Mollusca
(Animal Phylum)

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Mollusca

Mollusca
Temporal range: Cambrian–Recent

Tonicella lineata, a polyplacophoran or chiton, anterior end towards the right

Scientific classification

Kingdom:	Animalia
Superphylum:	Lophotrochozoa
Phylum:	**Mollusca** Linnaeus, 1758

Classes

"Aplacophora"
Bivalvia
Cephalopoda
Polyplacophora
Polyplacophora
Gastropoda
Monoplacophora
†Rostroconchia
Scaphopoda
incertae sedis

Diversity

85,000 recognized living species

The **Mollusca**, common name **molluscs** or **mollusks**, is a large phylum of invertebrate animals. There are around 85,000 recognized extant species of molluscs. This is the largest marine phylum, comprising about 23% of all the named marine organisms. Numerous molluscs also live in freshwater and terrestrial habitats. Molluscs are highly diverse, not only in size and in anatomical structure, but also in behaviour and in habitat.

The phylum Mollusca is typically divided into nine or ten taxonomic classes, of which two are extinct. The gastropods (snails and slugs) include by far the most classified species, accounting for 80% of the total. Cephalopod molluscs such as squid, cuttlefish and octopus are among the most neurologically advanced invertebrates. Either the giant squid or the colossal squid is the largest known species of animal without a backbone.

The two most universal features of the body structure of molluscs are a mantle with a significant cavity used for breathing and excretion, and the organization of the nervous system. Because of the great range of anatomical diversity, many textbooks base their descriptions on a hypothetical "generalized mollusc", with features common to many but not all classes within the Mollusca.

There is good evidence for the appearance of gastropods, cephalopods and bivalves in the Cambrian period 542 to 488.3 million years ago. However, the evolutionary history both of the emergence of molluscs from the ancestral group Lophotrochozoa, and of their diversification into the well-known living and fossil forms, is still vigorously debated. The most abundant metallic element in molluscs is calcium.

Molluscs have for many centuries been the source of important luxury goods, notably pearls, mother of pearl, Tyrian purple dye, and sea silk. Their shells have also been used as money in some pre-industrial societies.

There is a risk of food poisoning from toxins that accumulate in molluscs under certain conditions, and many countries have regulations that aim to minimize this risk. Blue-ringed octopus bites are often fatal, and the bite of *Octopus rubescens* can cause necrosis that lasts longer than one month if untreated, and headaches and weakness persisting for up to a week even if treated. Stings from a few species of large tropical cone shells can also kill. However, the sophisticated venoms of these cone snails have become important tools in neurological research and show promise as sources of new medications.

Schistosomiasis (also known as bilharzia, bilharziosis or snail fever) is transmitted to humans via water snail hosts, and affects about 200 million people. A few species of snails and slugs are serious agricultural pests, and in addition, accidental or deliberate introduction of various snail species into new territory has resulted in serious damage to some natural ecosystems.

Taxonomy

The phylum Mollusca is monophyletic and is typically divided into nine or ten taxonomic classes, of which two are extinct. The gastropods (snails and slugs) include by far the most classified species, accounting for 80% of the total. Cephalopod molluscs such as squid, cuttlefish and octopus are among the most neurologically advanced invertebrates. Either the giant squid or the colossal squid is the largest known species of animal without a backbone.

Opinions vary about the number of classes of molluscs—for example the table below shows eight living classes, and two extinct ones. However some authors combine the Caudofoveata and solenogasters into one class, the Aplacophora. Two of the commonly recognized classes are known only from fossils

Synonymy has been a great problem. The phylum Mollusca is certainly the marine group where the number of names, given in the last 250 years, and number of valid names of species are most at odds with each other. The great number of scientific journals and publications, most of which can only be consulted on payment, makes it difficult for the taxonomist to know whether or not a newly described species has actually been described before in the relevant literature. This causes many synonymies to remain unrecognized for decades. It is currently believed that synonyms represent at most 10-20% of the 1,635 new marine species (many of which are mollusks) that are on average being described each year.

Class	**Major organisms**	**Described living species**	**Distribution**
Caudofoveata	worm-like organisms	120	seabed 200–3,000 metres (660–9,800 ft)
Aplacophora	solenogasters, worm-like organisms	200	seabed 200–3,000 metres (660–9,800 ft)
Polyplacophora	chitons	1,000	rocky tidal zone and seabed
Monoplacophora	An ancient lineage of molluscs with cap-like shells	31	seabed 1,800–7,000 metres (5,900–23,000 ft); one species 200 metres (660 ft)
Gastropoda	All the snails and slugs including abalone, limpets, conch,	70,000	marine, freshwater, land

	nudibranchs, sea hares, sea butterfly		
Cephalopoda	squid, octopus, cuttlefish, nautilus	900	marine
Bivalvia	clams, oysters, scallops, geoducks, mussels	20,000	marine, freshwater
Scaphopoda	tusk shells	500	marine 6–7,000 metres (20–23,000 ft)
Rostroconchia †	fossils; probable ancestors of bivalves	extinct	marine
Helcionelloida †	fossils; snail-like organisms such as *Latouchella*	extinct	marine

Distinguishing features

The two most universal features of the body structure of molluscs are a mantle with a significant cavity used for breathing and excretion, and the organization of the nervous system. Because of the great range of anatomical diversity, many textbooks base their descriptions on a hypothetical "generalized mollusc", with features common to many but not all classes within the Mollusca.

Diversity

About 80% of all known mollusc species are gastropods (snails and slugs), including the cowry (a sea snail) pictured here.

Estimates of accepted described living species of molluscs vary from 50,000 to a maximum of 120,000 species. In 2009 Chapman estimated the number of described living species at 85,000. Haszprunar in 2001 estimated about 93,000 named species, which include 23% of all named marine organisms. Molluscs are second only to arthropods in numbers of living animal species—far behind the arthropods' 1,113,000 but well ahead of chordates' 52,000. It has been estimated that there are about 200,000 living species in total, and 70,000 fossil species, although the total number of mollusc species that ever existed, whether or not preserved, must be many times greater than the number alive today.

Molluscs have more varied forms than any other animal phylum. They include snails, slugs and other gastropods; clams and other bivalves; squids and other cephalopods; and other lesser-known but similarly distinctive sub-groups. The majority of species still live in the oceans, from the seashores to the abyssal zone, but some form a significant part of the freshwater fauna and the terrestrial ecosystems. Molluscs are extremely diverse in tropical and temperate regions but can be found at all latitudes. About 80% of all known mollusc species are gastropods. Cephalopoda such as squid, cuttlefish and octopus are among the neurologically most advanced of all invertebrates. The giant squid, which until recently had not been observed alive in its adult form, is one of the largest invertebrates.

However a recently caught specimen of the colossal squid, 10 metres (33 ft) long and weighing 500 kilograms (0.49 LT; 0.55 ST), may have overtaken it.

Freshwater and terrestrial molluscs appear exceptionally vulnerable to extinction. Estimates of the numbers of non-marine molluscs vary widely, partly because many regions have not been thoroughly surveyed. There is also a shortage of specialists who can identify all the animals in any one area to species. However, in 2004 the IUCN Red List of Threatened Species included nearly 2,000 endangered non-marine molluscs. For comparison, the great majority of molluscs species are marine but only 41 of these appeared on the 2004 Red List. 42% of recorded extinctions since the year 1500 are of molluscs, almost entirely non-marine species.

Definition

The words *mollusc* and mollusk are both derived from the French *mollusque*, which originated from the Latin *molluscus*, from *mollis*, soft. *Molluscus* was itself an adaptation of Aristotle's τᾀ μαλάκια, "the soft things", which he applied to cuttlefish. The scientific study of molluscs is known as malacology.

Molluscs have developed such a varied range of body structures that it is difficult to find synapomorphies (defining characteristics) that apply to all modern groups. The most general characteristic of molluscs is that they are unsegmented and bilaterally symmetrical. The following are present in all modern molluscs:

- The dorsal part of the body wall is a mantle (or pallium) which secretes calcareous spicules, plates or shells. It overlaps the body with enough spare room to form a mantle cavity.
- The anus and genitals open into the mantle cavity.
- There are two pairs of main nerve cords.

Other characteristics that commonly appear in textbooks have significant exceptions:

	Class						
Characteristic	**Aplacophora**	**Polyplacophora**	**Monoplacophora**	**Gastropoda**	**Cephalopoda**	**Bivalvia**	**Scaphopoda**
Radula, a rasping "tongue" with chitinous teeth	Absent in 20% of Neomeniomorpha	Yes	Yes	Yes	Yes	No	Internal, cannot extend beyond body
Broad, muscular foot	Reduced or absent	Yes	Yes	Yes	Modified into arms	Yes	Small, only at "front" end

Dorsal concentration of internal organs (visceral mass)	Not obvious	Yes	Yes	Yes	Yes	Yes	Yes
Large digestive ceca	No ceca in some aplacophora	Yes	Yes	Yes	Yes	Yes	No
Large complex metanephridia ("kidneys")	None	Yes	Yes	Yes	Yes	Yes	Small, simple

A "generalized mollusc"

Because of the enormous variations between groups of molluscs, many text books start the subject by describing a "generalized mollusc", which some suggest *may* resemble very early molluscs and which is rather similar to modern monoplacophorans.

The generalized mollusc has a single, "limpet-like" shell on top. The shell is secreted by a mantle that covers the upper surface. The underside consists of a single muscular "foot". The visceral mass, or visceropallium, is the soft, non-muscular metabolic region of the mollusc. It contains the body organs.

Mantle and mantle cavity

The mantle cavity is a fold in the mantle that encloses a significant amount of space. It is lined with epidermis. It is exposed, according to habitat, to sea, fresh water or air. The cavity was at the rear in the earliest molluscs but its position now varies from group to group. The anus, a pair of osphradia (chemical sensors) in the incoming "lane", the hindmost pair of gills and the exit openings of the nephridia ("kidneys") and gonads (reproductive organs) are in the mantle cavity. The whole soft body of bivalves lies within an enlarged mantle cavity.

Shell

The mantle edge secretes a shell (secondarily absent in a number of taxonomic groups, such as the nudibranchs) that consists of mainly chitin and conchiolin (a protein) hardened with calcium carbonate), except that the outermost layer in almost all cases is all conchiolin. Molluscs never use phosphate to construct their hard parts, with the questionable exception of *Cobcrephora*. While most mollusc shells are composed mainly of aragonite, those gastropods that lay eggs with a hard shell use calcite (sometimes with traces of aragonite) to construct the eggshells.

The shell consists of three layers: the outer layer (the periostracum) made of organic matter, a middle layer made of columnar calcite and an inner layer consisting of laminated calcite, that is often nacreous.

Foot

The underside consists of a muscular foot, which has adapted to different purposes in different classes. The foot carries a pair of statocysts, which act as balance sensors. In gastropods, it secretes mucus as a lubricant to aid movement. In forms that have only a top shell, such as limpets, the foot acts as a sucker attaching the animal to a hard surface, and the vertical muscles clamp the shell down over it; in other molluscs, the vertical muscles pull the foot and other exposed soft parts into the shell. In bivalves, the foot is adapted for burrowing into the sediment; in cephalopods it is used for jet propulsion, and the tentacles and arms are derived from the foot.

