragworms are commercially important as bait and as food sources for aquaculture, and there have been proposals to farm them in order to reduce over-fishing of their natural populations. Some marine polychaetes' predation on molluscs causes serious losses to fishery and aquaculture operations.

Scientists study aquatic annelids to monitor the oxygen content, salinity and pollution levels in fresh and marine water.

Accounts of the use of leeches for the medically dubious practise of blood-letting have come from China around 30 AD, India around 200 AD, ancient Rome around 50 AD and later throughout Europe. In the 19th century medical demand for leeches was so high that some areas' stocks were exhausted and other regions imposed restrictions or bans on exports, and *Hirudo medicinalis* is treated as an endangered species by both IUCN and CITES. More recently leeches have been used to assist in microsurgery, and their saliva has provided anti-inflammatory compounds and several important anticoagulants, one of which also prevents tumors from spreading.

Ragworms' jaws are strong but much lighter than the hard parts of many other organisms, which are biomineralized with calcium salts. These advantages have attracted the attention of engineers. Investigations showed that ragworm jaws are made of unusual proteins that bind strongly to zinc.

Evolutionary history

Fossil record

Since annelids are soft-bodied, their fossils are rare. Polychaetes' fossil record consists mainly of the jaws that some species had and the mineralized tubes that some secreted. Some Ediacaran fossils such as *Dickinsonia* in some ways resemble polychaetes, but the similarities are too vague for these fossils to be classified with confidence. The small shelly fossil *Cloudina*, from 549 to 542 million years ago, has been classified by some authors as an annelid, but by others as a cnidarian (i.e. in the phylum to which jellyfish and sea anemones belong). Until 2008 the earliest fossils widely accepted as annelids were the polychaetes *Canadia* and *Burgessochaeta*, both from Canada's Burgess Shale, formed about 505 million years ago in the early Cambrian. *Myoscolex*, found in Australia and a little older than the Burgess Shale, was possibly an annelid. However, it lacks some typical annelid features and has features which are not usually found in annelids and some of which are associated with other phyla. Then Simon Conway Morris and John Peel reported *Phragmochaeta* from Sirius Passet, about 518 million years old, and concluded that it was the oldest annelid known to date. There has been vigorous debate about whether the Burgess Shale fossil *Wiwaxia* was a mollusc or an annelid. Polychaetes diversified in the early Ordovician, about 488 to 474 million years ago. It is not until the early Ordovician that the first annelid jaws are found, thus the crown-group cannot have appeared before this date and probably appeared somewhat later. By the end of the Carboniferous, about 299 million years ago, fossils of most of the modern mobile polychaete groups had appeared. Many fossil tubes look like those made by modern sessile polychaetes, but the first tubes clearly produced by polychaetes date from the Jurassic, less than 199 million years ago.

The earliest good evidence for oligochaetes occurs in the Tertiary period, which began 65 million years ago, and it has been suggested that these animals evolved around the same time as flowering plants in the early Cretaceous, from 130 to 90 million years ago. A trace fossil consisting of a convoluted burrow partly filled with small fecal pellets may be evidence that earthworms were present in the early Triassic period from 251 to 245 million years ago. Body fossils going back to the mid Ordovician, from 472 to 461 million years ago, have been tentatively classified as oligochaetes, but these identifications are uncertain and some have been disputed.

Family tree

Traditionally the annelids have been divided into two major groups, the polychaetes and clitellates. In turn the clitellates were divided into oligochaetes, which include earthworms, and hirudinomorphs, whose best-known members are leeches. For many years there was no clear arrangement of the approximately 80 polychaete families into higher-level groups. In 1997 Greg Rouse and Kristian Fauchald attempted a "first heuristic step in terms of bringing polychaete systematics to an acceptable level of rigour", based on anatomical structures, and divided polychaetes into:

- Scolecida, less than 1,000 burrowing species that look rather like earthworms.
- Palpata, the great majority of polychaetes, divided into:
  - Canalipalpata, which are distinguished by having long grooved palps that they use for feeding, and most of which live in tubes.
  - Aciculata, the most active polychaetes, which have parapodia reinforced by internal spines (aciculae).

Also in 1997 Damhnait McHugh, using molecular phylogenetics to compare similarities and differences in one gene, presented a very different view, in which: the clitellates were an off-shoot of one branch of the polychaete family tree; the pogonophorans and echiurans, which for a few decades had been regarded as a separate phyla, were placed on other branches of the polychaete tree. Subsequent molecular phylogenetics analyses on a similar scale presented similar conclusions.

In 2007 Torsten Struck and colleagues compared 3 genes in 81 taxa, of which 9 were outgroups, in other words not considered closely related to annelids but included to give an indication of where the organisms under study are placed on the larger tree of life. For a cross-check the study used an analysis of 11 genes (including the original 3) in 10 taxa. This analysis agreed that clitellates, pogonophorans and echiurans were on various branches of the polychaete family tree. It also concluded that the classification of polychaetes into Scolecida, Canalipalpata and Aciculata was useless, as the members of these alleged groups were scattered all over the family tree derived from comparing the 81 taxa. In addition, it also placed sipunculans, generally regarded at the time as a separate phylum, on another branch of the polychaete tree, and concluded that leeches were a sub-group of oligochaetes rather than their sister-group among the clitellates. Rouse accepted the analyses based on molecular phylogenetics, and their main conclusions are now the scientific consensus, although the details of the annelid family tree remain uncertain.

In addition to re-writing the classification of annelids and 3 previously independent phyla, the molecular phylogenetics analyses undermine the emphasis that decades of previous writings placed on the importance of segmentation in the classification of invertebrates. Polychaetes, which these analyses found to be the parent group, have completely segmented bodies, while polychaetes' echiurans and sipunculan offshoots are not segmented and pogonophores are segmented only in the rear parts of their bodies. It now seems that segmentation can appear and disappear much more easily in the course of evolution than was previously thought. The 2007 study also noted that the ladder-like nervous system, which is associated with segmentation, is less universal than previously thought in both annelids and arthropods.

Annelids are members of the protostomes, one of the two major superphyla of bilaterian animals – the other is the deuterostomes, which includes vertebrates. Within the protostomes, annelids used to be grouped with arthropods under the super-group Articulata ("jointed animals"), as segmentation is obvious in most members of both phyla. However, the genes that drive segmentation in arthropods do not appear to do the same in annelids. Arthropods and annelids both have close relatives that are unsegmented. It is at least as easy to assume that they evolved segmented bodies independently as it is to assume that the ancestral protostome or bilaterian was segmented and that segmentation disappeared in many descendant phyla. The current view is that annelids are grouped with molluscs, brachiopods and several other phyla that have lophophores (fan-like feeding structures) and/or trochophore larvae as members of Lophotrochozoa. Bryzoa may be the most basal phylum (the one that first became distinctive) within the Lophotrochozoa, and the relationships between the other members are not yet known. Arthropods are now regarded as members of the Ecdysozoa ("animals that molt"), along with some phyla that are unsegmented.

The "Lophotrochozoa" hypothesis is also supported by the fact that many phyla within this group, including annelids, molluscs, nemerteans and flatworms, follow a similar pattern in the fertilized egg's development. When their cells divide after the 4-cell stage, descendants of these 4 cells form a spiral pattern. In these phyla the "fates" of the embryo's cells, in other words the roles their descendants will play in the adult animal, are the same and can be predicted from a very early stage. Hence this development pattern is often described as "spiral determinate cleavage".

Chapter- 2

Polychaete

Polychaetes
Temporal 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

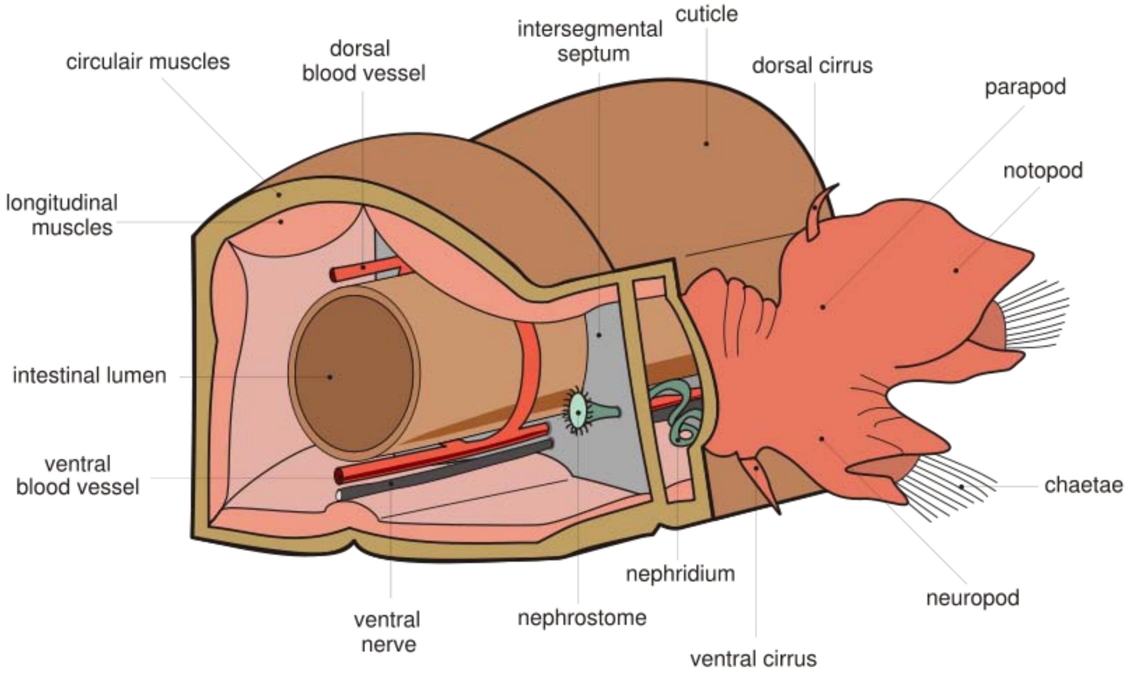
Polychaetes are segmented worms, generally less than 10 centimetres (3.9 in) in length, although ranging at the extremes from 1 millimetre (0.039 in) to 3 metres (9.8 ft). They are often brightly coloured, and may be iridescent or even luminescent. Each segment bears a pair of paddle-like and highly 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.