Circulation

Molluscs' circulatory systems are mainly open. Although molluscs are coelomates, their coeloms are reduced to fairly small spaces enclosing the heart and gonads. The main body cavity is a hemocoel through which blood and coelomic fluid circulate and which encloses most of the other internal organs. These hemocoelic spaces act as an efficient hydrostatic skeleton. The blood contains the respiratory pigment hemocyanin as an oxygen-carrier. The heart consists of one or more pairs of atria (auricles), which receive oxygenated blood from the gills and pump it to the ventricle, which pumps it into the aorta (main artery), which is fairly short and opens into the hemocoel.

The atria of the heart also function as part of the excretory system by filtering waste products out of the blood and dumping it into the coleom as urine. A pair of nephridia ("little kidneys") to the rear of and connected to the coelom extracts any re-usable materials from the urine and dumps additional waste products into it, and then ejects it via tubes that discharge into the mantle cavity.

Respiration

Most molluscs have only one pair of gills, or even only one gill. Generally the gills are rather like feathers in shape, although some species have gills with filaments on only one side. They divide the mantle cavity so that water enters near the bottom and exits near the top. Their filaments have three kinds of cilia, one of which drives the water current through the mantle cavity, while the other two help to keep the gills clean. If the osphradia detect noxious chemicals or possibly sediment entering the mantle cavity, the gills' cilia may stop beating until the unwelcome intrusions have ceased. Each gill has an incoming blood vessel connected to the hemocoel and an outgoing one to the heart.

Eating, digestion, and excretion

Most molluscs have muscular mouths with radulae, "tongues" bearing many rows of chitinous teeth, which are replaced from the rear as they wear out. The radula primarily functions to scrape bacteria and algae off rocks. This radula is associated with the odontophore, a cartilaginous supporting organ

Molluscs mouths also contain glands that secrete slimy mucus, to which the food sticks. Beating cilia (tiny "hairs") drive the mucus towards the stomach, so that the mucus forms a long string.

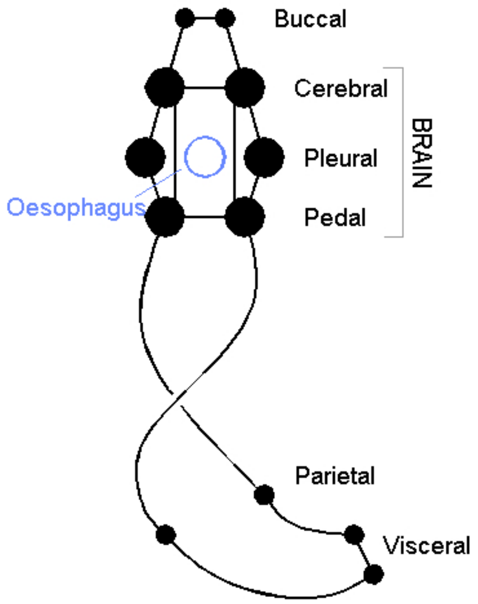
At the tapered rear end of the stomach and projecting slightly into the hindgut is the prostyle, a backward-pointing cone of feces and mucus, which is rotated by further cilia so that it acts as a bobbin, winding the mucus string onto itself. Before the mucus string reaches the prostyle, the acidity of the stomach makes the mucus less sticky and frees particles from it.

The particles are sorted by yet another group of cilia, which send the smaller particles, mainly minerals, to the prostyle so that eventually they are excreted, while the larger ones, mainly food, are sent to the stomach's cecum (a pouch with no other exit) to be digested. The sorting process is by no means perfect.

Periodically, circular muscles at the hindgut's entrance pinch off and excrete a piece of the prostyle, preventing the prostyle from growing too large. The anus is in the part of the mantle cavity that is swept by the outgoing "lane" of the current created by the gills. Carnivorous molluscs usually have simpler digestive systems.

As the head has largely disappeared in bivalves, their mouth has been equipped with labial palps (two on each side of the mouth) to collect the detritus from its mucus.

Nervous system



Simplified diagram of the mollusc nervous system

Molluscs have two pairs of main nerve cords (three in bivalves) the visceral cords serving the internal organs and the pedal ones serving the foot. Both pairs run below the level of the gut, and include ganglia as local control centers in important parts of the body. Most pairs of corresponding ganglia on both sides of the body are linked by commissures (relatively large bundles of nerves). The only ganglia above the gut are the cerebral ganglia, which sit above the esophagus (gullet) and handle "messages" from and to the eyes. The pedal ganglia, which control the foot, are just below the esophagus and their commissure and connections to the cerebral ganglia encircle the esophagus in a nerve ring.

The brain, in species that have one, encircles the esophagus. Most molluscs have a head with eyes, and all have a pair of sensor-containing tentacles, also on the head, that detect chemicals, vibrations and touch.

Reproduction

The simplest molluscan reproductive system relies on external fertilization, but there are more complex variations. All produce eggs, from which may emerge trochophore larvae, more complex veliger larvae, or miniature adults. Two gonads sit next to the coelom, a small cavity that surrounds the heart and shed ova or sperm into the coloem, from which the nephridia extract them and emit them into the mantle cavity. Molluscs that use such a system remain of one sex all their lives and rely on external fertilization. Some molluscs use internal fertilization and/or are hermaphrodites, functioning as both sexes; both of these methods require more complex reproductive systems.

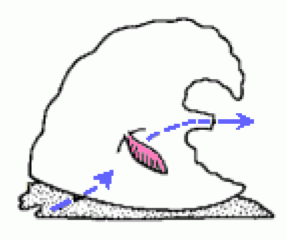
The most basic molluscan larva is a trochophore, which is planktonic and feeds on floating food particles by using the two bands of cilia round its "equator" to sweep food into the mouth, which uses more cilia to drive them into the stomach, which uses further cilia to expel undigested remains through the anus. New tissue grows in the bands of mesoderm in the interior, so that the apical tuft and anus are pushed further apart as the animal grows. The trochophore stage is often succeeded by a veliger stage in which the prototroch, the "equatorial" band of cilia nearest the apical tuft, develops into the velum ("veil"), a pair of cilia-bearing lobes with which the larva swims. Eventually the larva sinks to the seafloor and metamorphoses into the adult form. Whilst metamorphosis is the usual state in molluscs, the cephalopods differ in exhibiting direct development: the hatchling is a 'miniaturized' form of the adult.

Evolution

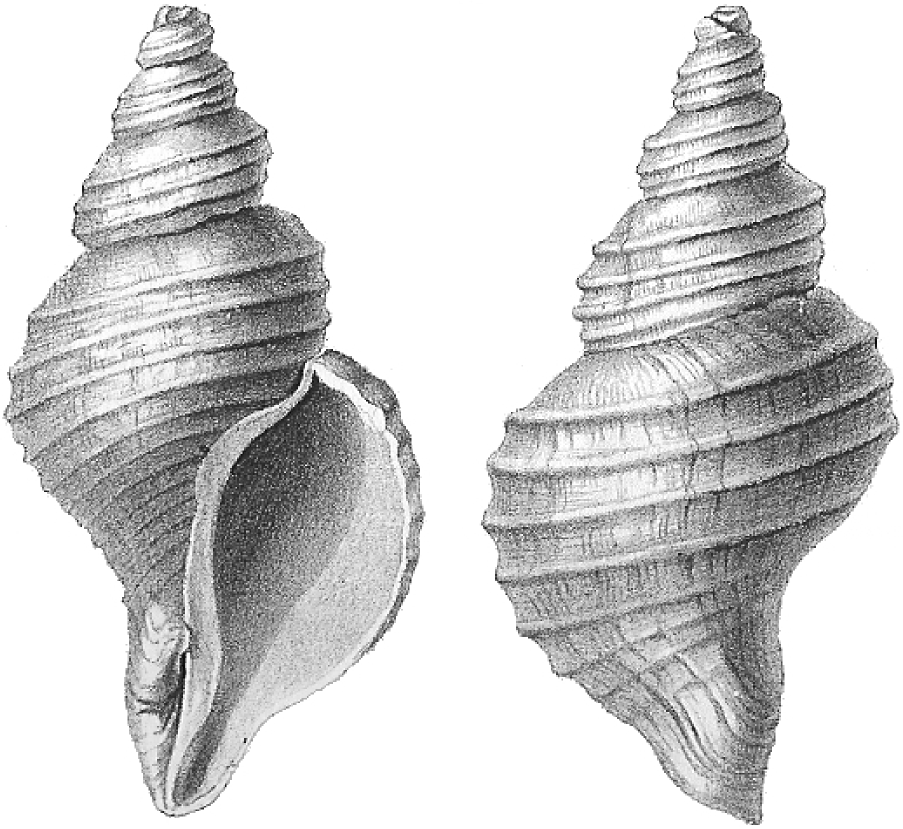
Fossil record

There is good evidence for the appearance of gastropods, cephalopods and bivalves in the Cambrian period 542 to 488.3 million years ago. However, the evolutionary history both of the emergence of molluscs from the ancestral group Lophotrochozoa, and of their diversification into the well-known living and fossil forms, is still vigorously debated.

There is debate about whether some Ediacaran and Early Cambrian fossils really are molluscs. *Kimberella*, from about 555 million years ago, has been described as "mollusc-like", but others are unwilling to go further than "probable bilaterian". There is an even sharper debate about whether *Wiwaxia*, from about 505 million years ago, was a mollusc, and much of this centers on whether its feeding apparatus was a type of radula or more similar to that of some polychaete worms. Nicholas Butterfield, who opposes the idea that *Wiwaxia* was a mollusc, has written that earlier microfossils from 515 to 510 million years ago are fragments of a genuinely mollusc-like radula. This appears to contradict the concept that the ancestral molluscan radula was mineralized.



The tiny Helcionellid fossil *Yochelcionella* is thought to be an early mollusk



Spirally coiled shells appear in many gastropods

However, the Helcionellids, which first appear over 540 million years ago in Early Cambrian rocks from Siberia and China, are thought to be early molluscs with rather snail-like shells. Shelled molluscs therefore predate the earliest trilobites. Although most helcionellid fossils are only a few millimeters long, specimens a few centimeters long have also been found, most with more limpet-like shapes. There have been suggestions that the tiny specimens were juveniles and the larger ones adults.

Some analyses of helcionellids concluded that these were the earliest gastropods. However other scientists are not convinced that Early Cambrian fossils show clear signs of the torsion that identifies modern gastropods twists the internal organs so that the anus lies above the head.

For a long time it was thought that *Volborthella*, some fossils of which pre-date 530 million years ago, was a cephalopod. However discoveries of more detailed fossils showed that *Volborthella*'s shell was not secreted but built from grains of the mineral silicon dioxide (silica), and that it was not divided into a series of compartments by septa as those of fossil shelled cephalopods and the living *Nautilus* are. *Volborthella*'s classification is uncertain. The Late Cambrian fossil *Plectronoceras* is now thought to be the earliest clearly cephalopod fossil, as its shell had septa and a siphuncle, a strand of tissue that *Nautilus* uses to remove water from compartments that it has vacated as it grows, and which is also visible in fossil ammonite shells. However, *Plectronoceras* and other early cephalopods crept along the seafloor instead of swimming, as their shells contained a "ballast" of stony deposits on what is thought to be the underside and had stripes and blotches on what is thought to be the upper surface. All cephalopods with external shells except the nautiloids became extinct by the end of the Cretaceous period 65 million years ago. However, the shell-less Coleoidea (squid, octopus, cuttlefish) are abundant today.

The Early Cambrian fossils *Fordilla* and *Pojetaia* are regarded as bivalves. "Modern-looking" bivalves appeared in the Ordovician period, 488 to 443 million years ago. One bivalve group, the rudists, became major reef-builders in the Cretaceous, but became extinct in the Cretaceous-Tertiary extinction. Even so, bivalves remain abundant and diverse.

The Hyolitha is a class of extinct animals with a shell and operculum that may be molluscs. Authors who suggest that they deserve their own phylum do not comment on the position of this phylum in the tree of life

Phylogeny

The phylogeny (evolutionary "family tree") of molluscs is a controversial subject. In addition to the debates about whether *Kimberella* and any of the "halwaxiids" were molluscs or closely related to molluscs, there are debates about the relationships between the classes of living molluscs. In fact some groups traditionally classifed as molluscs may have to be redefined as distinct but related.

Molluscs are generally regarded members of the Lophotrochozoa, a group defined by having trochophore larvae and, in the case of living Lophophorata, a feeding structure called a lophophore. The other members of the Lophotrochozoa are the annelid worms and seven marine phyla. The diagram on the right summarizes a phylogeny presented in 2007.

Because the relationships between the members of the family tree are uncertain, it difficult to identify the features inherited from the last common ancestor of all molluscs. For example, it is uncertain whether the ancestral mollusc was metameric (composed of repeating units)—if it was, that would suggest an origin from an annelid-like worm. Scientists disagree about this: Giribet and colleagues concluded in 2006 that the repetition of gills and of the foot's retractor muscles were later developments, while in 2007 Sigwart concluded that the ancestral mollusc was metameric, and that it had a foot used for creeping and a "shell" that was mineralized. In one particular one branch of the family tree, the shell of conchiferans is thought to have evolved from the spicules (small spines) of aplacophorans; however this is difficult to reconcile with the embryological origins of spicules.

The molluscan shell appears to have originated from a mucus coating, which eventually stiffened into a cuticle. This would have been impermeable and thus forced the development of more sophisticated respiratory apparatus in the form of gills. Eventually, the cuticle would have become mineralized, using the same genetic machinery (*engrailed*) as most other bilaterian skeletons. The first mollusc shell almost certainly was reinforced with the mineral aragonite.

However, an analysis in 2009 that used both morphological and molecular phylogenetics comparisons concluded that the molluscs are not monophyletic; in particular, that Scaphopoda and Bivalvia are both separate, monophyletic lineages unrelated to the remaining molluscan classes—in other words that the traditional phylum Mollusca is polyphyletic, and that it can only be made monophyletic if scaphopods and bivalves are excluded. A 2010 analysis managed to recover the traditional conchiferan and seriala groups, but similarly concluded that the molluscs are not monophyletic, this time suggesting that solenogastres are more closely related to the non-molluscan taxa used as an outgroup than to other molluscs. Current molecular data is insufficient to constrain the molluscan phylogeny, and since the methods used to determine the confidence in clades are prone to over-estimation, it is risky to place too much emphasis even on the areas that different studies agree.

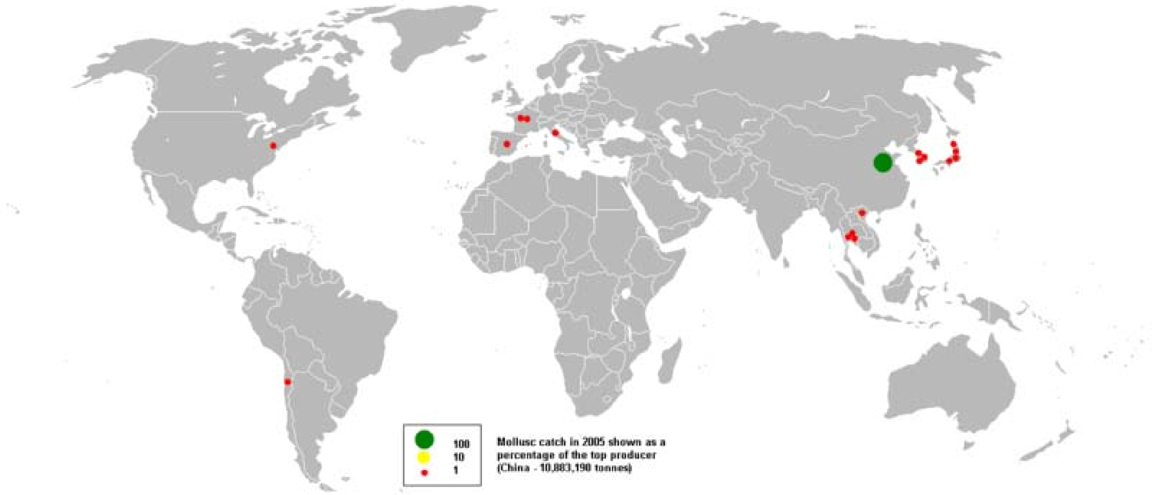
Human interaction

Molluscs have for many centuries been the source of important luxury goods, notably pearls, mother of pearl, Tyrian purple dye, and sea silk. Their shells have also been used as money in some pre-industrial societies.

There is a risk of food poisoning from toxins that accumulate in molluscs under certain conditions, and many countries have regulations that aim to minimize this risk. Blue-ringed octopus bites are often fatal, and the bite of *Octopus rubescens* can cause necrosis that lasts longer than one month if untreated, and headaches and weakness persisting for up to a week even if treated. Stings from a few species of large tropical cone shells can also kill. However, the sophisticated venoms of these cone snails have become important tools in neurological research and show promise as sources of new medications.

Schistosomiasis (also known as bilharzia, bilharziosis or snail fever) is transmitted to humans via water snail hosts, and affects about 200 million people. A few species of snails and slugs are serious agricultural pests, and in addition, accidental or deliberate introduction of various snail species into new territory has resulted in serious damage to some natural ecosystems.

Uses by humans



Mollusc output in 2005

Molluscs, especially bivalves such as clams and mussels, have been an important food source since at least the advent of anatomically modern humans—and this has often resulted in over-fishing. Other commonly eaten molluscs include octopuses and squids, whelks, oysters, and scallops. In 2005, China accounted for 80% of the global mollusc catch, netting almost 11,000,000 tonnes (11,000,000 LT; 12,000,000 ST). Within Europe, France remained the industry leader. Some countries regulate importation and handling of molluscs and other seafood, mainly to minimize the poison risk from toxins that accumulate in the animals.

Saltwater pearl oyster farm in Seram, Indonesia

Most molluscs that have shells can produce pearls, but only the pearls of bivalves and some gastropods whose shells are lined with nacre are valuable. The best natural pearls are produced by pearl oyster.s *Pinctada margaritifera* and *Pinctada mertensi*, which live in the tropical and sub-tropical waters of the Pacific Ocean. Natural pearls form when a small foreign object gets stuck between the mantle and shell.

There are two methods of culturing pearls, by inserting either "seeds" or beads into oysters. The "seed" method uses grains of ground shell from freshwater mussels, and over-harvesting for this purpose has endangered several freshwater mussel species in the southeastern USA. The pearl industry is so important in some areas that significant sums of money are spent on monitoring the health of farmed molluscs.

Other luxury and high-status products were made from molluscs. Tyrian purple, made from the ink glands of murex shells, "... fetched its weight in silver" in the fourth-century BC, according to Theopompus. The discovery of large numbers of Murex shells on Crete suggests that the Minoans may have pioneered the extraction of "Imperial purple" during the Middle Minoan period in the 20th–18th century BC, centuries before the Tyrians. Sea silk is a fine, rare and valuable fabric produced from the long silky threads (byssus) secreted by several bivalve molluscs, particularly *Pinna nobilis*, to attach themselves to the sea bed. Procopius, writing on the Persian wars circa 550 CE, "stated that the five hereditary satraps (governors) of Armenia who received their insignia from the Roman Emperor were given chlamys (or cloaks) made from *lana pinna* (Pinna "wool," or byssus). Apparently only the ruling classes were allowed to wear these chlamys."

Mollusc shells, including those of cowries, were used as a kind of money in several pre-industrial societies. However these "currencies" generally differed in important ways from the standardized government-backed and -controlled money familiar to industrial societies. Some shell "currencies" were not used for commercial transactions but mainly as social status displays at important occasions such as weddings. When used for commercial transactions they functioned as commodity money, in other words as a tradable commodity whose value differed from place to place, often as a result of difficulties in transport, and which was vulnerable to incurable inflation if more efficient transport or "goldrush" behavior appeared.

Stings and bites

The blue-ringed octopus's rings are a warning signal—this octopus is alarmed, and its bite can kill.

When handled alive, a few species of molluscs can sting or bite and, with some species, this can present a serious risk to the human handling the animal. To put this into perspective however, deaths from mollusc venoms are less than 10% of the number of deaths from jellyfish stings.

All octopuses are venomous but only a few species pose a significant threat to humans. Blue-ringed octopuses in the genus *Hapalochlaena*, which live around Australia and New Guinea, bite humans only if severely provoked, but their venom kills 25% of human victims. Another tropical species, *Octopus apollyon*, causes severe inflammation that can last for over a month even if treated correctly.

Live cone snails can be dangerous to shell-collectors but are useful to neurology researchers

All species of cone snails are venomous and can sting when handled, although many species are too small to pose much of a risk to humans. These are carnivorous gastropods that feed on marine invertebrates (and in the case of larger species on fish). Their venom is based on a huge array of toxins, some fast-acting and others slower but deadlier—they can afford to do this because their toxins require less time and energy to be produced compared with those of snakes or spiders. Many painful stings have been reported, and a few fatalities, although some of the reported fatalities may be exaggerations. Only the few larger species of cone snail that can capture and kill fish are likely to be seriously dangerous to humans. The effects of individual cone shell toxins on victims' nervous systems are so precise that they are useful tools for research in neurology, and the small size of their molecules makes it easy to synthesize them.

The traditional belief that a giant clam can trap the leg of a person between its valves, thus drowning them, is a myth.

Pests

Skin vesicles created by the penetration of *Schistosoma*

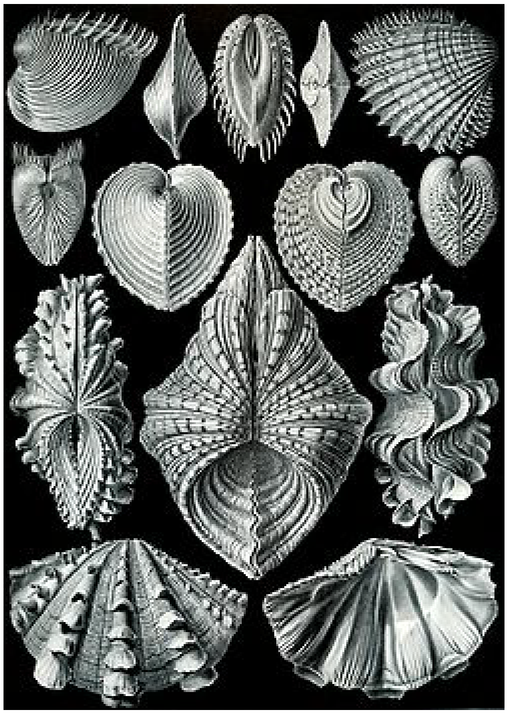
Schistosomiasis (also known as bilharzia, bilharziosis or snail fever) is "second only to malaria as the most devastating parasitic disease in tropical countries. An estimated 200 million people in 74 countries are infected with the disease — 100 million in Africa alone." The parasite has 13 known species, of which two infect humans. The parasite itself is not a mollusc, but all the species have freshwater snails as intermediate hosts.