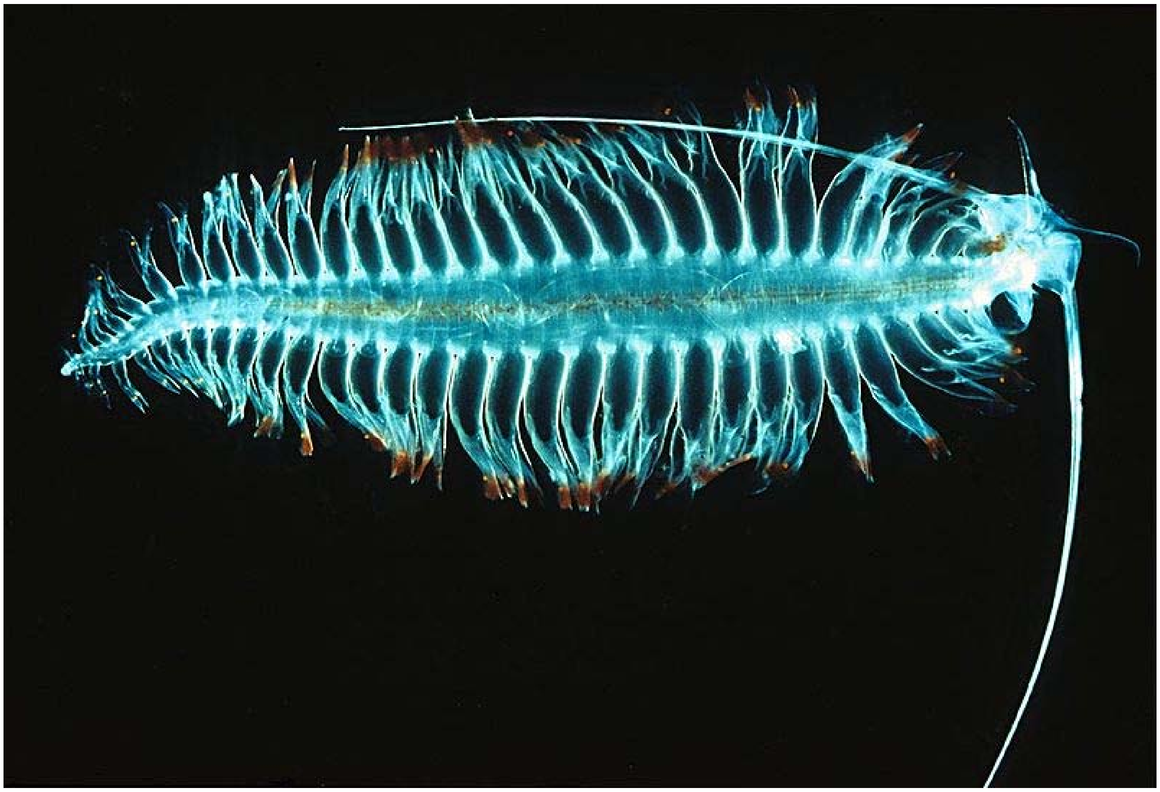
Ecology

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

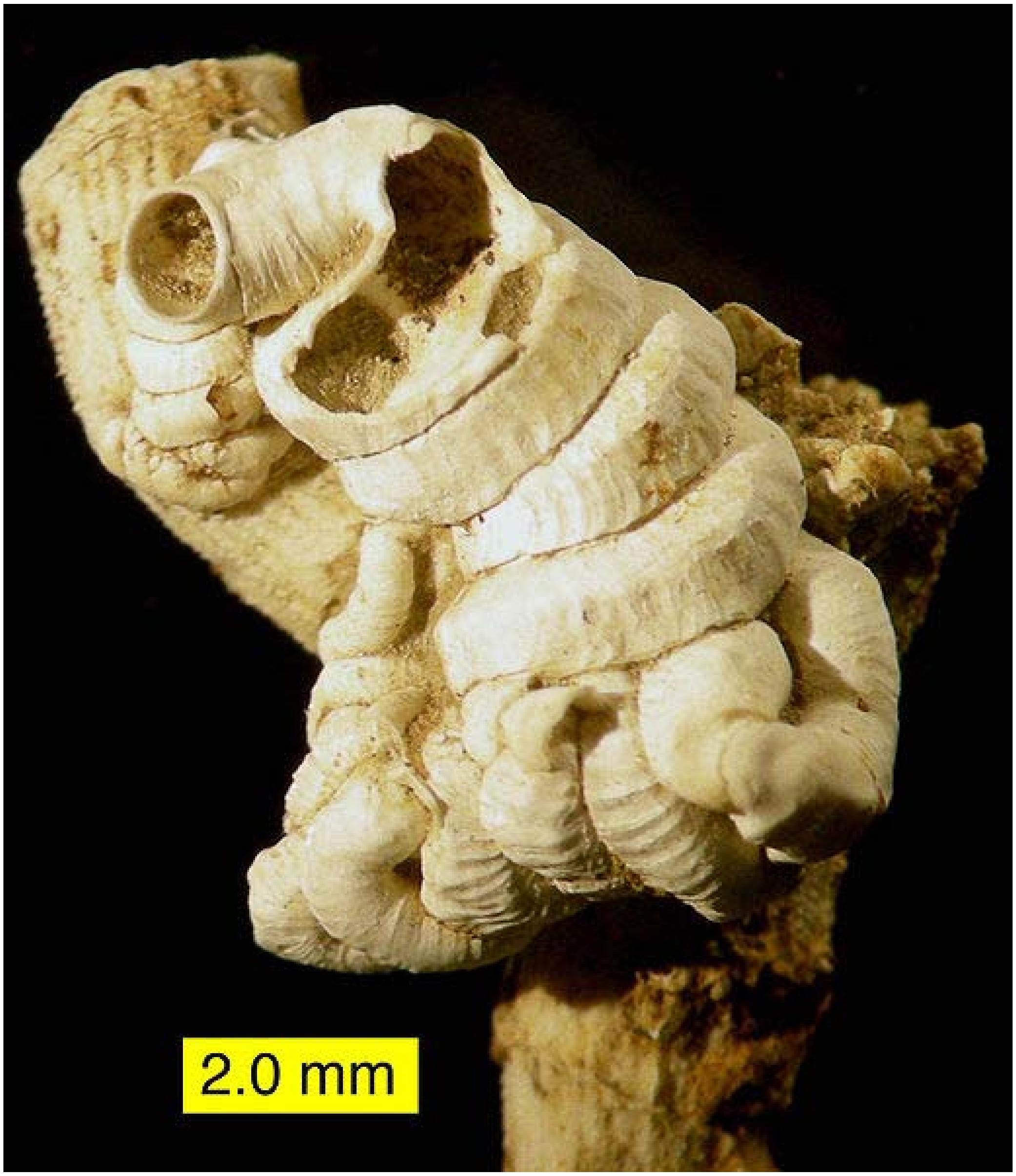
Most polychaetes have separate sexes, rather than being hermaphroditic. The most primitive species have a pair of gonads in every segment, but, in most species, there has been some degree of specialisation. The gonads shed immature gametes directly into the body cavity, where they complete their development. 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 Sphaeodoridae
- Family Syllidae
- Family Typhloscolecidae

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

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

Chapter- 3

Clitellata and Oligochaeta

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.

Oligochaeta

Oligochaeta

Earthworm (*Lumbricus terrestris*)

Scientific classification

Kingdom:	Animalia
Phylum:	Annelida
Class:	Clitellata
Subclass:	**Oligochaeta**

Orders

Haplotaxida
Lumbriculida
Moniligastrida

Oligochaeta 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

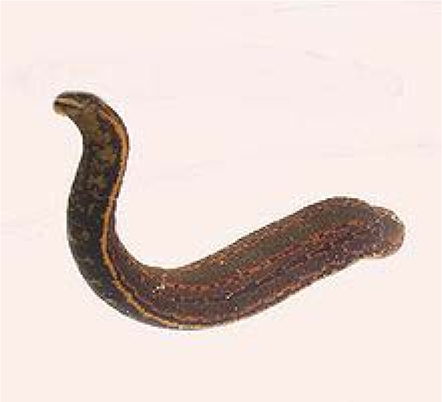
- Randiellidae (Erséus & Strehlow, 1986)
- Tubificidae (Vejdovsky, 1884 (including Naidinae Ehrenberg, 1831))
- Narapidae (Righi, 1983)
- Opistocystidae (Cernosvitov, 1936)
- Dorydrilidae (Cook, 1971)
- Parvidrilidae (Erséus, 1999)
- Phreodrilidae (Beddard, 1891)
- Propappidae (Coates, 1986)
- Haplotaxidae (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.

Chapter- 4

Leech

Leech



Hirudo medicinalis

Scientific classification	
Kingdom:	Animalia
Phylum:	Annelida
Class:	Nasteh
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.

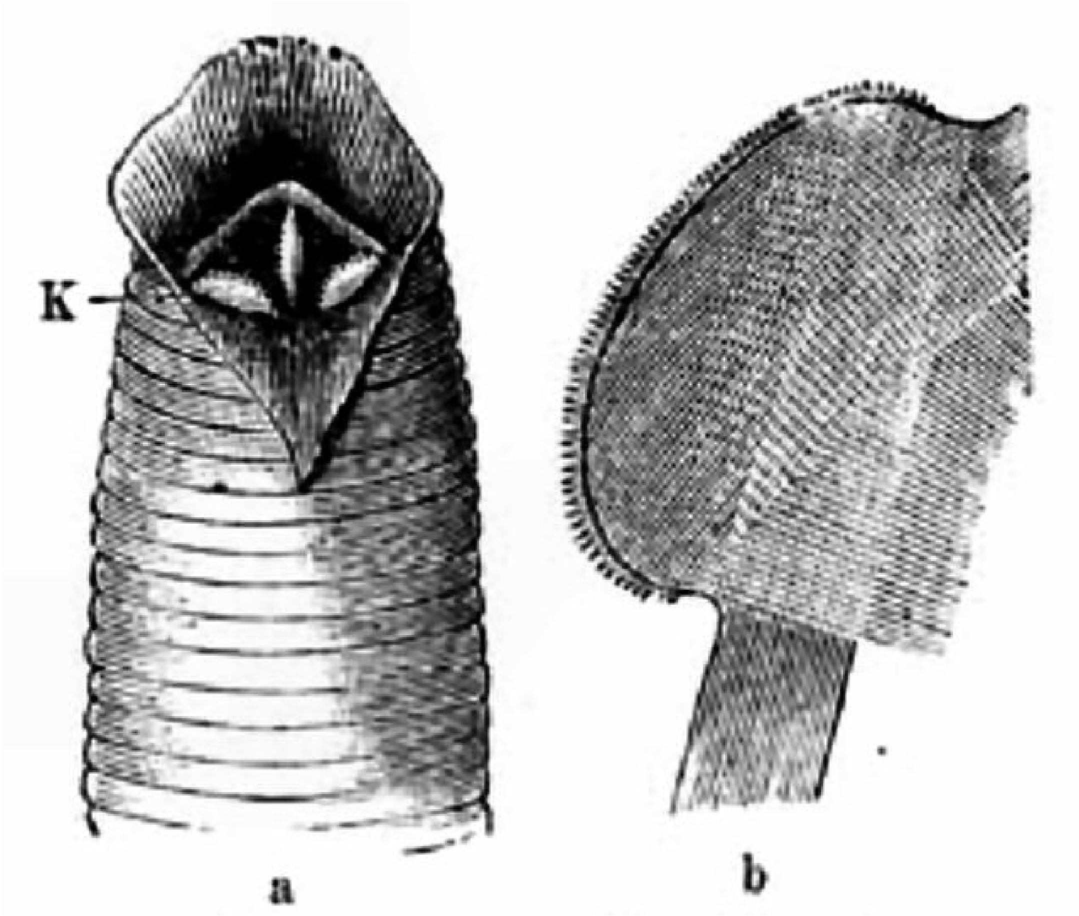
- Arhynchobdellida: Leeches which lack a proboscis and which may or may not have jaws armed with teeth. Arhynchobellids are divided into two orders:
    - Gnathobdela: In this order of "jawed" leeches, armed with teeth, is found the quintessential leech: the European medical (bloodsucking) leech, *Hirudo 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. 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,then to the gizzard, 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.