Some species of molluscs, particularly certain snails and slugs, can be serious crop pests, and when introduced into new environments can unbalance local ecosystems. One such pest, the giant African snail *Achatina fulica*, has been introduced to many parts of Asia, as well as to many islands in the Indian Ocean and Pacific Ocean. In the 1990s this species reached the West Indies. Attempts to control it by introducing the predatory snail *Euglandina rosea* proved disastrous, as the predator ignored *Achatina fulica* and went on to extirpate several native snail species instead.

Chapter- 2

Bivalvia

Bivalvia
Temporal range: early Cambrian–Recent



"Acephala", from Ernst Haeckel's *Kunstformen der Natur* (1904)

Scientific classification

Kingdom:	Animalia
Phylum:	Mollusca
Class:	**Bivalvia** Linnaeus, 1758

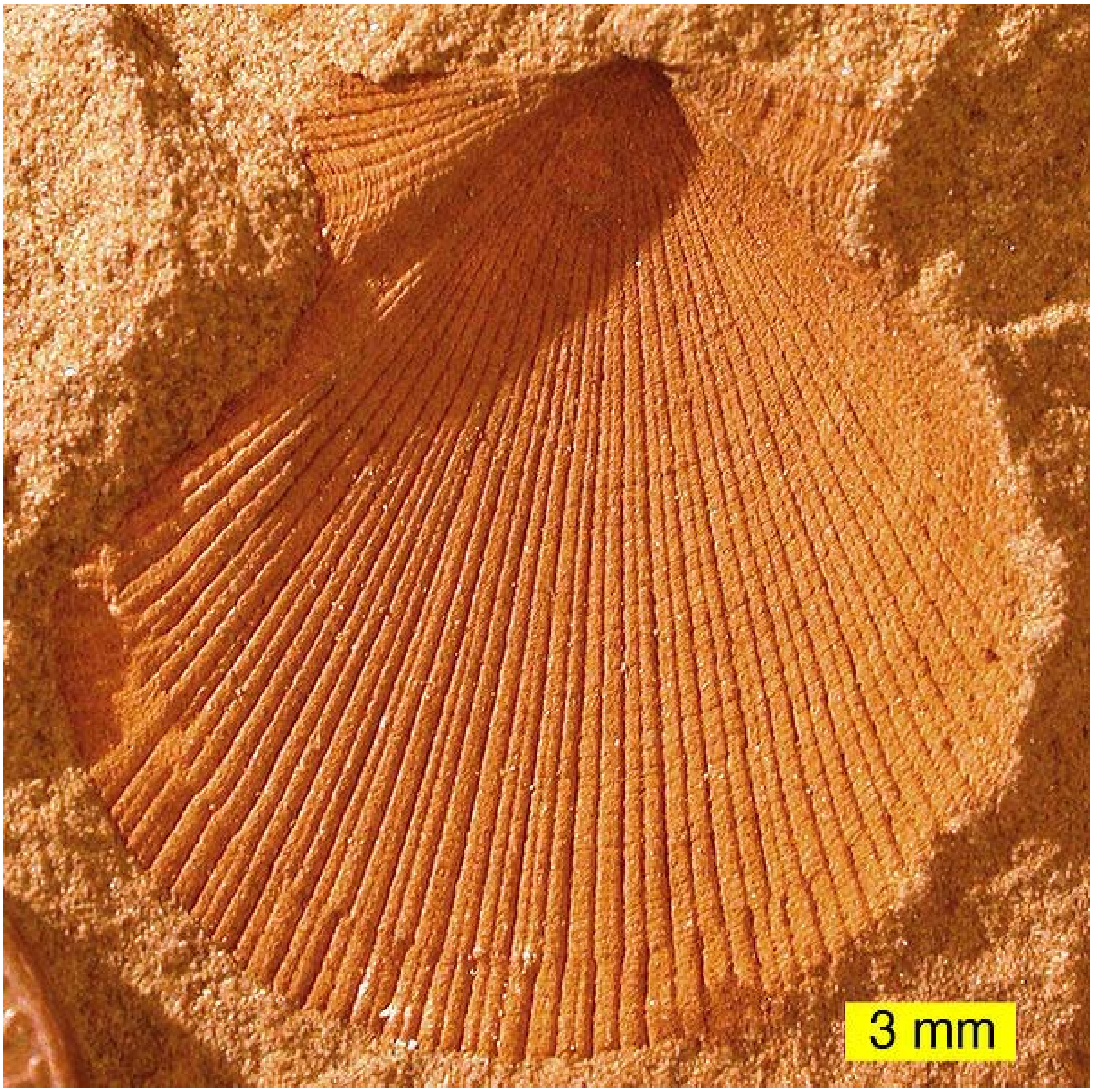
Subclasses

Anomalosdesmata
Cryptodonta

Heterodonta
Paleoheterodonta
Palaeotaxodonta
Pteriomorphia

Mussels in the intertidal zone in Cornwall, England

Fossil gastropod and attached mytilid bivalves in a Jurassic limestone (Matmor Formation) in southern Israel



Aviculopecten subcardiformis; an extinct pectenoid bivalve from the Logan Formation of Wooster, Ohio (external mold)

Bivalvia is a class of marine and freshwater mollusks known for some time as **Pelecypoda**, but now commonly referred to simply as **bivalves**. As with Gastropoda and Cephalopoda, the term Pelecypoda is in reference to the animal itself while Bivalvia simply describes the shell. Other names for the class include Acephala, Bivalva, and Lamellibranchia. The total number of bivalves currenty amounts to 9,200 species in 1,260 genera and 106 families. The global marine bivalves (including brackish water and estuarine species) contain about 8,000 species, combined in 4 subclasses and 99 families with 1,100 genera. The largest recent families are Veneridae with more than 680 species or Tellinidae and Lucinidae with over 500 species. The freshwater bivalves have 7 additional families, of which the Unionidae contain about 700 species.

Bivalves have a shell consisting of two asymmetrically rounded halves called *valves* that are mirror images of each other, joined at one edge by a flexible ligament called the *hinge*. The shell is typically bilaterally symmetrical, with the hinge lying in the sagittal plane. Recent Bivalves cover a large range of shell sizes from 0.52 mm in *Condylonucula maya* to 1,532 mm in *Kuphus polythalamia*

Bivalves are unique among the molluscs, having lost their odontophore and radula in their transition to filter feeding.

Some bivalves are epifaunal; they attach to surfaces. Others are infaunal; they bury themselves in sediment. These forms typically have a strong digging foot. Some bivalves such as scallops can swim.

The term *bivalve* is derived from the Latin *bis*, meaning 'two', and *valvae*, meaning *leaves of a door* Other bivalved animals include brachiopods, ostracodes, and conchostrachans.

Taxonomy

No consensus exists on bivalve phylogeny. Many conflicts exist due to taxonomies based on single organ systems and conflicting naming schemes. More recent taxonomies use multiple organ systems, fossil records, as well as molecular phylogenetics to draw more robust phylogenies. Due to the numerous fossil lineages, DNA sequence data is of limited use should the subclasses turn out to be paraphyletic.

In his 1935 work *Handbuch der systematischen Weichtierkunde* (Handbook of Systematic Malacology), Johannes Thiele introduced a mollusc taxonomy based upon the 1909 work by Cossmann and Peyrot. Thiele's system divided the bivalves into three orders:

- *Taxodonta* – taxodont dentition
- *Anisomyaria* – either a single adductor muscle or one adductor muscle much larger than the other
- *Eulamellibranchiata* – all forms with lamellibranch ctenidia

The last was divided into four sub-orders: *Schizodonta*, *Heterodonta*, *Adapedonta* and *Anomalodesmata*.

The systematic layout presented here follows Norman D. Newell's 1965 classification based on hinge tooth morphology:

Subclass	**Order**
Palaeotaxodonta	*Nuculoida
	†Praecardioida
Cryptodonta	
	Solemyoida

Pteriomorphia	Arcoida (ark shells)
	†Cyrtodontoida
	Limoida (file shells)
	Mytiloida (true mussels)
	Ostreoida (oysters, formerly included in Pterioida)
	†Praecardioida
	Pterioida (pearl oysters, pen shells)
	†Trigonioida
Paleoheterodonta	Unionoida (freshwater mussels)
Heterodonta	†Modiomorpha
	†Cycloconchidae
	†Hippuritoida
	†Lyrodesmatidae
	Myoida (most "soft shell calms" razor clams)
	†Redoniidae
	Veneroida (most "hard shell calms", cockles, etc)
Anomalodesmata	Pholadomyoida

The monophyly of the Anomalodesmata is disputed, but this is of less consequence as that group does not include higher-level prehistoric taxa. The standard view now is that Anomalodesmata resides within the subclass Heterodonta.

An alternative systematic scheme exists according to gill morphology. This distinguishes between Protobranchia, Filibranchia, and Eulamellibranchia. The first corresponds to Newells Palaeotaxodonta and Cryptodonta, the second to his Pteriomorphia, with the last corresponding to all other groups. In addition, Franc separated the Septibranchia from his eulamellibranchs, but this would seem to make the latter paraphyletic.

In May 2010 a new taxonomy of the Bivalvia was published in the journal Malacologia. In this classification 324 families were recognized as valid, 214 of which are known exclusively as fossils and 110 families occur in the Recent with or without a fossil record. This publication consisted of two parts:

- Nomenclator of Bivalve Names of the Family-Group and above
- Classification of Bivalve Families (under the redaction of Rüdiger Bieler, Joseph G. Carter and Eugene V. Coan)

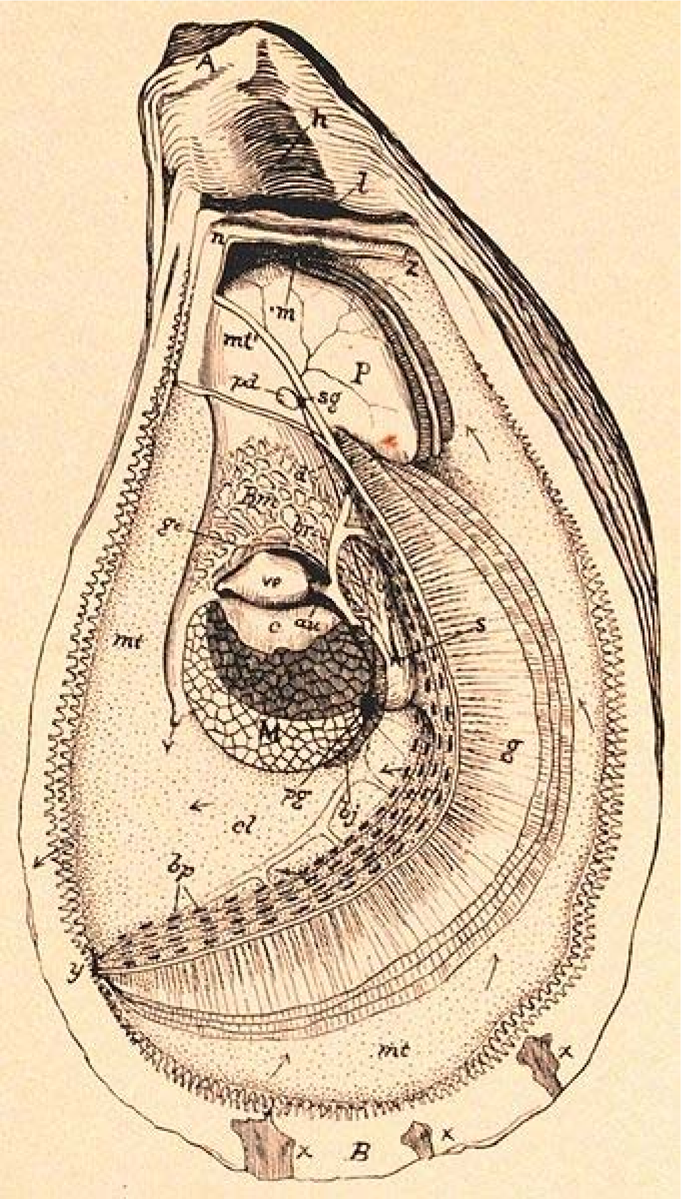
Biodiversity the number of recent bivalves

Huber gives a total number of about 9,200 living bivalves combined in 106 families. He states that the number of 20,000 living species, often encountered in literature, could not be verified and shows the following table.