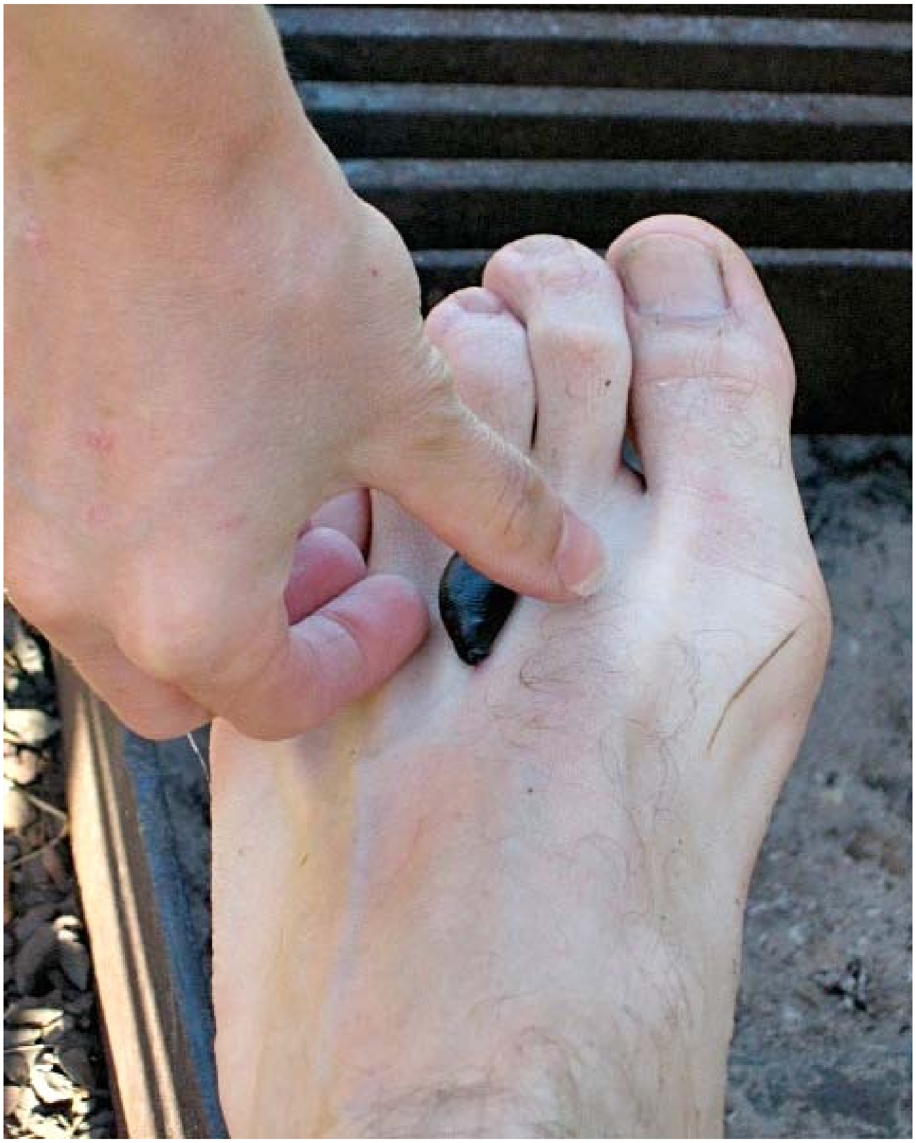
Leech bites

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 can 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.

Common but medically inadvisable techniques to remove a leech are 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, which may be anywhere from 20 min. to 2 hours or more. Usually an hour is needed After finishing his dinner the leech will detach and move away or just roll off that portion of the body. 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. Bleeding time will vary with location (some areas of the back bleed less than areas on the calves or thighs for example). Bleeding time may vary from just a few hours to perhaps as much as three days. This is a function of not only the hirudin but of other compounds(unspecified) that reduce the surface tension of the blood. Another factor would be if the patient were on anti-clotting medications at the time of leech therapy. 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.

Chapter- 5

Echiura and Haplodrili

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.

Echiurans 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

Echiurans 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.

Haplodrili

Haplodrili, or **Archiannelida**, is a primitive marine worm part of the annelid phylum. Zoologist Ray Lankester gave it its name of Haplodrili, while zoologist Berthold Hatschek named it Archiannelida.

Overview

Polygordius and Protodrilus live in sand, but while the former moves by means of the contraction of its body-wall muscles, Protodrilus can progress by the action of the bands of cilia surrounding its segments, and of the longitudinal ciliated ventral groove. Saccocirrus, which also lives in sand, and more closely resembles the Polychaeta, has throughout the greater length of its body on each segment a pair of small uniramous parapodia bearing a bunch of simple setae. No other member of the group is known to have any trace of setae or parapodia at any stage of development.

Commonality

These three genera have the following characters in common. The body is small and resembles polychaete larvae, epidermis ciliated, the number of segments varies from five and up or can be completely absent, small prostomium with or without appendages, parapodia absent, septa reduced or absent, the nervous system consists of a brain and longitudinal ventral nerve cords closely connected with the epidermis (withotit distinct ganglia), widely separated in Saccocirrus, closely approximated in Protodrilus, fused together in Polygordius; the coelom is well developed and the dorsal and ventral longitudinal mesenteries are complete; the nephridia are simple, and open into the coelom. Polygordius differs from Protodrilus and Saccocirrus in the absence of a distinct suboesophageal muscular pouch, and in the absence of a peculiar closed cavity in the head region, which is especially well developed in Saccocirrus, and probably represents the specialized coelom of the first segment.

Moreover, in Saccocirrus the genital organs of a transverse section of Saccocirrus showing on the left side the organs in a genital segment of a male, and on the right side the organs in a genital segment of a female.

Chapter- 6

Earthworm

Earthworms

Lumbricus terrestris, the Common Earthworm

Scientific classification

Kingdom:	Animalia
Phylum:	Annelida
Class:	Clitellata
Order:	Haplotaxida
Suborder:	**Lumbricina**

Families

Acanthodrilidae
Ailoscolidae
Alluroididae
Almidae (disputed)

Criodrilidae
Eudrilidae
Exxidae
Glossoscolecidae
Hormogastridae
Lumbricidae
Lutodrilidae
Megascolecidae
Microchaetidae
Ocnerodrilidae
Octochaetidae
Sparganophilidae

Earthworm is the common name for the largest members of Oligochaeta (which is either a class or subclass depending on the author) in the phylum Annelida. In classical systems they were placed in the order **Opisthopora**, on the basis of the male pores opening posterior to the female pores, even though the internal male segments are anterior to the female. Theoretical cladistic studies have placed them instead in the suborder **Lumbricina** of the order Haplotaxida, but this may again soon change. Folk names for the earthworm include "dew-worm", "Rainworm", "night crawler" and "angleworm" (due to its use as fishing bait).

Earthworms are also called **megadriles** (or big worms), as opposed to the microdriles (or small worms) in the families Tubificidae, Lumbriculidae, and Enchytraeidae, among others. The megadriles are characterized by having a distinct clitellum (which is much more obvious than the single-layered one of the microdriles) and a vascular system with true capillaries.

Anatomy

The basic body plan of an earthworm is a tube, the digestive system, within a tube, the muscular slimy, moist outer body. The body is annular, formed of segments that are most specialized in the anterior. Earthworms have a simple closed circulatory system. They have two main blood vessels that extend through the length of their body: a ventral blood vessel which leads the blood to the posterior end, and a dorsal blood vessel which leads to the anterior end. The dorsal vessel is contractile and pumps blood forward, where it is pumped into the ventral vessel by a series of "hearts" (aortic arches) which vary in number in the different taxa. The blood is distributed from the ventral vessel into capillaries on the body wall and other organs and into a vascular sinus in the gut wall, where gases and nutrients are exchanged. This arrangement may be complicated in the various groups by suboesophageal, supraoesophageal, parietal and neural vessels, but the basic arrangement holds in all earthworms. Most earthworms are decomposers feeding on undecayed leaf and other plant matter, others are more geophagous.

Reproduction

Earthworm reproduction

Earthworms are hermaphrodites: They typically have two pairs of testes, surrounded by 2 pairs of testes sacs. There are 2 or 4 pairs of seminal vesicles which produce, store and release the sperm via the male pores, and ovaries and ovipores in segment 13 that release eggs via female pores on segment 14. However, most also have one or more pairs of spermathecae (depending on the species) that are internal sacs which receive and store sperm from the other worm in copulation. Some species use external spermatophores for transfer instead.

Earthworm cocoons from *L. terrestris*

An earthworm cocoon from *L. rubellus*

Copulation and reproduction are separate processes in earthworms. The mating pair overlap front ends ventrally and each exchanges sperm with the other. The clitellum becomes very reddish to pinkish in color. The cocoon, or egg case, is secreted by the clitellum band which is near the front of the worm, but behind the spermathecae. Some time after copulation, long after the worms have separated, the clitellum secretes the cocoon which forms a ring around the worm. The worm then backs out of the ring, and as it does so, injects its own eggs and the other worm's sperm into it. As the worm slips out, the ends of the cocoon seal to form a vaguely lemon-shaped incubator (cocoon) in which the embryonic worms develop. They emerge as small, but fully formed earthworms, except for a lack of the sex structures, which develop later in about 60 to 90 days. They attain full size in about one year, sometimes sooner. Scientists predict that the average lifespan under field conditions is 4–8 years, still most garden varieties live only one to two years. Several common earthworm species are mostly parthenogenetic, that is, with asexual reproduction resulting in clones.

Digestion

There is a digestion system in an earthworm. The process of nutrition begins in the mouth, where food is sucked in by a muscular pharynx. From there, food goes down the esophagus through peristalsis(muscle contractions.) After this, the food is stored in the crop, which retains food and has the ability to expand. From there, food goes into the gizzard where sand and muscular contractions churn the food and increase the surface area. From there, food enters the intestine which has the ability to absorb food, then food exits through the anus. A rectum is unnecessary because an earthworm is in a moist environment and thus does not require water reclamation.

Regeneration

Earthworms have the ability to regenerate lost segments, but this ability varies between species and depends on the extent of the damage. Stephenson (1930) devoted a chapter of his monograph to this topic, while G.E. Gates spent 20 years studying regeneration in a variety of species, but “because little interest was shown”, Gates (1972) only published a few of his findings that, nevertheless, show it is theoretically possible to grow two whole worms from a bisected specimen in certain species. Gates’s reports included:

- *Eisenia fetida* (Savigny, 1826) with head regeneration, in an anterior direction, possible at each intersegmental level back to and including 23/24, while tails were regenerated at any levels behind 20/21.
- *Lumbricus terrestris* Linneus, 1758 replacing anterior segments from as far back as 13/14 and 16/17 but tail regeneration was never found.
- *Perionyx excavatus* Perrier, 1872 readily regenerated lost parts of the body, in an anterior direction from as far back as 17/18, and in a posterior direction as far forward as 20/21.
- *Lampito mauritii* Kinberg, 1867 with regeneration in anterior direction at all levels back to 25/26 and tail regeneration from 30/31; head regeneration was sometimes believed to be caused by internal amputation resulting from *Sarcophaga* sp. larval infestation.
- *Criodrilus lacuum* Hoffmeister, 1845 also has prodigious regenerative capacity with ‘head’ regeneration from as far back as 40/41.

An unidentified Tasmanian earthworm shown growing a second head is reported here:.

Behavior

Rainstorms and "Stranding" Behavior

Earthworms can sometimes be found on the surface of the ground following heavy rain storms, as a storm may flood the soil with excessive water. However, if the surface where they find themselves is unexpectedly paved, rocky, or compacted (hardened), they may become stranded, potentially suffering injury or death from causes such as heat, exposure, dehydration, or predation. Note, there are some earthworm species that can survive for several days in water if it is sufficiently oxygenated.

Earthworms may also come to the surface during rain in order to mate, and therefore, an alternative hypothesis concerning "stranding" behavior is that as some species (notably *Lumbricus terrestris*) come to the surface to mate they may become stranded. However, this behavior is limited to only a few species and *L. terrestris* is rarely, if ever, one of those found stranded on impermeable surfaces, this hypothesis does not seem likely to be true.

Another hypothesis is that the worms may be using the moist conditions on the surface to travel more quickly than they can underground, thus moving to and colonizing new areas more quickly. Since the relative humidity of the surface and air is higher during and after rain, they do not become dehydrated quite as rapidly. However, if true, this is a very risky behavior near dawn, in high summer, or in the daytime, since earthworms die quickly when exposed to direct sunlight with its high heat, light and strong UV content, and are more vulnerable to predators such as birds.

An earthworm being eaten by an American Robin

A further hypothesis is that, because there are many other organisms beside the earthworm in the ground as well, and these organisms all tend to increase respiration as water content of the soil increases, carbon dioxide gas may dissolve into the rainwater forming a higher than usual acid content carbonic acid in the soil area. As the soil becomes too acidic for the worms, they seek a more neutral environment on the surface.

Locomotion and importance to soil

Close up of an earthworm in garden soil

Earthworms travel underground by the means of waves of muscular contractions which alternately shorten and lengthen the body. The shortened part is anchored to the surrounding soil by tiny claw-like bristles (setae) set along its segmented length. In all the body segments except the first, last and clitellum, there is a ring of S-shaped setae embedded in the epidermal pit of each segment (perichaetine). The whole burrowing process is aided by the secretion of lubricating mucus. Worms can make gurgling noises underground when disturbed as a result of the worm moving through its lubricated tunnels. They also work as biological "pistons" forcing air through the tunnels as they move. Thus earthworm activity aerates and mixes the soil, and is constructive to mineralization and nutrient uptake by vegetation. Certain species of earthworm come to the surface and graze on the higher concentrations of organic matter present there, mixing it with the mineral soil. Because a high level of organic matter mixing is associated with soil fertility, an abundance of earthworms is beneficial to the organic gardener. In fact as long ago as 1881 Charles Darwin wrote: *It may be doubted whether there are many other animals which have played so important a part in the history of the world, as have these lowly organized creatures.*

Benefits

The major benefits of earthworm activities to soil fertility can be summarized as:

- **Biological**. In many soils, earthworms play a major role in converting large pieces of organic matter (e.g. dead leaves) into rich humus, and thus improving soil fertility. This is achieved by the worm's actions of pulling down below any organic matter deposited on the dried dirt, such as leaf fall or manure, either for food or when it needs to plug its burrow. Once in the burrow, the worm will shred the leaf and partially digest it, then mingle it with the earth by saturating it with intestinal secretions. Worm casts (see below) can contain 40% more humus than the top 9" of soil in which the worm is living.

Faeces in form of casts

- **Chemical**. As well as dead organic matter, the earthworm also ingests any other soil particles that are small enough—including stones up to 1/20 of an inch (1.25mm) across—into its gizzard wherein minute fragments of grit grind everything into a fine paste which is then digested in the intestine. When the worm excretes this in the form of casts which are deposited on the surface or deeper in the soil, minerals and plant nutrients are made available in an accessible form. Investigations in the US show that fresh earthworm casts are 5 times richer in available nitrogen, 7 times richer in available phosphates and 11 times richer in available potash than the surrounding upper 6 inches (150 mm) of soil. In conditions where there is plenty of available humus, the weight of casts produced may be greater than 4.5 kg (10 lb) per worm per year, in itself an indicator of why it pays the gardener or farmer to keep worm populations high.
- **Physical**. By its burrowing actions, the earthworm is of great value in keeping the soil structure open, creating a multitude of channels which allow the processes of both aeration and drainage to occur. Permaculture co-founder Bill Mollison points out that by sliding in their tunnels, earthworms "act as an innumerable army of pistons pumping air in and out of the soils on a 24 hour cycle (more rapidly at night)". Thus the earthworm not only creates passages for air and water to traverse, but is itself a vital component in the living biosystem that is healthy soil. Earthworms continue to move through the soil due to the excretion of mucus into the soil that acts as a lubricant for easier movement of the worm.

The earthworm's existence cannot be taken for granted. Dr. W. E. Shewell Cooper observed "tremendous numerical differences between adjacent gardens" (*Soil, Humus And Health*), and worm populations are affected by a host of environmental factors, many of which can be influenced by good management practices on the part of the gardener or farmer.

Darwin estimated that arable land contains up to 53,000 worms per acre (13/m^2), but more recent research from Rothamsted Experimental Station has produced figures suggesting that even poor soil may support 250,000/acre (62/m^2), whilst rich fertile farmland may have up to 1,750,000/acre (432/m^2), meaning that the weight of earthworms beneath the farmer's soil could be greater than that of his livestock upon its surface. One thing is certain however: rich, fertile soil that is cared for organically and well-fed and husbanded by its steward will reap its reward in a healthy worm population, whilst denuded, overworked, and eroded land will almost certainly contain fewer, scrawny, undernourished specimens.

Earthworms as invasive species

From a total of around 6,000 species, only about 120 species are widely distributed around the world. These are the peregrine or cosmopolitan earthworms.

Australia

Australia has 650 known species of native earthworm that survive in both rich and in nutrient-poor conditions where they may be sensitive to changes in the environment. Introduced species are commonly found in agricultural environments along with persistent natives. Most of the 75 or so exotics have been accidentally introduced into Australia. The total species numbers are predicted to exceed 2,000.

North America

A total of approximately 182 earthworm taxa in 12 families are reported from America north of Mexico, i.e., USA & Canada, of which 60 (ca. 33%) are exotic/introduced. Only two genera of Lumbricid earthworms are indigenous to North America while introduced genera have spread to areas where earthworms did not formerly exist, especially in the north where forest development relies on a large amount of undecayed leaf matter. When worms decompose that leaf layer, the ecology may shift making the habitat unsurvivable for certain species of trees, ferns and wildflowers. Another possible ecologic impact of greater earthworm numbers: larger earthworms (e.g. the night crawler, *Lumbricus terrestris*, and the Alabama jumper, *Amynthas agrestis*) can be eaten by adult salamanders, and when the salamanders do consume the earthworms they are more successful at reproduction. However, those earthworms are too large for juvenile salamanders to consume, which leads to a net loss in salamander population.

Currently there is no economically feasible method for controlling invasive earthworms in forests. Earthworms normally spread slowly, but can be quickly introduced by human activities such as construction earthmoving, or by fishermen releasing bait, or by plantings.

United Kingdom

A recent threat to earthworm populations in the UK is the New Zealand Flatworm (*Artiposthia triangulata*), which feeds upon the earthworm, but in the UK has no natural predator itself. At present sightings of the New Zealand flatworm have been mainly localised, but this is no reason for complacency as it has spread extensively since its introduction in 1960 through contaminated soil and plant pots. Any sightings of the flatworm should be reported to the Scottish Crop Research Institute, which is monitoring its spread.

Special habitats

While, as the name *earthworm* suggests, the main habitat of earthworms is in soil, the situation is more complicated than that. The brandling worm *Eisenia fetida* lives in decaying plant matter and manure. *Arctiostrotus vancouverensis* from Vancouver Island and the Olympic Peninsula is generally found in decaying conifer logs or in extremely acidic humus. *Aporrectodea limicola* and *Sparganophilus* and several others are found in mud in streams. Some species are arboreal. Even in the soil species, there are special habitats, such as soils derived from serpentine which have an earthworm fauna of their own.

Ecology

Earthworms are classified into three main ecophysiological categories: (1) leaf litter/compost dwelling worms (epigeic) e.g. *Eisenia fetida*; (2) topsoil or subsoil dwelling worms (endogeics); and (3) worms that construct permanent deep burrows through which they visit the surface to obtain plant material for food, such as leaves (anecic), e.g. *Lumbricus terrestris*.

Permanent vertical burrow

Earthworm populations depend on both physical and chemical properties of the soil, such as soil temperature, moisture, pH, salts, aeration and texture, as well as available food, and the ability of the species to reproduce and disperse. One of the most important environmental factors is pH, but earthworms vary in their preferences. Most earthworms favor neutral to slightly acidic soil. However, *Lumbricus terrestris* are still present in a pH of 5.4 and *Dendrobaena octaedra* at a pH of 4.3 and some Megascolecidae are present in extremely acid humic soils. Soil pH may also influence the numbers of worms that go into diapause. The more acidic the soil, the sooner worms go into diapause, and remain in diapause the longest time at a pH of 6.4.

Ocypus olens trying to prey on *Lumbricus* sp.

Earthworms form the base of many food chains. They are preyed upon by many species of birds (e.g. starlings, thrushes, gulls, crows, European Robins and American Robins), snakes, mammals (e.g. bears, foxes, hedgehogs, moles) and invertebrates (e.g. ground beetles and other beetles, snails, slugs). Earthworms have many internal parasites including Protozoa, Platyhelminthes, Nematodes; they can be found in the worms' blood, seminal vesicles, coelom, intestine, or in the cocoons.

The application of chemical fertilizers, sprays and dusts can have a disastrous effect on earthworm populations. Nitrogenous fertilizers tend to create acid conditions, which are fatal to the worms, and often dead specimens are to be found on the surface following the application of substances like DDT, lime sulphur and lead arsenate. In Australia, changes in farming practices such as the application of superphosphates on pastures and a switch from pastoral farming to arable farming had a devastating effect on populations of the Giant Gippsland earthworm leading to their classification as a protected species.

Therefore, the most reliable way to maintain or increase the levels of worm population in the soil is to avoid the application of artificial chemicals. Adding organic matter, preferably as a surface mulch, on a regular basis will provide them with their food and nutrient requirements, and also creates the optimum conditions of heat (cooler in summer and warmer in winter) and moisture to stimulate their activity.

Economic impact

Various species of worms are used in vermiculture, the practice of feeding organic waste to earthworms to decompose and compost food waste. These are usually *Eisenia fetida* (or its close relative *Eisenia andrei*) or the Brandling worm, also known as the Tiger worm or Red Wiggler, and are distinct from soil-dwelling earthworms.

Earthworms are sold all over the world. The earthworm market is sizable. According to Doug Collicut, "In 1980, 370 million worms were exported from Canada, with a Canadian export value of $13 million and an American retail value of $54 million."

Earthworms are also sold as food for human consumption. Noke is a culinary term used by the Māori of New Zealand, to refer to earthworms which are considered delicacies.

Taxonomy and distribution

The families, with distribution of the main ones:

- Acanthodrilidae: Africa, midland and southeastern North America, Central and South America, Australia and Oceania.
- Ailoscolidae
- Alluroididae
- Almidae (disputed): Africa, South America.
- Criodrilidae
- Eudrilidae: Tropical Africa.

- Exxidae: Central America/Caribbean.
- Glossoscolecidae: Central and northern South America.
- Hormogastridae: Europe.
- Lumbricidae: Temperate Northern Hemisphere from Vancouver Island, Canada to Japan, mostly Eurasia.
- Lutodrilidae
- Megascolecidae: South East Asia, Australasia and Oceania, northwestern North America.
- Microchaetidae
- Ocnerodrilidae: Central and South America, Africa.
- Octochaetidae: Central/South America, western Africa, India, New Zealand, Australia.
- Sparganophilidae: North America.

Chapter- 7

Machaerid and Scolecodont

Machaerid

Machaerid **Temporal range: Ordovician (or earlier?) – Carboniferous**	
Scientific classification	
Kingdom:	Animalia
Phylum:	?Annelida
Families	
plumulitids turrilepadids lepidocoleids	

Machaeridians are a group of armoured, segmented annelid worms, known from the Early Ordovician (Late Tremadoc) to Carboniferous. The group consist of three distinct families: the plumulitids, turrilepadids and lepidocoleids.

Fossils

Only the calcitic scleretomes ("armour plates") of these worms tend to be preserved in the fossil record. These are tiny, and usually found disarticulated: articulated specimens reach about a centimeter in length, and are incredibly rare – hence the limited degree of study since their description in 1857. Scleritomes which bear a strong resemblance to the machaeridians are found in the small shelly fauna of the early Cambrian, 530 million years ago, suggesting an early origin of the group.

The machaeridians are characterized by having serialized rows of calcitic shell plates. The dorsal sclerites were convex and almost isometric; lateral sclerites were flatter and longer. The plates comprised two calcite layers: the outer layer is thin and formed by lamellar deposition, whereas new elements were added to the thicker inner layer as it grew. Scales are ridged with growth lines, implying that they grew episodically. A few taxa experimented with different approaches to scale formation; some were only very weakly calcified and may have mainly been organic in nature. They were never moulted, and each scale could be moved with an attached muscle.

The front two segments of the machaeridians were commonly different from the rest, bearing fewer spiny projections.

The plumulitids are flattened from above and looks much like the coat of mail armour of chitons. The two other families are laterally compressed and some lepidocoleids formed a dorsal hinge, which make these machaeridians look like a string of bivalves.

Ecology

Machaeridians are often found in association with stylophorans - the cornutes and mitrates. This suggests that they possessed a similar ecology. They probably fed on organic detritus, perhaps even the faeces of the accompanying stylophorans.

Their scales almost certainly performed a defensive role.