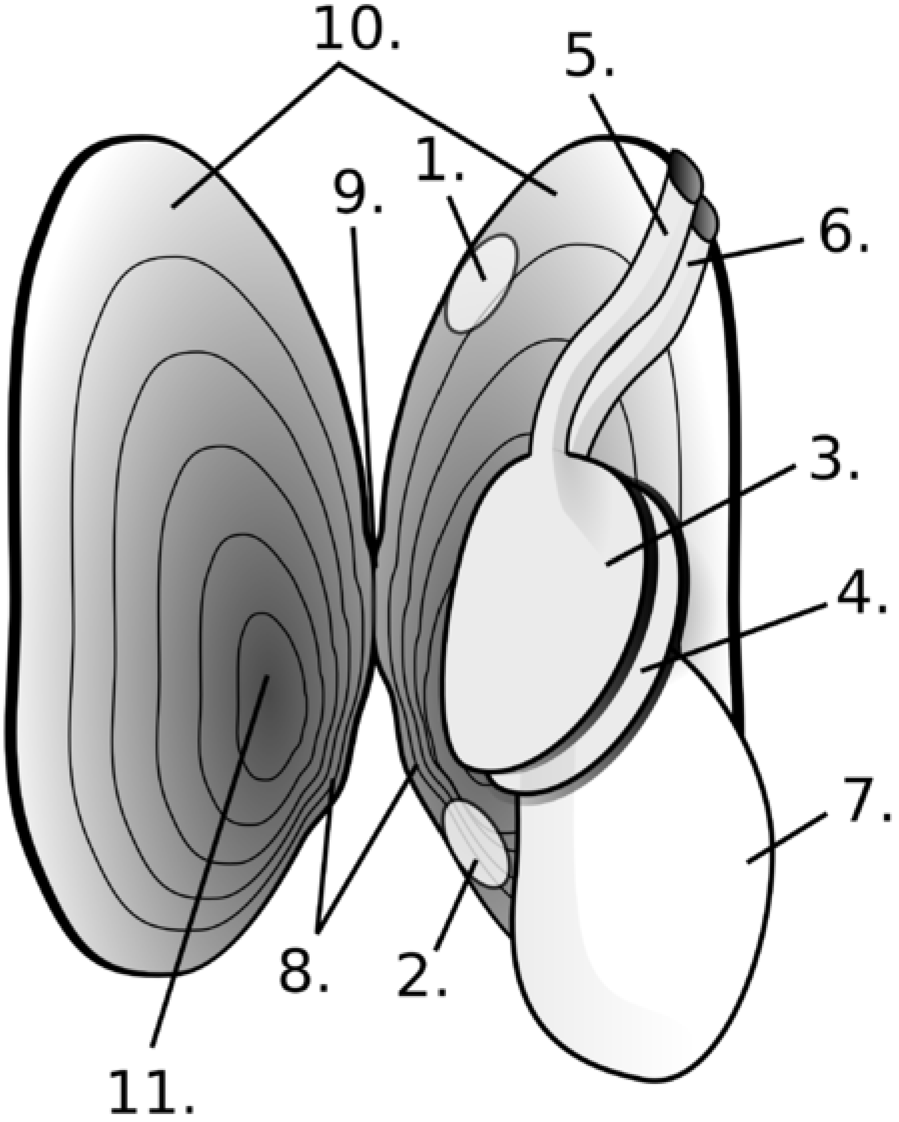
Number of	**Families**	**Genera**	**Species**
PROTOBRANCHIA	**10**	**49**	**700**
Nuculoidea	**1**	**8**	**170**
Sapretoidea	**1**	**ca. 5**	**10**
Solemyoidea	**1**	**2**	**30**
Manzanelloidea	**1**	**2**	**20**
Nuculanoidea	**6**	**32**	**460**
PTERIOMORPHA	**25**	**240 (incl. 2 freshwater)**	**2000 (incl. 11 freshwater)**
Mytiloidea	**1**	**50 (1 freshwater)**	**400 (5 freshwater)**
Arcoidea	**7**	**60 (1 freshwater)**	**570 (6 freshwater)**
Pinnoidea	**1**	**3 (+)**	**50**
Pterioidea	**5**	**9**	**80**
Ostreoidea	**2**	**23**	**80**
Dimyoidea	**1**	**3**	**15**
Anomioidea	**2**	**9**	**30**
Plicatuloidea	**1**	**1**	**20**
Pectinoidea	**4**	**68**	**500**
Limoidea	**1**	**8**	**250**
PALAEOHETERODONTA	**7 (incl. 6 freshwater)**	**171 (incl. 170 freshwater)**	**908 (incl. 900 freshwater)**
Trigonioidea	**1**	**1**	**8**
Unionoidea	**(6 freshwater)**	**(170 freshwater)**	**(900 freshwater)**
HETERODONTA	**64 (incl. 1 freshwater)**	**800 (incl. 16 freshwater)**	**5600 (incl. 270 freshwater)**
Crassatelloidea	**5**	**65**	**420**
Thyasiroidea	**1**	**ca. 12**	**ca. 100**

Lucinoidea	2	ca. 85	ca. 500
Galeommatoidea	ca. 4	ca. 100	ca. 500
Cyamioidea	3	22	140
Solenoidea	2	17 (2 freshwater)	130 (4 freshwater)
Hiatelloidea	1	5	25
Gastrochaenoidea	1	7	30
Chamoidea	1	6	70
Cardioidea	2	38	260
Tellinoidea	5	110 (2 freshwater)	900 (15 freshwater)
Glossoidea	2	20	110
Arcticoidea	2	6	13
Cyrenoidea	1	6 (3 freshwater)	60 (30 freshwater)
Sphaerioidea	(1 freshwater)	(5 freshwater)	(200 freshwater)
Veneroidea	4	104	750
Hemidonacoidea	1	1	6
Cyrenoidoidea	1	1	6
Ungulinoidea	1	16	100
Mactroidea	4	46	220
Dreissenoidea	1	3 (2 freshwater)	20 (12 freshwater)
Myoidea	3	15 (1 freshwater)	130 (1 freshwater)
Pholadoidea	2	34 (1 freshwater)	200 (3 freshwater)
Limoidea	1	8	250
(ANOMALODESMATA)	(14)	(71)	(770)
Pholadomyoidea	2	3	20
Clavagelloidea	1	2	20
Pandoroidea	7	30	250
Verticordioidea	2	16	160
Cuspidarioidea	2	20	320