The organisms would have had limited ability to flex to the right and left (in the sagittal plane), but would have been able to roll up. While most possessed bilateral symmetry, the scales on the right and left side of *Turrilepas wrightiana* are different in shape and form. The Plumulitid machaeridians would have moved across the surface of the sea floor using parapodia, whereas the fully-armoured Turrelepids and Lepidocoelids burrowed in a peristaltic fashion reminiscent of their evolutionary cousins, the earthworms. This burrowing role has subjected them to the same evolutionary pressures which affect burrowing bivalves; convergent evolution as a result of their shared function probably contributed to early suggestions that the machaeridians should be classified with the molluscs.

Taxonomic affinity

The group had been variously assigned to the echinoderms, barnacles, annelids and mollusks, before the discovery of a fossil preserving soft tissue allowed a firm classification to the annelids, in 2008. This annelid affinity came as some surprise, as it is the only instance of this group developing calcitic armour. The exact relationship to crown group annelids are still unresolved, but some characters indicate a relationship to Aphroditacean annelids (Vinther et al. 2008). Caron (2008) suggested that machaeridians must be a stem group based on number of specialised features. However, one cannot assess crown group/stem group affinities based on autapomorphies, but on shared morphological traits or the lack thereof. He also suggested that machaeridians might be polyphyletic, but machaerdians are a well defined group with a number of shared characters and morphological gradations between all three families.

Scolecodont

An Ordovician scolecodont from Estonia

A **scolecodont** is the jaw of a **polychaete** annelid, a common type of fossil-producing segmented worm useful in invertebrate paleontology. **Scolecodonts** are common and diverse microfossils, which range from the Cambrian period (around half a billion years ago at the start of the Paleozoic era) to the present. They diversified profusely in the Ordovician, and are most common in the Ordovician, Silurian and Devonian marine deposits of the Paleozoic era.

Relatedly, more problematic worm-like fossils have been described in even older, Neoproterozoic era deposits in the Ediacaran Hills of southern Australia and in mid-Cambrian deposits of Burgess shale in British Columbia.

Since the other classes of annelids (specifically, the earthworms and leeches) lack hard parts, only the sea-dwelling **polychaetes** are frequently represented in the fossil record. Polychaetes are commonly fossilized due to their chitinous teeth and their dwelling tubes made of durable calcite (a calcium carbonate), hardened mucus (a.k.a. parchment), and/or chitin-like cement.

Scolecodonts belonging to the extinct families Atraktoprionidae, Hadoprionidae, Kalloprionidae, Mochtyellidae, Paulinitidae, Polychaetaspidae, Ramphoprionidae, Rhytiprionidae, Skalenoprionidae, Symmetroprionidae, Xanioprionidae, and the still-extant (living) family Oenonidae (which includes the Arabellidae) are known from Silurian rocks in Scotland. Scolecodonts representing the present-day families Onuphidae and Dorvilleidae first appeared in Mesozoic era deposits.

Chapter- 8

Chordate

Chordata Temporal range: Early Cambrian – Recent, 540–0 Ma	

X-ray tetra (*Pristella maxillaris*), one of the few chordates with a visible backbone. The spinal cord is housed within its backbone.

Scientific classification	
Kingdom:	Animalia
Superphylum:	Deuterostomia
Phylum:	**Chordata** Bateson, 1885

Chordates (phylum **Chordata**) are animals which are either vertebrates or one of several closely related invertebrates. They are united by having, for at least some period of their life cycle, a notochord, a hollow dorsal nerve cord, pharyngeal slits, an endostyle, and a post-anal tail. The phylum Chordata consists of three subphyla: Urochordata, represented by tunicates; Cephalochordata, represented by lancelets; and Craniata, which includes Vertebrata. The Hemichordata have been presented as a fourth chordate subphylum, but they are now usually treated as a separate phylum. Urochordate larvae have both a notochord and a nerve cord which are lost in adulthood. Cephalochordates have a notochord and a nerve cord (but no brain or specialist sensory organs) and a very simple circulatory system. Craniates are the only sub-phylum whose members have skulls. In all craniates except for hagfish, the dorsal hollow nerve cord is surrounded with cartilaginous or bony vertebrae and the notochord is generally reduced; hence, hagfish are not regarded as vertebrates. The chordates and three sister phyla, the Hemichordata, the Echinodermata and the Xenoturbellida, make up the deuterostomes, one of the two superphyla that encompass all fairly complex animals.

Attempts to work out the evolutionary relationships of the chordates have produced several hypotheses, but the current consensus is that chordates are monophyletic, meaning that Chordata contains all and only the descendants of a single common ancestor *which is itself a chordate*, and that craniates' nearest relatives are cephalochordates. All of the earliest chordate fossils have been found in the Early Cambrian Chengjiang fauna, and include two species that are regarded as fish, which implies that they are vertebrates. Because the fossil record of chordates is poor, only molecular phylogenetics offers a reasonable prospect of dating their emergence. However, the use of molecular phylogenetics for dating evolutionary transitions is controversial.

It has also proved difficult to produce a detailed classification within the living chordates. Attempts to produce evolutionary "family trees" give results that differ from traditional classes because several of those classes are not monophyletic. As a result vertebrate classification is in a state of flux.

Definition

Chordates form a phylum of creatures that are based on a bilateral body plan, and is defined by having at some stage in their lives all of the following:

- A notochord, in other words a fairly stiff rod of cartilage that extends along the inside of the body. Among the vertebrate sub-group of chordates the notochord develops into the spine, and in wholly aquatic species this helps the animal to swim by flexing its tail.
- A dorsal neural tube. In fish and other vertebrates this develops into the spinal cord, the main communications trunk of the nervous system.
- Pharyngeal slits. The pharynx is the part of the throat immediately behind the mouth. In fish the slits are modified to form gills, but in some other chordates they are part of a filter-feeding system that extracts particles of food from the water in which the animals live.
- A muscular tail that extends backwards behind the anus.
- An endostyle. This is a groove in the ventral wall of the pharynx. In filter-feeding species it produces mucus to gather food particles, which helps in transporting food to the esophagus. It also stores iodine, and may be a precursor of the vertebrate thyroid gland.

Sub-divisions

Craniata

Craniate: Hagfish

Craniates, one of the three sub-divisions of chordates, have distinct skulls. Michael J. Benton comments that "craniates are characterized by their heads, just as chordates, or possibly all deuterostomes, are by their tails."

Most are vertebrates, in which the notochord is replaced by the spinal column.

This consists of a series of bony or cartilaginous cylindrical vertebrae, generally with neural arches that protect the spinal cord and with projections that link the vertebrae. Hagfish have incomplete braincases and no vertebrae, and are therefore not regarded as vertebrates, but as members of the craniates, the group from which vertebrates are thought to have evolved. The position of lampreys is ambiguous. They have complete braincases and rudimentary vertebrae, and therefore may be regarded as vertebrates and true fish. However molecular phylogenetics, which uses biochemical features to classify organisms, has produced both results that group them with vertebrates and others that group them with hagfish.

Cephalochordata: "The Lancelets"

Cephalochordate: Lancelet

Cephalochordates are small, "vaguely fish-shaped" animals that lack brains, clearly defined heads and specialized sense organs. These burrowing filter-feeders may be either the closest living relatives of craniates or surviving members of the group from which all other chordates evolved.

Urochordata: "The Tunicates"

Tunicates: sea squirts

Most tunicates appear as adults in two major forms, both of which are soft-bodied filter-feeders that lack the standard features of chordates: "sea squirts" are sessile and consist mainly of water pumps and filter-feeding apparatus; salps float in mid-water, feeding on plankton, and have a two-generation cycle in which one generation is solitary and the next forms chain-like colonies. However all tunicate larvae have the standard chordate features, including long, tadpole-like tails; they also have rudimentary brains, light sensors and tilt sensors. The third main group of tunicates, Appendicularia (also known as Larvacea) retain tadpole-like shapes and active swimming all their lives, and were for a long time regarded as larvae of sea squirts or salps. Because of their larvae's long tails tunicates are also called urochordates ("tail chordates").

Closest non-chordate relatives

The Hemichordates

Enteropneust hemichordate: *Balanoglossus*

Hemichordates ("half chordates") have some features similar to those of chordates: branchial openings that open into the pharynx and look rather like gill slits; stomochords, similar in composition to notochords but running in a circle round the "collar", which is ahead of the mouth; and a dorsal nerve cord — but also a smaller ventral nerve cord.

There are two living groups of hemichordates. The solitary enteropneusts, commonly known as "acorn worms", have long probosces and worm-like bodies with up to 200 branchial slits, are up to 2.5 metres (8.2 ft) long, and burrow though seafloor sediments. Pterobranchs are colonial animals, often less than 1 millimetre (0.039 in) long individually, whose dwellings are inter-connected. Each filter feeds by means of a pair of branched tentacles, and has a short, shield-shaped proboscis. The extinct graptolites, colonial animals whose fossils look like tiny hacksaw blades, lived in tubes similar to those of pterobranchs.

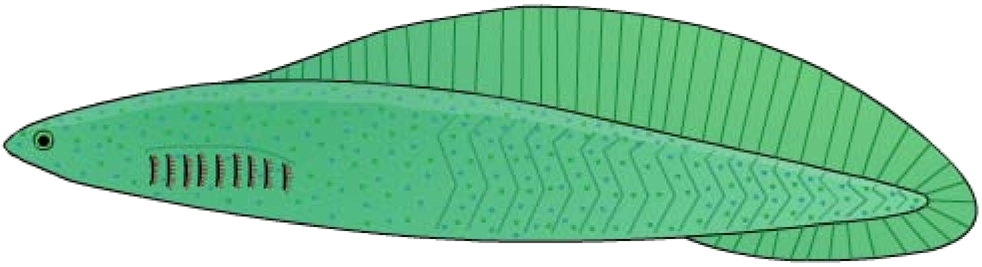
The Echinoderms

Echinoderm: starfish

Echinoderms differ from chordates and their other relatives in three conspicuous ways: instead of having bilateral symmetry they have radial symmetry, meaning their body pattern is shaped like a wheel; they have tube feet; and their bodies are supported by skeletons made of calcite, a material not used by chordates. The hard calcified shell keeps their bodies well protected from the environment, and these skeletons enclose their bodies but are also covered by a thin skin. The feet are powered by another unique feature of echinoderms, a water vascular system of canals that also function as a "lung" and are surrounded by muscles that act as pumps. Crinoids look rather like flowers, and use their feather-like arms to filter food particles out of the water; most live anchored to rocks, but a few can move very slowly. Other echinoderms are mobile and take a variety of body shapes, for example starfish, sea urchins and sea cucumbers.

Origins

The majority of animals more complex than jellyfish and other Cnidarians are split into two groups, the protostomes and deuterostomes, and chordates are deuterostomes. It seems very likely that 555 million year old *Kimberella* was a member of the protostomes. If so, this means that the protostome and deuterostome lineages must have split some time before *Kimberella* appeared — at least 558 million years ago, and hence well before the start of the Cambrian 542 million years ago. The Ediacaran fossil *Ernietta*, from about 549 to 543 million years ago, may represent a deuterostome animal.



Haikouichthys, from about 518 million years ago in China, may be the earliest known fish.

Fossils of one major deuterostome group, the echinoderms (whose modern members include starfish, sea urchins and crinoids), are quite common from the start of the Cambrian, 542 million years ago. The Mid Cambrian fossil *Rhabdotubus johanssoni* has been interpreted as a pterobranch hemichordate. Opinions differ about whether the Chengjiang fauna fossil *Yunnanozoon*, from the earlier Cambrian, was a hemichordate or chordate. Another fossil, *Haikouella lanceolata*, also from the Chengjiang fauna, is interpreted as a chordate and possibly a craniate, as it shows signs of a heart, arteries, gill filaments, a tail, a neural chord with a brain at the front end, and possibly eyes — although it also had short tentacles round its mouth. *Haikouichthys* and *Myllokunmingia*, also from the Chengjiang fauna, are regarded as fish. *Pikaia*, discovered much earlier but from the Mid Cambrian Burgess Shale, is also regarded as a primitive chordate. On the other hand fossils of early chordates are very rare, since non-vertebrate chordates have no bones or teeth, and only one has been reported for the rest of the Cambrian.