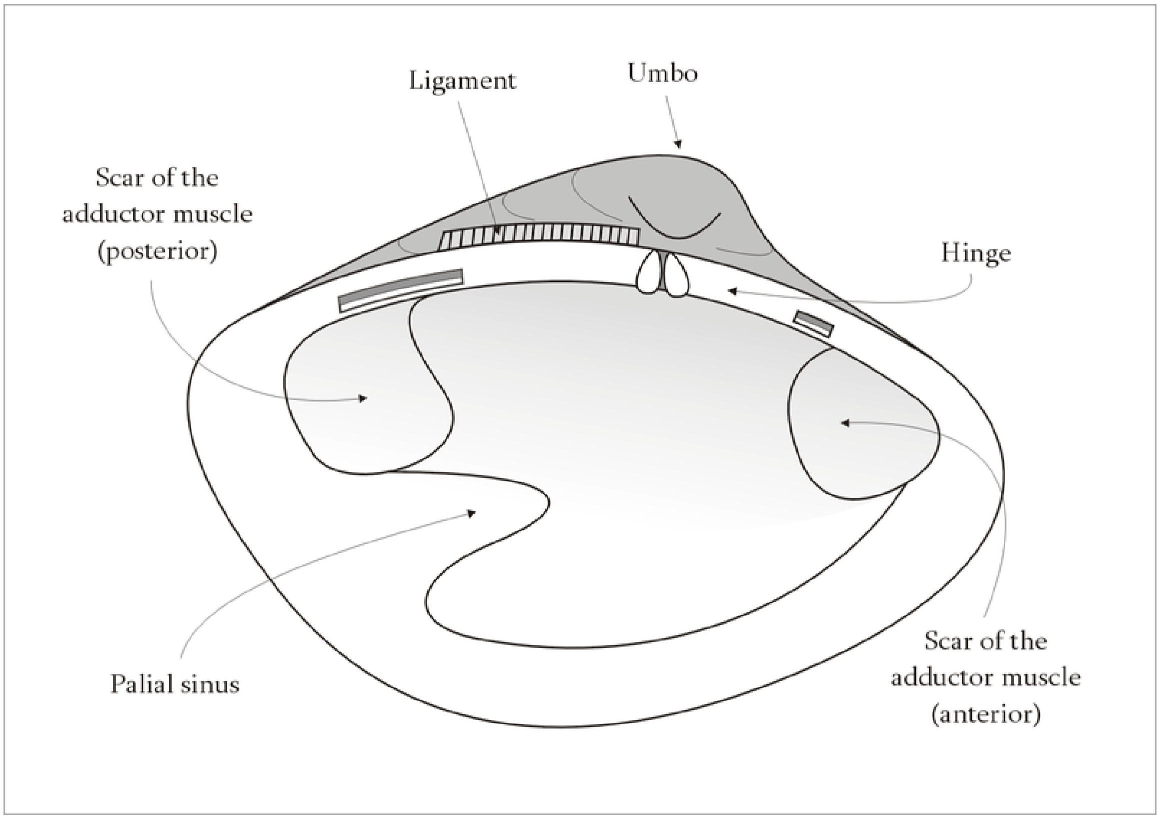
Anatomy



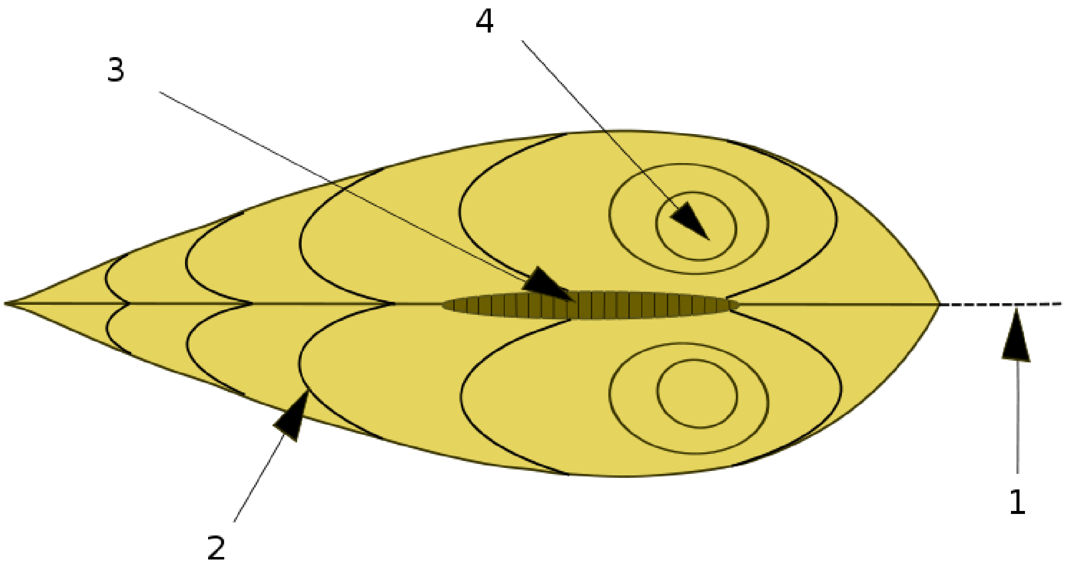
Drawing of oyster anatomy



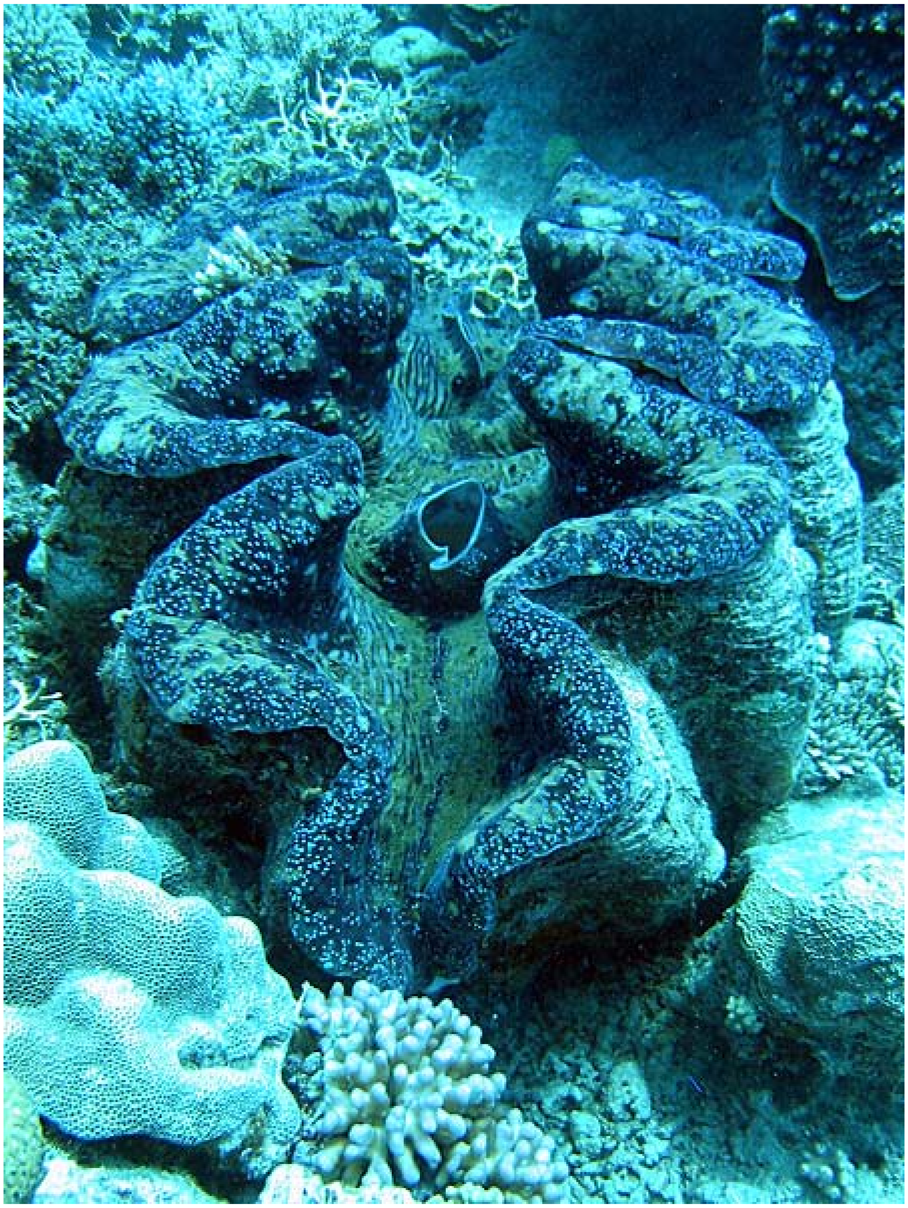
Drawing of anatomy of Freshwater pearl mussel *Margaritifera margaritifera*



A diagram of the internal shell anatomy of the left hand valve of a bivalve such as a venerid



Main parts in the shell of a bivalve: 1: sagittal plane, 2: growth lines, 3: ligament, 4: umbo



Giant clam, *Tridacna gigas*

Bivalve shells vary greatly in shape; some are globular, others flattened, while others are elongated to aid burrowing. The shipworms of the family Teredinidae have greatly elongated bodies, but the shell valves are much reduced and restricted to the anterior end of the body, where they function as burrowing organs that permit the animal to dig tunnels through wood.

Nervous system

The sedentary habit of the bivalves has led to the development of a simpler nervous system than in other molluscs; they have no brain. In all but the simplest forms the neural ganglia are united into two cerebropleural ganglia on either side of the oesophagus. The pedal ganglia, controlling the foot, are at its base, and the visceral ganglia (which can be quite large in swimming bivalves) under the posterior adductor muscle. These ganglia are both connected to the cerebropleural ganglia by nerve fibres. There may also be siphonal ganglia in bivalves with a long siphon.

Senses

The sensory organs of bivalves are not well developed and are largely a function of the posterior mantle margins. The organs are usually tentacle mechanoreceptors or chemoreceptors.

Scallops have complex eyes with a lens and retina, but most other bivalves have much simpler eyes, if any. There are also light-sensitive cells in all bivalves that can detect a shadow falling over the animal.

Many bivalves possess a number of tentacles, which have chemoreceptor cells to taste the water, as well as being sensitive to touch. These are typically found near the siphons, but in some species may fringe the entire mantle cavity.

Another notable sensory organ found in bivalves is the osphradium, a patch of sensory cells located below the posterior adductor muscle. It may serve to taste the water, or measure its turbidity, but it is probably not homologous with the structure of the same name found in snails and slugs.

In the septibranchs the inhalant siphon is surrounded by vibration-sensitive tentacles for detecting prey.

Statocysts within the organism help the bivalve to sense and correct its orientation.

Muscles

The muscular system is composed of the posterior and anterior adductor muscles, although the anterior muscles may be reduced or even lost in some species.

The paired anterior and posterior pedal retractor muscles operate the animal's foot. In some bivalves, such as oysters and scallops, these retractors are absent.

Circulation and respiration

Bivalves have an open circulatory system that bathes the organs in hemolymph. The heart has three chambers; two auricles receiving blood from the gills, and a single ventricle. The ventricle is muscular and pumps hemolymph into the aorta, and through this to the rest of the body. Many bivalves have only a single aorta, but most also have a second, usually smaller, aorta serving the hind parts of the animal.

Oxygen is absorbed into the hemolymph in the gills, which hang down into the mantle cavity, and also assist in filtering food particles from the water. The wall of the mantle cavity is a secondary respiratory surface, and is well supplied with capillaries. Some species, however, have no gills, with the mantle cavity being the only location of gas exchange. Bivalves adapted to tidal environments can survive for several hours out of water by closing their shells and keeping the mantle cavity filled with water.

The hemolymph usually lacks any respiratory pigment, although some species are known to possess haemoglobin dissolved directly into the serum.

Mantle and shell

The world's largest clam (187 cms), a *Sphenoceramus steenstrupi* fossil from Greenland in the Geological Museum in Copenhagen

In bivalves the mantle forms a thin membrane surrounding the body which secretes the valves, ligament and hinge teeth. The mantle lobes secrete the valves and the mantle crest secretes the ligament and hinge teeth. The mantle is attached to the shell by the mantle retractor muscles at the pallial line. In some bivalves the mantle edges fuse to form siphons, which take in and expel water for suspension feeding.

The shell is composed of two calcareous valves, which are made of either calcite (as with oysters) or both calcite and aragonite, usually with the aragonite forming an inner layer (as with the Pterioida). The outermost layer is the periostracum, composed of a horny organic substance. This forms the familiar coloured layer on the shell.

The shell is added to in two ways; at the open edge and by a gradual thickening throughout the animal's life.

The shell halves are held together at the animal's dorsum by the ligament, which is composed of the tensilium and resilium. The ligament opens the shell.

Digestive system

Modes of feeding

The majority of bivalves are filter feeders, using their gills to capture particulate food from the water. In almost all species, the water current enters the shell from the posterior ventral surface of the animal, and then passes upwards through the gills in a U-shape, so that it exits just above the intake. In burrowing species, there may be elongated siphons stretching from the body to the surface, one each for the inhalant and exhalant streams of water.

The gills of filter-feeding bivalves have become highly modified to increase their ability to capture food. For example, the cilia on the gills, which originally served to remove unwanted sediment, are adapted to capture food particles, and transport them in a steady stream of mucus to the mouth. The filaments of the gills are also much longer than those in more primitive bivalves, and are folded over to create a groove through which food can be transported. The structure of the gills varies considerably, and can serve as a useful means for classifying bivalves into groups.

Some bivalves feed by scraping detritus from the bottom, and this may be the primitive mode of feeding for the group, before the gills became adapted for filter feeding. These primitive bivalves hold onto the substratum with a pair of tentacles at the edge of the mouth, each of which has a single palp, or flap. The tentacles are covered in mucus, which traps the food particles, and transports them back to the palps using cilia. The palps then serve to sort the particles, ejecting those that are too large to be digestible.

A few bivalves, such as *Poromya*, are carnivorous, eating much larger prey than the tiny phytoplankton consumed by the filter feeders. In these animals, the gills are relatively small, and form a perforated barrier separating the main mantle cavity from a smaller chamber through which the water is exhaled. Muscles pump water through the cavity, sucking in small crustaceans and worms. The prey are then seized in the palps and consumed.

The unusual genus *Entovalva* is parasitic, and lives only in the gut of sea cucumbers.

Digestive tract

The digestive tract of typical bivalves consists of an oesophagus, stomach, and intestine. A number of digestive glands open into the stomach, often via a pair of diverticula; these secrete enzymes to digest food in the stomach, but also include cells that phagocytose food particles, and digest them intracellularly.

In the filter feeding bivalves, an elongated rod of solidified mucus referred to as the **crystalline style** projects into the stomach from an associated sac. Cilia in the sac cause the style to rotate, winding in a stream of food-containing mucus from the mouth, and churning the stomach contents. This constant motion propels food particles into a sorting region at the rear of the stomach, which distributes smaller particles into the digestive glands, and heavier particles into the intestine.

Carnivorous bivalves have a greatly reduced style, and a chitinous gizzard that helps grind up the food before digestion.

Excretory system

Like most other molluscs, the excretory organs of bivalves are nephridia. There are two nephridia, each consisting of a long, glandular tube, which opens into the body cavity just beneath the heart, and a bladder. Waste is voided from the bladders through a pair of openings near the front of the upper part mantle cavity, where it can easily be washed away in the stream of exhalant water.

Reproduction

The sexes are usually separate, but some hermaphroditism is known. Bivalves practice external fertilization. The gonads are located close to the intestines, and either open into the nephridia, or through a separate pore into the mantle cavity.

Typically bivalves start life as a trochophore, later becoming a veliger. Freshwater bivalves of the Unionoida have a different life cycle: they become a glochidium, which attaches to any firm surface to avoid the danger of being swept downsteam. Glochidia can be serious pests of fish if they lodge in the fish gills.

Some of the species in the freshwater mussel family, Unionidae, commonly known as *pocketbook mussels* have evolved a remarkable reproductive strategy. The edge of the female's body that protrudes from the valves of the shell develops into an imitation of a small fish complete with markings and false eyes. This decoy moves in the current and attracts the attention of real fish. Some fish see the decoy as prey, while others see a conspecific. Whatever they see, they approach for a closer look and the mussel releases huge numbers of larvae from her gills, dousing the inquisitive fish with her tiny, parasitic young. These glochidia larvae are drawn into the fish's gills where they attach and trigger a tissue response that forms a small cyst in which the young mussel resides. It feeds by breaking down and digesting the tissue of the fish within the cyst.

Behaviour

A large number of venerid bivalves with their siphons visible

The radical structure of the bivalves reflects their behaviour in several ways. The most significant is the use of the closely-fitting valves as a defense against predation and, in intertidal species, against desiccation. The entire animal can be contained within the shell, which is held shut by the powerful adductor muscles. This defense is difficult to overcome except by specialist predators such as sea stars and oystercatchers.

Feeding

Most bivalves are filter feeders although some have taken up scavenging and predation. Nephridia remove the waste material. Buried bivalves feed by extending a siphon to the surface (indicated by the presence of a pallial sinus, the size of which is proportional to the burrowing depth, and represented by their hinge teeth).

Feeding types

There are four feeding types, defined by their gill structure:

- **Protobranchs** use their ctenidia solely for respiration, and the labial palps to feed
- **Septibranchs** possess a septum across the mantle cavity which pumps in food.
- **Filibranchs** and **lamellibranchs** trap food with a mucous coating on the ctenidia; the filibranchs and lamellibranchs are differentiated by the way the ctenidia are joined

Movement

Razor shells can dig themselves into the sand with great speed to escape predation. Scallops, and file clams can swim to escape a predator, clapping their valves together to create a jet of water. Cockles can use their foot to leap from danger. However these methods can quickly exhaust the animal. In the razor shells the siphons can break off only to grow back later.

Defensive secretions

The file shells can produce a noxious secretion when threatened, and the fan shells of the same family have a unique, acid-producing organ.

Comparison with brachiopods

Anadara, a bivalve with taxodont dentition from the Pliocene of Cyprus

Bivalves are superficially similar to brachiopods, but the construction of the shell is completely different in the two groups. In brachiopods, the two valves are on the dorsal and ventral surfaces of the body, while in bivalves, they are on the left and right sides.

Bivalves appeared late in the Cambrian explosion and came to dominate over brachiopods during the Palaeozoic. By the Permian-Triassic extinction event bivalves were undergoing a huge radiation while brachiopods were devastated, losing 95% of their diversity.

It had long been considered that bivalves are better adapted to aquatic life than the brachiopods were, causing brachiopods to be out-competed and relegated to minor niches in later strata. These taxa appeared in textbooks as an example of replacement by competition. Evidence included the use of an energetically-efficient ligament-muscle system for opening valves, requiring less food to subsist. However the prominence of bivalves over brachiopods might instead be due to chance disparities in their response to extinction events.

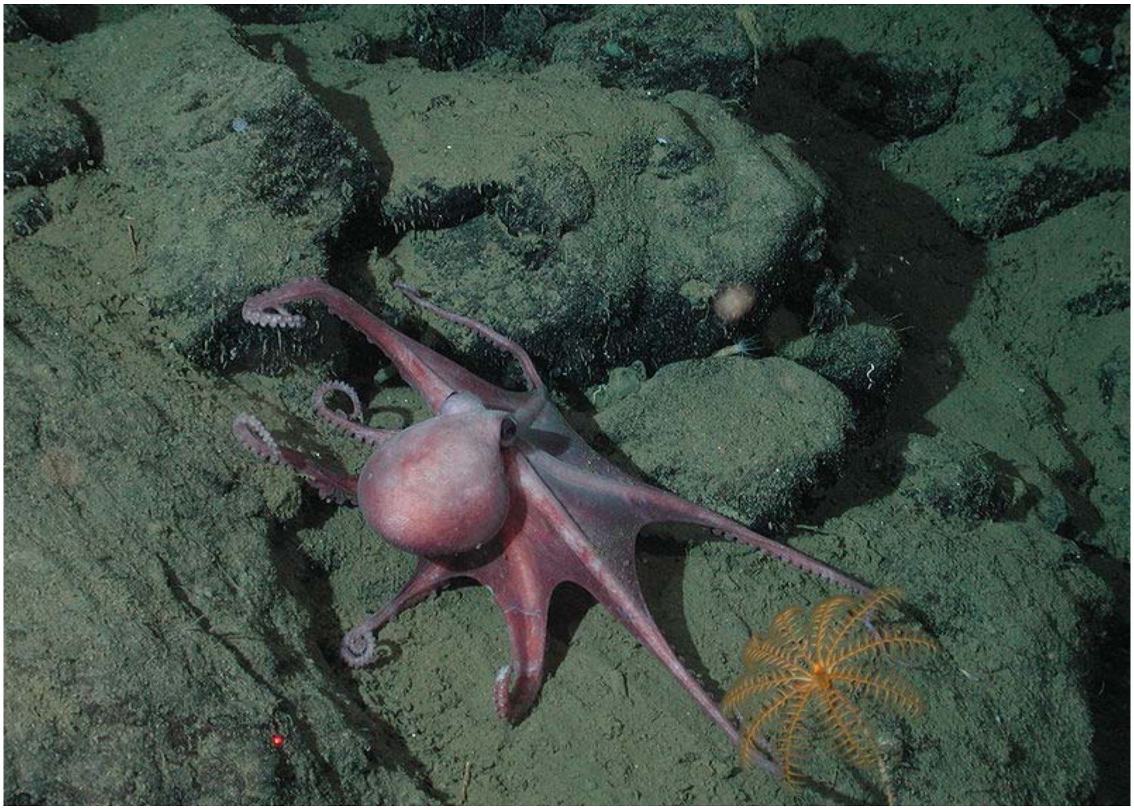
Chapter- 3

Cephalopod

A **cephalopod** is any member of the molluscan class **Cephalopoda** (Greek plural *Κεφαλόποδα* (kephalópoda); "head-feet"). These exclusively marine animals are characterized by bilateral body symmetry, a prominent head, and a set of arms or tentacles (muscular hydrostats) modified from the primitive molluscan foot. Fishermen sometimes call them **inkfish**, referring to their common ability to squirt ink. The study of cephalopods is a branch of malacology known as **teuthology**.

Cephalopods became dominant during the Ordovician period, represented by primitive nautiloids. The class now contains two, only distantly related, extant subclasses: Coleoidea, which includes octopuses, squid, and cuttlefish; and Nautiloidea, represented by *Nautilus* and *Allonautilus*. In the Coleoidea, the molluscan shell has been internalized or is absent, whereas in the Nautiloidea, the external shell remains. About 800 living species of cephalopods have been identified. Two important extinct taxa are the Ammonoidea (ammonites) and Belemnoidea (belemnites).

Distribution



Top: A pair of *Sepia officinalis* in shallow water
Bottom: *Benthoctopus* sp. on the Davidson Seamount at 2,422 m depth

There are around 800 extant species of cephalopod, although new species continue to be described. An estimated 11,000 extinct taxa have been described, although the soft-bodied nature of cephalopods means they are not easily fossilised.

Cephalopods are found in all the oceans of Earth. None of them can tolerate freshwater, but the brief squid, *Lolliguncula brevis*, found in Chesapeake Bay may be a notable exception in that it tolerates brackish water.

Cephalopods occupy most of the depth of the ocean, from the abyssal plane to the sea surface. Their diversity is greatest near the equator (~40 species retrieved in nets at 11°N by a diversity study) and decreases towards the poles (~5 species captured at 60°N).

Nervous system and behaviour

Top: An octopus opening a container with a screw cap
Bottom: Hawaiian bobtail squid, *Euprymna scolopes*, burying itself in the sand, leaving only the eyes exposed

Cephalopods are widely regarded as the most intelligent of the invertebrates, and have well developed senses and large brains (larger than those of gastropods). The nervous system of cephalopods is the most complex of the invertebrates, and their brain-to-body-mass ratio falls between that of warm- and cold-blooded vertebrates. The giant nerve fibers of the cephalopod mantle have been widely used as experimental material in neurophysiology for many years; their large diameter (due to lack of myelination) makes them relatively easy to study.

Cephalopods are social creatures; when isolated from their own kind, they will take to shoaling with fish.

Some cephalopods are able to fly distances up to 50 m. While the organisms are not particularly aerodynamic, they achieve these rather impressive ranges by use of jet-propulsion; water continues to be expelled from the funnel while the organism is in flight.

Senses

Cephalopods have advanced vision, can detect gravity with statocysts, and have a variety of chemical sense organs. Octopuses use their tentacles to explore their environment and can use them for depth perception.

The primitive nautilus eye functions similarly to a pinhole camera.

Vision

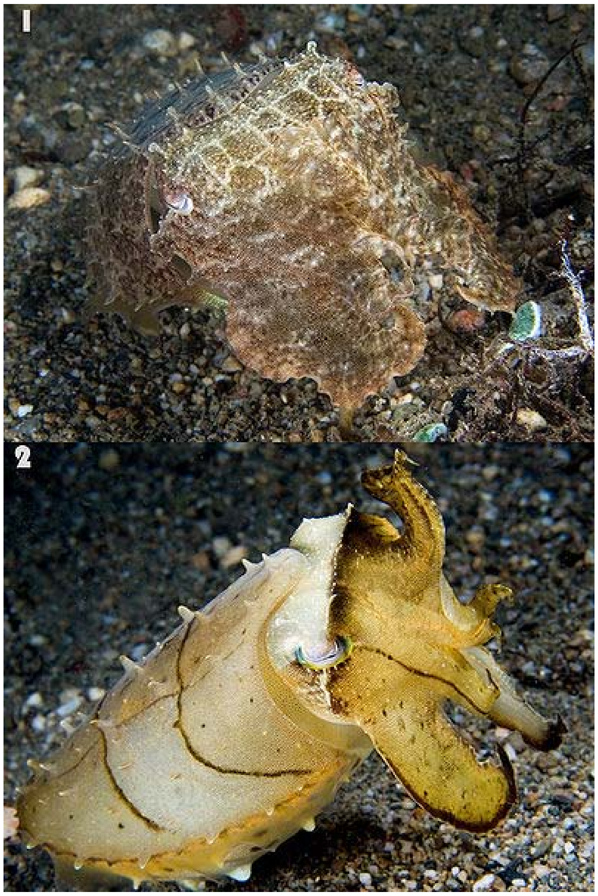
Most cephalopods rely on vision to detect predators and prey, and to communicate with one another. Consequently, cephalopod vision is acute: training experiments have shown that the common octopus can distinguish the brightness, size, shape, and horizontal or vertical orientation of objects. The morphological construction gives cephalopod eyes the same performance as sharks'; however, their construction differs, as cephalopods lack a cornea, and have an everted retina. Cephalopods' eyes are also sensitive to the plane of polarization of light. Surprisingly—given their ability to change color—all octopuses and most cephalopods are color blind. When camouflaging themselves, they use their chromatophores to change brightness and pattern according to the background they see, but their ability to match the specific color of a background may come from cells such as iridophores and leucophores that reflect light from the environment. They also produce visual pigments throughout their body, and may sense light levels directly from their body. Evidence of color vision has been found in the sparkling enope squid (*Watasenia scintillans*), which achieves color vision by the use of three distinct retinal molecules (A1, sensitive to red; A2, to purple, and A4, to yellow?) which bind to its opsin.