The evolutionary relationships between the chordate groups and between chordates as a whole and their closest deuterostome relatives have been debated since 1890. Studies based on anatomical, embryological, and paleontological data have produced different "family trees". Some closely linked chordates and hemichordates, but that idea is now rejected. Combining such analyses with data from a small set of ribosome RNA genes eliminated some older ideas, but open the possibility that tunicates (urochordates) are "basal deuterostomes", in other words surviving members of the group from which echinoderms, hemichordates and chordates evolved. Most researchers agree that, within the chordates, craniates are most closely related to cephalochordates, but there are also reasons for regarding tunicates (urochordates) as craniates' closest relatives. One other phylum, Xenoturbellida, appears to be basal within the deuterostomes, in other words closer to the original deuterostomes than to the chordates, echinoderms and hemichordates.

Since chordates have left a poor fossil record, attempts have been made to calculate the key dates in their evolution by molecular phylogenetics techniques, in other words by analysing biochemical differences, mainly in RNA. One such study suggested that deuterostomes arose before 900 million years ago and the earliest chordates around 896 million years ago. However molecular estimates of dates often disagree with each other and with the fossil record, and their assumption that the molecular clock runs at a known constant rate has been challenged.

Classification

Taxonomy

The following schema is from the third edition of *Vertebrate Palaeontology*. The invertebrate chordate classes are from Fishes of the World. While it is structured so as to reflect evolutionary relationships (similar to a cladogram), it also retains the traditional ranks used in Linnaean taxonomy.

- **Phylum Chordata**
  - Subphylum **Tunicata** (Urochordata) — (tunicates; 3,000 species)
    - Class **Ascidiacea**
    - Class **Thaliacea** (salps)
    - Class **Appendicularia** (larvacea)
  - Subphylum **Cephalochordata** (Acraniata) — (lancelets; 30 species)
  - Subphylum **Vertebrata** (Craniata) (vertebrates — animals with backbones; 57,674 species)
      -
      - Class '**Agnatha**' paraphyletic (jawless vertebrates; 100+ species)
        - Subclass Myxinoidea (hagfish; 65 species)
        - Subclass Petromyzontida (lampreys)
        - Subclass Conodonta
        - Subclass **Pteraspidomorphi** (Paleozoic jawless fish)
          - Order Anaspida
          - Order Thelodonti (Paleozoic jawless fish)
    - Infraphylum **Gnathostomata** (jawed vertebrates)
        -
        - Class **Placodermi** (Paleozoic armoured forms)
        - Class **Chondrichthyes** (cartilaginous fish; 900+ species)
        - Class **Acanthodii** (Paleozoic "spiny sharks")
        - Class **Osteichthyes** (bony fish; 30,000+ species)
          - Subclass **Actinopterygii** (ray-finned fish; about 30,000 species)
          - Subclass **Sarcopterygii** (lobe-finned fish)
      - Superclass **Tetrapoda** (four-legged vertebrates; 28,000+ species)
        - Class **Amphibia** (amphibians; 6,000 species)
          - Series **Amniota** (with amniotic egg)
        - Class **Reptilia** (reptiles; 8,225+ species)

    - Subclass **Anapsida** (extinct "proto-reptiles" and possibly turtles)
    - Subclass **Synapsida** (mammal-like "reptiles"; 4,500+ species, progenitors of mammals)
    - Subclass **Diapsida** (majority of reptiles, progenitors of birds)
- Class **Mammalia** (mammals; 5,800 species)
- Class **Aves** (birds; 8,800–10,000 species)

Chapter- 9

Craniata

Craniata
Temporal range: Early Cambrian - Recent

A Pacific Hagfish, an example of a craniate

Scientific classification	
Kingdom:	Animalia
Phylum:	Chordata
(unranked):	**Craniata** Linnaeus 1758:240

Subphyla

Petromyzontida (lampreys)
(disputed)
Myxini (hagfishes)
Vertebrata

Craniata (sometimes **Craniota**) is a proposed clade of chordate animals that contains the Myxini (hagfish), Petromyzontida (including lampreys), and Gnathostomata (jawed vertebrates) as living representatives. As the name suggests, Craniata are animals with a (hard bone or cartilage) skull in Chordata.

Craniata as an unranked taxon replaces the former use of Vertebrata (Vertebrata *sensu lato*). The main difference of the old and new (Vertebrata *sensu stricto*) interpretation of

Vertebrata is that Myxini and sometimes the Petromyzontida are no longer included in Vertebrata. The Myxini lack proper vertebrae, which are characteristic for vertebrates according to the new interpretation, whereas traditionally, and confusingly, they were not (Hickman et al., 2007).

Characteristics

In the simplest sense craniates are chordates with heads, thus excluding members of chordate subphyla Urochordata (tunicates) and Cephalochordata (lancelets), but including Myxini, which have cartilaginous skulls and tooth-like structures composed of keratin. Craniata also includes all lampreys and armored jawless fishes, sharks and rays, bony fish, amphibians, reptiles and mammals. The craniate head consists of a brain, sense organs including eyes, and a skull.

In addition to distinct crania (sing. *cranium*), craniates possess many derived characteristics which have allowed for more complexity to follow. Molecular-genetic analysis of craniates reveals that, compared to less complex animals, they developed duplicate sets of many gene families that are involved in cell signaling, transcription, and morphogenesis.

In general, craniates are much more active than tunicates and lancelets and as a result have greater metabolic demands, as well as several anatomical adaptations. Aquatic craniates have gill slits which are connected to muscles and nerves which pump water through the slits (as opposed to lancelets, whose pharyngeal slits are used only for suspension feeding), engaging in both feeding and gas exchange. Muscles line the alimentary canal, moving food through the canal, allowing higher craniates like mammals to develop more complex digestive systems for optimal food processing. Craniates have cardiovascular systems which include a heart with two or more chambers, red blood cells, and O_2 transporting hemoglobin, as well as kidneys.

Systematics and taxonomy

Linnaeus (1758) used the terms 'Craniata' and 'Vertebrata' interchangeably to include lampreys, jawed fishes, and terrestrial vertebrates (tetrapods). Hagfishes were classified as Vermes, possibly representing a transitional form between 'worms' and fishes. Dumeril (1806) grouped hagfishes and lampreys in the taxon 'Cyclostomi', characterized by horny teeth borne on a tongue-like apparatus, a large notochord as adults, and pouch-shaped gills (Marspibranchii). Cyclostomes were regarded as either degenerate cartilaginous fishes or primitive vertebrates. Cope (1889) coined the name 'Agnatha' (jawless) for a group that included the cyclostomes and a number of fossil groups in which jaws could not be observed. Vertebrates were subsequently divided into two major sister-groups; Agnatha and Gnathostomata (jawed vertebrates). Stensiö (1927) suggested that the two groups of living agnathans (i.e., cyclostomes) arose interpedently from different groups of fossil agnathans. Løvtrup (1977) argued that lampreys are more closely related to gnathostomes based on a number of uniquely derived characters, including: arcualia (serially arranged paired cartilages above the notochord), extrinsic eyeball muscles, radial muscles in the fins, a closely-set atrium and ventricle of the heart, nervous regulation of the heart (by the vagus nerve), a typhlosole (spirally coiled valve of the intestinal wall), true lymphocytes, a differentiated anterior lobe of the pituitary gland (adenohypophysis), three inner ear maculae (patches of acceleration sensitive 'hair cells' used in balance) organized into two or three vertical semicircular canals, neuromast organs (composed of vibration sensitive hair cells) in the laterosensory canals, an electroreceptive lateral line (with voltage sensitive hair cells) and electrosensory lateral line nerves, and a cerebellum (i.e., the multi-layered roof of the hindbrain with unique structure [characteristic neural architecture including direct inputs from the lateral line and large output Purkinje cells) and function [integrating sensory perception and coordinating motor control]. In other words, the 'cyclostome' characteristics (e.g., horny teeth, "tongue", gill pouches) are either instances of convergent evolution for feeding and gill ventilation in animals with an eel-like body shape, or represent primitive craniate characteristics subsequently lost or modified in gnathostomes. Janvier (1978) proposed to use the names 'Vertebrata' and 'Craniata' as two distinct and nested taxa.

Validity

The validity of the taxon "Craniata" was recently examined by Delarbre et al. (2002) using mtDNA sequence data, concluding that Myxini is more closely related to Hyperoartia than to Gnathostomata - i.e., that modern jawless fishes form a clade called Cyclostomata. The argument is that if Craniata is indeed monophyletic, Vertebrata would return to its old content (Gnathostomata + Cyclostomata) and the name Craniata, being superfluous, would become a junior synonym.

However, mtDNA may not be a reliable marker for phylogenetic analysis of such ancient divergence times, due to its rapid rate of mutation. Further, the root of the molecular phylogeny for Craniata may be difficult to resolve due to the very poor representation of deep branches among living taxa; in other words that the taxon sampling afforded by extant taxa alone results in very long branches, within the basal craniate lineages, and among their closest relatives (i.e., *Branchiostoma*). Because extinction has eliminated so much of the important transitional states needed to reconstruct the early branching order of craniate lineages, the molecular tree of these taxa may effectively be an unrooted network.

Chapter- 10

Lancelet

Lancelets

Lancelet (*Branchiostoma lanceolatum*)

Scientific classification	
Kingdom:	Animalia
Phylum:	Chordata
Subphylum:	Cephalochordata
Class:	**Leptocardii**
Order:	**Amphioxiformes**

Families

Asymmetronidae
Branchiostomidae

The **lancelets** (from lancet), also known as **amphioxus**, are the modern representatives of the subphylum Cephalochordata, usually said to be the sister group of the craniates. They are usually found buried in sand in shallow parts of temperate or tropical seas. In Asia, they are harvested commercially as food for humans and domesticated animals. They are an important object of study in zoology as they provide indications about the origins of the vertebrates. Lancelets serve as an intriguing comparison point for tracing how vertebrates have evolved and adapted. Although lancelets split from vertebrates more than 520 million years ago, their genomes hold clues about evolution, particularly how vertebrates have employed old genes for new functions. They are regarded as similar to the archetypal vertebrate form.

The genome of the Florida lancelet (*Branchiostoma floridae*) has been sequenced.

Physical features

Lancelets grow up to about 5 centimetres (2.0 in) long, reaching 7 centimetres (2.8 in) at the longest. They have a translucent, somewhat fish-like body, but without any paired fins or other limbs. A relatively poorly developed tail fin is present, but they are not especially good swimmers. While they do possess some cartilage-like material stiffening the gill slits, mouth, and tail, they have no true skeleton.

In common with vertebrates, lancelets have a hollow nerve cord running along the back, pharyngeal slits and a tail that runs past the anus. Also like vertebrates, the muscles are arranged in blocks called myomeres.

Unlike vertebrates, the dorsal nerve cord is not protected by bone but by a simpler notochord made up of a cylinder of cells that are closely-packed to form a toughened rod. The lancelet notochord, unlike the vertebrate spine, extends into the head. This gives the subphylum its name (*cephalo-* meaning 'relating to the head'). The nerve cord is only slightly larger in the head region than in the rest of the body, so that lancelets cannot be said to possess a true brain. Neither do they have any eyes, or other complex sense organs comparable to those of vertebrates.

Lancelets also have oral *cirri*, thin tentacle-like strands that hang in front of the mouth and act as sensory devices and as a filter for the water passing into the body. Water passes from the mouth into the large pharynx, which is lined by numerous gill-slits. The ventral surface of the pharynx contains a groove, called the endostyle, which, connected to a structure known as Hatschek's pit, produces a film of mucus. Ciliary action pushes the mucus in a film over the surface of the gill slits, trapping suspended food particles as it does so. The mucus is collected in a second, dorsal, groove, and passed back to the rest of the digestive tract. Having passed through the gill slits, the water enters an atrium surrounding the pharynx, then exits the body via the *atriopore*.

The remainder of the digestive system consists of a simple tube running from the pharynx to the anus. A single blind-ending caecum branches off from the underside of the gut, with a lining able to phagocytose the food particles; a feature never found in vertebrates. It used to be thought that the caecum might be homologous to the liver of vertebrates, but this is now thought to be less likely.

Lancelets have no respiratory system, breathing solely through their skin, which consists of a simple epithelium. Despite the name, little if any respiration occurs in the gill slits, which are solely devoted to feeding. The circulatory system does resemble that of primitive fish in its general layout, but is much simpler, and does not include a heart. There are no blood cells, and no haemoglobin.

The excretory system consists of segmented "kidneys" containing protonephridia instead of nephrons, and quite unlike those of vertebrates. Also unlike vertebrates, there are numerous, segmented gonads.

Taxonomy

The Cephalochordata is traditionally seen as a sister subphylum to the vertebrates, with which it is grouped together into a clade (sometimes called Notochordata) which in turn is the sister group to the simpler still Urochordata. Newer research suggests this may not be the case. The Cephalochordata may be the most basal subphylum of the chordates, while the sister group of the vertebrates may be the urochordates. However, other recent molecular studies (cit. in Benton 2005: 8) place cephalochordates nearer to vertebrates, and "[m]ost authors regard amphioxus as the closest relative of the Vertebrata on the basis of 10–15 [morphological] features that are not seen in tunicates".

The asymmetric nature of juveniles is unique to the cephalochordates and demonstrates (as do certain other features, including the seriated gonads) that lancelets are more derived than would be expected. This is a reminder that the "living fossil" representative of a basal clade has as long an evolutionary history as any other living thing, and thus is more derived than the actual primitive ancestor it otherwise so closely resembles.

The following are the species recognised by ITIS. Other sources, for instance Tudge, show that there might be up to thirty species.

- Family Asymmetronidae
    - Genus *Asymmetron*
        - *Asymmetron lucayanum*
        - *Asymmetron maldivense*
    - Genus *Epigonichthys*
        - *Epigonichthys australis*
        - *Epigonichthys bassanus*
        - *Epigonichthys cingalense*
        - *Epigonichthys cultellus*
        - *Epigonichthys hectori*
        - *Epigonichthys lucayanum*
        - *Epigonichthys maldivensis*
- Family Branchiostomidae
    - Genus *Branchiostoma*
        - *Branchiostoma belcheri*
        - *Branchiostoma californiense*
        - *Branchiostoma capense*
        - *Branchiostoma caribaeum*
        - *Branchiostoma clonaseum*
        - *Branchiostoma floridae*
        - *Branchiostoma lanceolatum*
        - *Branchiostoma minucauda*

- *Branchiostoma moretonensis*
- *Branchiostoma valdiviae*
- *Branchiostoma virginiae*

Chapter- 11

Tunicate

Tunicate
Temporal range: Cambrian stage 3–Recent

Sea Tulips, *Pyura spinifera*

Scientific classification

Kingdom:	Animalia
Phylum:	Chordata
Subphylum:	**Tunicata** Giribet et al., 2000

Classes

Appendicularia
Ascidiacea
Sorberacea
Thaliacea

Tunicates, also known as **urochordates**, are members of the subphylum **Tunicata** or **Urochordata**, a group of underwater saclike filter feeders with incurrent and excurrent siphons that is classified within the phylum Chordata. While most tunicates live on the ocean floor, others – such as salps, doliolids and pyrosomes – live above in the pelagic zone as adults. They were historically known as **Ascadia**, and are now commonly known as **sea squirts** and **sea pork**.

Most tunicates feed by filtering sea water through pharyngeal slits, but some are submarine predators such as the *Megalodicopia hians*. Like other chordates, tunicates have a notochord during their early development but lack myomeric segmentation throughout the body and tail as adults. Tunicates lack the kidney-like metanephridial organs, and the original coelom body-cavity develops into a pericardial cavity and gonads. Except for the pharynx, heart and gonads, the organs are enclosed in a membrane called an epicardium, which is surrounded by the jelly-like mesenchyme. Tunicates begin life in a mobile larval stage that resembles a tadpole, later developing into a barrel-like and usually sedentary adult form.

Tunicates apparently evolved in the early Cambrian period, beginning *c* 540 million years ago. Despite their simple appearance, tunicates are closely related to vertebrates, which include fish and all land animals with bones.

Life cycle

Most tunicates are hermaphrodites. The eggs are kept inside their body until they hatch, while sperm is released into the water where it fertilizes other individuals when brought in with incoming water.

Some larval forms appear very much like primitive chordates with a notochord (stiffening rod). Superficially, the larva resemble small tadpoles. They swim with a tail, and may have a simple eye, or ocellus, and balancing organ, or statolith. Some forms have a calcereous spicule that may be preserved as a fossil. They have appeared from the Jurassic to the present, with one proposed Neoproterozoic form, *Yarnemia*.

The larval ends when the tunicate finds a suitable rock to affix to and cements itself in place. The larval form is not capable of feeding, though it may have a digestive system, and is only a dispersal mechanism. Many physical changes occur to the tunicate's body, one of the most interesting being the digestion of the cerebral ganglion, which controls movement and is the equivalent of the human brain. From this comes the common saying that the sea squirt "eats its own brain". In some classes, the adults remain pelagic (swimming or drifting in the open sea), although their larvae undergo similar metamorphoses to a higher or lower degree.

Once grown, adults can develop a thick covering, called a *tunic*, to protect their barrel-shaped bodies from enemies.

During embryonic development, tunicates exhibit "determinate cleavage", where the fate of the cells is set early on with reduced cell numbers and genomes that are rapidly evolving. In contrast, the amphioxus and vertebrates show cell determination relatively late in development and cell cleavage is indeterminate. The genome evolution of amphioxus and vertebrates is also relatively slow.

Feeding

Clavelina moluccensis, the bluebell tunicate

Tunicate colonies of *Botrylloides violaceus* with oral tentacles at openings of oral siphons visible

Colonial Ascidians in the Yaquina Bay

Tunicates are suspension feeders. They have two openings in their body cavity: an in-current and an ex-current siphon. The in-current siphon is used to intake food and water, and the ex-current siphon expels waste and water. The tunicate's primary food source is plankton. Plankton gets entangled in the mucus secreted from the endostyle. The tunicate's pharynx is covered by miniature hairs called ciliate cells which allow the consumed plankton to pass down through to the esophagus. Their guts are U-shaped, and their anuses empty directly to the outside environment. Tunicates are also the only animals able to create cellulose.

Tunicate blood is particularly interesting. It contains high concentrations of the transition metal vanadium and vanadium-associated proteins as well as higher than usual levels of lithium. Some tunicates can concentrate vanadium up to a level one million times that of the surrounding seawater. Specialized cells can concentrate heavy metals, which are then deposited in the tunic.

Classification

Tunicates are more closely related to craniates (including hagfish, lampreys, and jawed vertebrates) than to lancelets, echinoderms, hemichordates, *Xenoturbella* or other invertebrates. The clade comprising Tunicates and Vertebrates is called Olfactores.

The Tunicata contains about 3,000 species, usually divided into the following classes:

- Ascidiacea (Aplousobranchia, Phlebobranchia, and Stolidobranchia)
- Thaliacea (Pyrosomida, Doliolida, and Salpida)
- Appendicularia (Larvacea)
- Sorberacea

Although the traditional classification is followed for now, newer evidence suggests that the Ascidiacea is an artificial group of paraphyletic status. The new classification would be:

- Stolidobranchia
- Aplousobranchia, Phlebobranchia and Thaliacea
- Appendicularia
- Sorberacea would belong somewhere in Ascidiacea, or be in a taxon on its own

The species *Ciona intestinalis* and *Ciona savignyi* have attracted interest in biology for developmental studies. Both species' mitochondrial and nuclear genomes have been sequenced. Moreover, the nuclear genome of the appendicularian *Oikopleura dioica* appears to be one of the smallest among metazoans.

Sea squirts have become a testing ground in the controversy about the extent to which cross-species gene transfer and hybridization have influenced animal evolution. In 1990, Donald I. Williamson of the University of Liverpool (U.K.) fertilised sea squirt (*Ascidia mentula*) eggs with sea urchin (*Echinus esculentus*) sperm resulting in fertile adults that resembled urchins, but Michael W. Hart of Simon Fraser University failed to find sea-squirt DNA in tissue samples from the supposed hybrids. Williamson claims to have repeated the experiment with sea urchin eggs and sea squirt sperm, producing sea urchin larvae which developed into squirt-like juveniles. On the other hand, Syvanen and Ducore of the University of California have suggested that sea squirts descended from a hybrid between a chordate and a likely extinct protostome ancestor at a time before the diversification of round worms and arthropods. This study also examined whether there was evidence of a sea urchin/tunicate hybridization event that could possibly explain the distribution of genes in modern sea squirts—none could be seen.

Fossil record

The star-shaped holes (*Catellocaula vallata*) in this Upper Ordovician bryozoan represent a tunicate preserved by bioimmuration in the bryozoan skeleton

Undisputed fossils of tunicates are rare. The best known (and earliest) is *Shankouclava shankouense* from the Lower Cambrian Maotianshan Shale at Shankou village, Anning, near Kunming (South China). There is also a common bioimmuration of a tunicate (*Catellocaula vallata*) found in Upper Ordovician bryozoan skeletons of the upper midwestern United States.

There are also two enigmatic species from the Ediacaran period - *Ausia fenestrata* from the Nama Group of Namibia and a second new *Ausia*-like genus from the Onega Peninsula, White Sea of northern Russia. Results of new study have shown possible affinity of these Ediacaran organisms to the ascidians. These two organisms lived in the shallow waters of a sea, slightly more than 555-548 million years ago and are likely the oldest evidence of the chordate lineage of metazoans.

A Precambrian fossil known as *Yarnemia* has been referred to the Urochordata, however this assignment is doubtful. Complete body fossils of tunicates are rare, but in some tunicate families, microscopic spicules are generated which may be preserved as microfossils. Such spicules have occasionally been described from Jurassic and later rocks. Few paleontologists are familiar with them; tunicate spicules may be mistaken for sponge spicules.

Invasive species

Over the past few years, urochordates (notably of the genera *Didemnum* and *Styela*) have been invading coastal waters in many countries, and are spreading quickly. These mat-like organisms can smother other sea life, have very few natural predators, and are causing much concern. They form colonies which are yellowish cream in color, and look like thick sponge-like masses that overgrow themselves on stationary objects on the sea floor such as gravel, mollusc shells, and possibly other encrusting species. These colonies are flexible, irregular, long, flat, and often exist as branched outgrowths projected from the surface. Some of the outgrowths result from the colony encrusting worm tubes or other cylindrical objects but many are solid with a firm gelatinous core. The individuals of the colony are called zooids and many zooids with individual siphonal openings cover the surface of the colony.

Transportation of invasive tunicates is usually in the ballast water or on the hulls of ships. Current research indicates that many tunicates previously thought to be indigenous to Europe and the Americas are, in fact, invaders. Some of these invasions may have occurred centuries or even millennia ago. In some areas, tunicates are proving to be a major threat to aquaculture operations.

The U.S. Geological Survey, NOAA Fisheries, and the University of Rhode Island are investigating this phenomenon as they have been spotted in 2004 in Georges Bank. They requested that any information or sightings of these invading colonies be reported to United States Geological Survey to aid in their investigation.

Medical uses

Tunicates contain a host of potentially useful chemical compounds, including:

- Didemnins, effective against various types of cancer, as antivirals and immunosuppressants
- Aplidine, effective against various types of cancer
- Trabectedin, effective against various types of cancer

In the May 2007 issue of The *FASEB* Journal, researchers from Stanford University showed that tunicates can correct abnormalities over a series of generations, and they suggest that a similar regenerative process may be possible for humans. The mechanisms underlying the phenomenon may lead to insights about the potential of cells and tissues to be reprogrammed and regenerate compromised human organs. Gerald Weissman, editor-in-chief of the journal, said "This study is a landmark in regenerative medicine; the Stanford group has accomplished the biological equivalent of turning a sow's ear into a silk purse and back again."

Chapter- 12

Vertebrate

Vertebrates
Temporal range: Cambrian-Recent, 525–0 Ma

Individual organisms from each major vertebrate group. Clockwise, starting from top left:

Fire Salamander, Saltwater Crocodile, Southern Cassowary, Black-and-rufous Giant Elephant Shrew, Ocean Sunfish

Scientific classification

Kingdom:	Animalia
Phylum:	Chordata
(unranked):	Craniata
Subphylum:	**Vertebrata** Cuvier, 1812

Simplified grouping

- Fishes
- Tetrapods

Vertebrates are members of the subphylum **Vertebrata**, chordates with backbones and spinal columns. About 58,000 species of vertebrates have been currently described. Vertebrata is the largest subphylum of chordates, and contains many familiar groups of large land animals. Vertebrates are the animals from the groups of jawless fishes, bony fishes, sharks and rays, amphibians, reptiles, mammals, and birds. Extant vertebrates range in size from the carp species *Paedocypris*, at as little as 7.9 mm (0.3 inch), to the Blue Whale, at up to 33 m (110 ft). Vertebrates make up about 5% of all described animal species; the rest are invertebrates, which lack backbones.

The vertebrates traditionally include the hagfish, which do not have proper vertebrae, though their closest living relatives, the lampreys, do have vertebrae. For this reason, the vertebrate subphylum is sometimes referred to as "Craniata", as all members do possess a cranium.

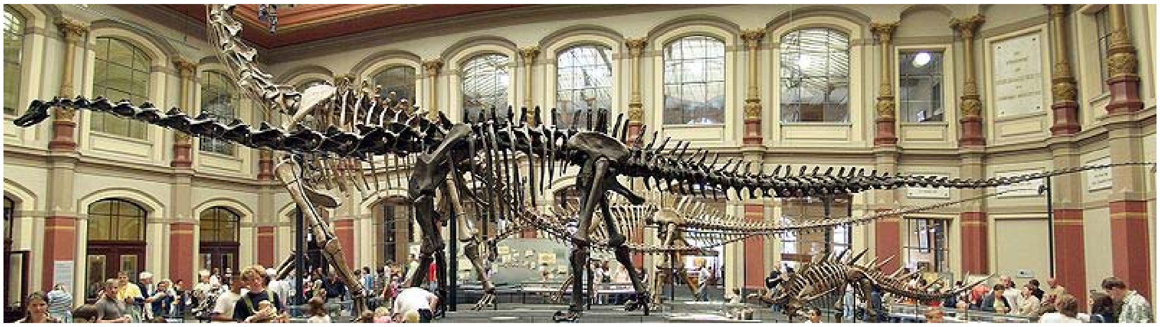
Etymology

The word *vertebrate* derives from the Latin word *vertebratus* (Pliny), meaning *joint of the spine*. It is closely related to the word *vertebra*, which refers to any of the bones or segments of the spinal column.

Anatomy and morphology

All vertebrates are built along the basic chordate body plan: a stiff rod running through the length of the animal (vertebral column or notochord), with a hollow tube of nervous tissue (the spinal cord) above it and the gastrointestinal tract below. In all vertebrates the mouth is found at or right below the anterior end of the animal, while the anus opens to the exterior before the end of the body. The remaining part of the body continuing aft of the anus forms a tail with vertebrae and spinal cord, but no gut.

The defining characteristic of a vertebrate is the vertebral column, in which the notochord (a stiff rod of uniform composition) has been replaced by a segmented series of stiffer elements (vertebrae) separated by mobile joints (intervertebral discs, derived embryonically and evolutionarily from the notochord). However, a few vertebrates have secondarily lost this anatomy, retaining the notochord into adulthood, as in the sturgeon and the *Latimeria*. Jawed vertebrates are typified by paired appendages (fins or legs, which may be secondarily lost), but this is not part of the definition of vertebrates as a whole.



Fossilized skeleton of *Diplodocus*, showing an extreme example of the backbone that characterizes the vertebrates. Exhibited at the Museum für Naturkunde (*Museum of Natural Science*), Berlin.

Evolutionary history

Vertebrates originated about 525 million years ago during the Cambrian explosion, which was an event of massive rise in organism diversity that occurred in the Cambrian period. The earliest known vertebrate is believed to be the *Myllokunmingia*. Molecular analysis since 1999 have suggested that the hagfishes are most closely related to lampreys, and so also are vertebrates. Others consider them a sister group of vertebrates in the common taxon of Craniata. Another early vertebrate is *Haikouichthys ercaicunensis*, also from the Chengjiang fauna 524 million years ago. All of these groups lacked a jaw in the common sense.

The first jawed vertebrates appeared in the Ordovician and became common in the Devonian, often known as the "Age of Fishes". The two groups of bony fishes, the actinopterygii and sarcopterygii, evolved and became common. The Devonian also saw the demise of virtually all jawless fishes, save for lampreys and hagfish, as well as the rise of the first labyrinthodonts, transitional between fish and amphibians. The Placodermi, a group of fishes that dominated much of the late Silurian and the majority of the Devonian period, also became extinct at the end of the Devonian.

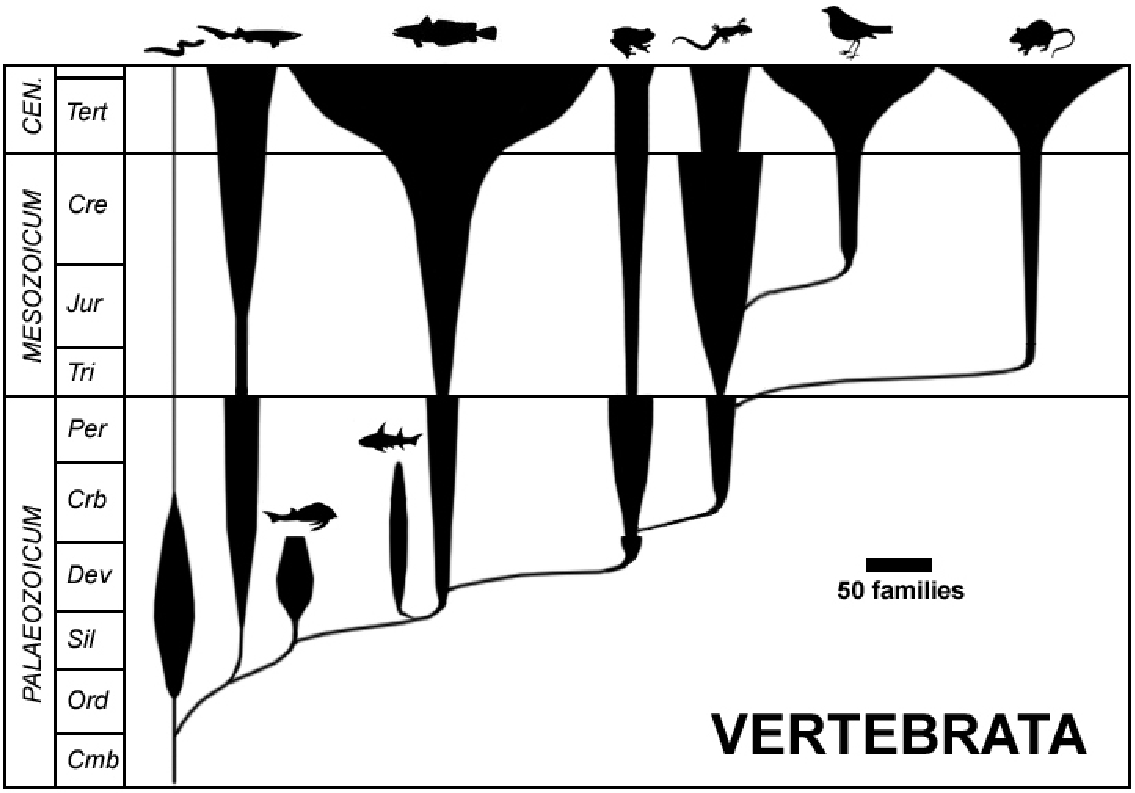
The reptiles appeared from labyrinthodont stock in the subsequent Carboniferous period. The anapsid and synapsid reptiles were common during the late Paleozoic, while the diapsids became dominant during the Mesozoic. The dinosaurs gave rise to the birds in the Jurassic. The demise of the dinosaurs at the end of the Cretaceous promoted expansion of the mammals, which had developed from the therapsids, a group of synapsid reptiles, during the Late Triassic Period. The post-dinosaur world have seen great diversification of bony fishes, frogs, birds and mammals.

Over half of all living vertebrate species (about 32,000 species) are fishes (non-tetrapod craniates), a diverse set of lineages that inhabit all the world's aquatic ecosystems, from snow minnows (Cypriniformes) in Himalayan lakes at elevations over 4,600 meters (15,000 feet) to flatfishes (order Pleuronectiformes) in the Challenger Deep, the deepest ocean trench at about 11,000 meters (36,000 feet). Fishes of myriad varieties are the main predators in most of the world's water bodies, both freshwater and marine. The rest of the vertebrate species are tetrapods, a single lineage that includes amphibians (frogs, with more than 5,800 species; salamanders, with about 580 species; and caecilians, with about 175 species); mammals (with over 5,400 species); and reptiles and birds (with more than 18,000 species). Tetrapods dominate the megafauna of most terrestrial environments (including fossorial and arboreal realms) and also include many partially or fully aquatic groups (e.g., sea snakes, penguins, cetaceans).

Classification

There are several ways of classifying animals. Evolutionary systematics relies on anatomy, physiology and evolutionary history, which is determined through similarities in anatomy and, if possible, the genetics of organisms. Phylogenetic classification is based solely on phylogeny. Evolutionary systematics gives an overview; phylogenetic systematics gives detail. The two systems are thus complementary rather than opposed.

Traditional classification



Traditional spindle diagram of the evolution of the vertebrates at class level

Conventional classification has living vertebrates grouped into seven classes based on traditional interpretations of gross anatomical and physiological traits. This classification is the one most commonly encountered in school textbooks, overviews, non-specialist, and popular works:

- **Subphylum Vertebrata**
    - Class Agnatha (jawless fish)
    - Class Chondrichthyes (cartilaginous fishes)
    - Class Osteichthyes (bony fishes)
    - Class Amphibia (amphibians)
    - Class Reptilia (reptiles)
    - Class Aves (birds)
    - Class Mammalia (mammals)

While this traditional classification is orderly most of the groups are paraphyletic, i.e. do not contain all descendants of the class's common ancestor. Descendants of the first reptiles do for instance include the birds and mammals as well as reptiles. Quite a few scientists working with vertebrates use a classification based purely on phylogeny, organized by their known evolutionary history and sometimes disregarding the conventional interpretations of their anatomy and physiology. An example based on Janvier (1981, 1997), Shu *et al.* (2003), and Benton (2004) is given here:

- **Subphylum Vertebrata**
    - Superclass Agnatha or Cephalaspidomorphi (lampreys and other jawless fishes, some ancestral to other vertebrates)
    - **Infraphylum Gnathostomata** (vertebrates with jaws)
            -
            - Class †Placodermi (extinct armoured fishes)
            - Class Chondrichthyes (cartilaginous fishes)
            - Class †Acanthodii (extinct spiny "sharks")
        - **Superclass Osteichthyes** (bony fishes)
            - Class Actinopterygii (ray-finned bony fishes)
            - Class Sarcopterygii (lobe-finned fishes, some ancestral to tetrapods)
        - **Superclass Tetrapoda** (four-limbed vertebrates)
            - Class Amphibia (amphibians, some ancestral to the amniotes)
            - Class †Synapsida (extinct mammal-like "reptiles", some ancestral to mammals, sometimes classed with Reptilia)
            - Class Mammalia (mammals)
            - Class Reptilia (reptiles, some ancestral to birds)
            - Class Aves (birds)

Most of the classes listed are not "complete" taxa: the agnathans have given rise to the jawed vertebrates; the bony fishes have given rise to the land vertebrates; the traditional "amphibians" have given rise to the reptiles (traditionally including the mammal-like "reptiles"), which in turn have given rise to the birds and mammals.