Unlike many other cephalopods, nautiluses do not have good vision; their eye structure is highly developed, but lacks a solid lens. They have a simple "pinhole" eye through which water can pass. Instead of vision, the animal is thought to use olfaction as the primary sense for foraging, as well as locating or identifying potential mates.

Hearing

Cephalopods can use their statocysts to detect sound.

Use of light



This broadclub cuttlefish (*Sepia latimanus*) can go from camouflage tans and browns (top) to yellow with dark highlights (bottom) in less than a second.

Most cephalopods possess chromatophores - that is, coloured pigments - which they can use in a startling array of fashions. As well as providing camouflage with their background, some cephalopods bioluminesce, shining light downwards to disguise their shadows from any predators that may lurk below. The bioluminescence is produced by bacterial symbionts; the host cephalopod is able to detect the light produced by these organisms. Bioluminescence may also be used to entice prey, and some species use colourful displays to impress mates, startle predators, or even communicate with one another. It is not certain whether bioluminescence is actually of epithelial origin or if it is a bacterial production.

Colouration

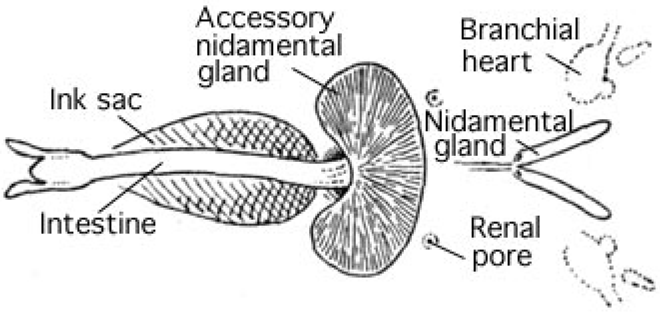
Colouration can be changed in milliseconds as they adapt to their environment, and the pigment cells are expandable by muscular contraction. Colouration is typically more pronounced in near-shore species than those living in the open ocean, whose functions tend to be restricted to camouflage by breaking their outline.

Evidence of original colouration has been detected in cephalopod fossils dating as far back as the Silurian; these orthoconic individuals bore concentric stripes, which are thought to have served as camouflage. Devonian cephalopods bear more complex colour patterns, whose function may be more complex.

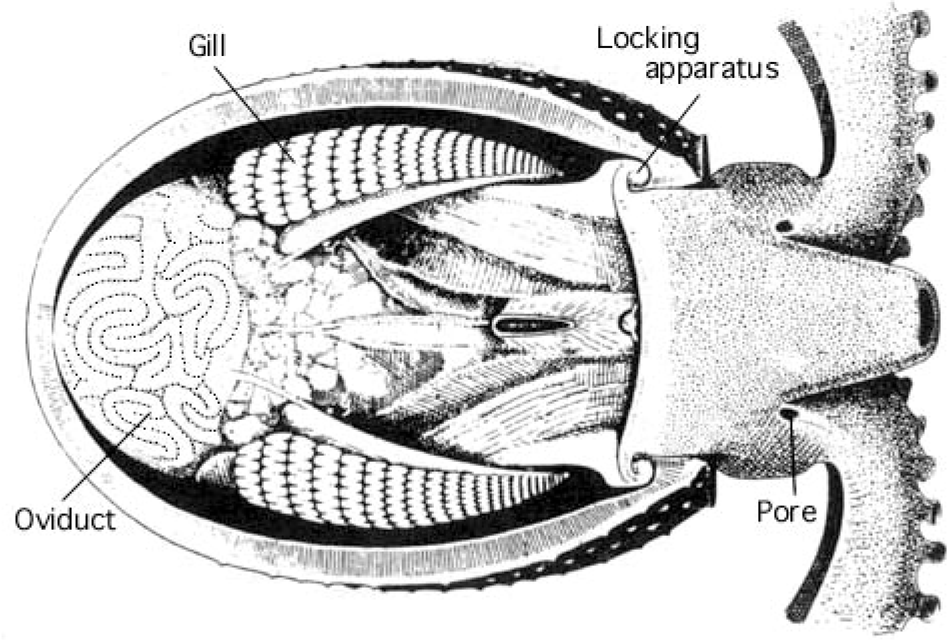
Ink

With the exception of the Nautilidae and the species of octopus belonging to the suborder Cirrina, all known cephalopods have an ink sac, which can be used to expel a cloud of dark ink to confuse predators. This sac is a muscular bag which originated as an extension of the hind gut. It lies beneath the gut and opens into the anus, into which its contents – almost pure melanin – can be squirted; its proximity to the base of the funnel means the ink can be distributed by ejected water as the cephalopod uses its jet propulsion. The ejected cloud of melanin is usually mixed, upon expulsion, with mucus, produced elsewhere in the mantle, and therefore forms a thick cloud, resulting in visual (and possibly chemosensory) impairment of the predator, like a smokescreen. However, a more sophisticated behaviour has been observed, in which the cephalopod releases a cloud, with a greater mucus content, that approximately resembles the cephalopod that released it (this decoy is referred to as a pseudomorph). This strategy often results in the predator attacking the pseudomorph, rather than its rapidly departing prey.

The inking behaviour of cephalopods has led to a common name of "inkfish", primarily used in fisheries science and the fishing industry, paralleling the terms white fish, oily fish, and shellfish.



Viscera of Chtenopteryx sicula



Viscera of Ocythoe tuberculata

Circulatory system

Cephalopods are the only mollusks with a closed circulatory system. Coleoids have two gill hearts (also known as branchial hearts) that move blood through the capillaries of the gills. A single systemic heart then pumps the oxygenated blood through the rest of the body.

Like most molluscs, cephalopods use hemocyanin, a copper-containing protein, rather than hemoglobin, to transport oxygen. As a result, their blood is colorless when deoxygenated and turns blue when exposed to air.

Respiration

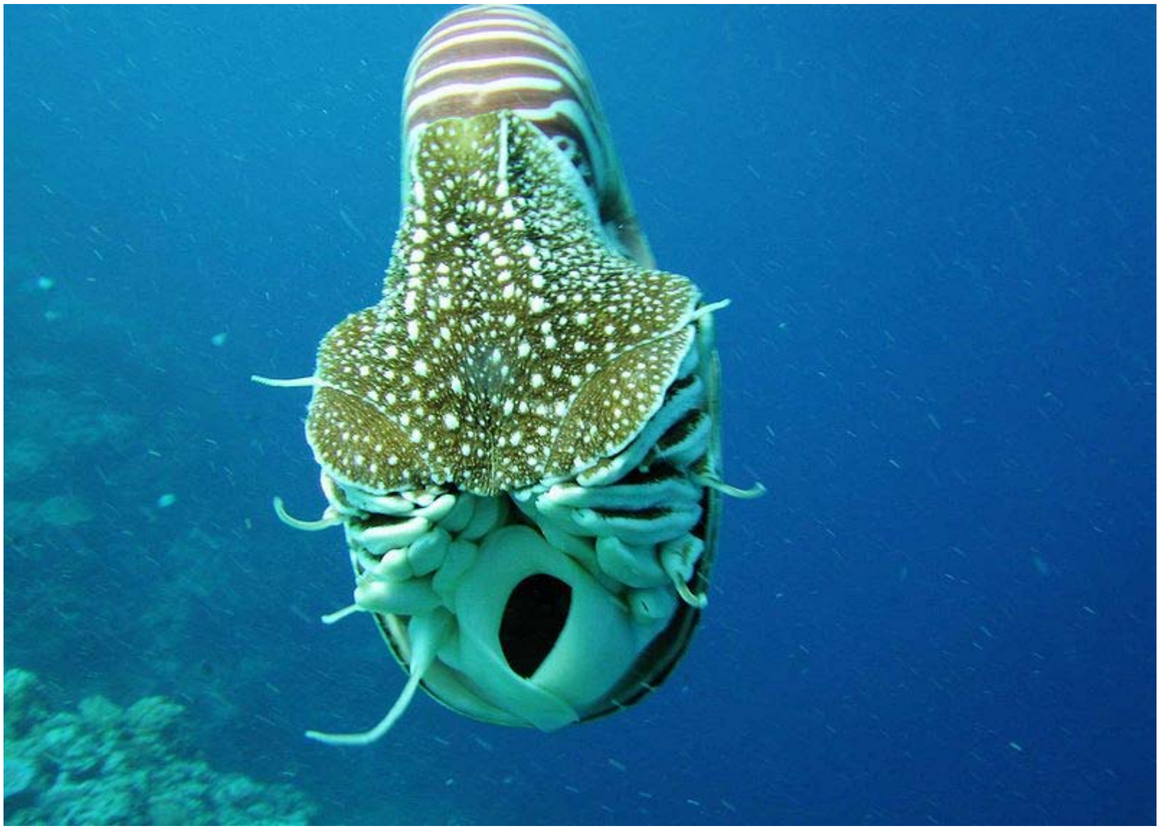
Cephalopods exchange gasses with the seawater by forcing water through their gills, which are attached to the roof of the organism. Water enters the mantle cavity on the outside of the gills, and the entrance of the mantle cavity closes. When the mantle contracts, water is forced through the gills, which lie between the mantle cavity and the funnel. The water's expulsion through the funnel can be used to power jet propulsion. The gills, which are much more efficient than those of other molluscs, are attached to the ventral surface of the mantle cavity. There is a trade-off with gill size regarding lifestyle. To achieve fast speeds, gills need to be small - water will be passed through them quickly when energy is needed, compensating for their small size. However, organisms which spend most of their time moving slowly along the bottom do not naturally pass much water through their cavity for locomotion; thus they have larger gills, along with complex systems to ensure that water is constantly washing through their gills, even when the organism is stationary. The water flow is controlled by contractions of the radial and circular mantle cavity muscles.

The gills of cephalopods are supported by a skeleton of robust fibrous proteins; the lack of mucopolysaccharides distinguishes this matrix from cartilage. The gills are also thought to be involved in excretion, with NH_4^+ being swapped with K^+ from the seawater.

Locomotion and buoyancy

Octopuses swim headfirst, with arms trailing behind

While all cephalopods can move by jet propulsion, this is a very energy-consuming way to travel compared to the tail propulsion used by fish. The relative efficiency of jet propulsion decreases further as animal size increases; paralarvae are far more efficient than juvenile and adult individuals. Since the Paleozoic era, as competition with fish produced an environment where efficient motion was crucial to survival, jet propulsion has taken a back role, with fins and tentacles used to maintain a steady velocity. Whilst jet propulsion is never the sole mode of locomotion, the stop-start motion provided by the jets continues to be useful for providing bursts of high speed - not least when capturing prey or avoiding predators. Indeed, it makes cephalopods the fastest marine invertebrates, and they can out-accelerate most fish. The jet is supplemented with fin motion; in the squid, the fins flap each time that a jet is released, amplifying the thrust; they are then extended between jets (presumably to avoid sinking). Oxygenated water is taken into the mantle cavity to the gills and through muscular contraction of this cavity, the spent water is expelled through the hyponome, created by a fold in the mantle. The size difference between the posterior and anterior ends of this organ control the speed of the jet the organism can produce. The velocity of the organism can be accurately predicted for a given mass and morhpology of animal. Motion of the cephalopods is usually backward as water is forced out anteriorly through the hyponome, but direction can be controlled somewhat by pointing it in different directions. Some cephalopods accompany this expulsion of water with a gunshot-like popping noise, thought to function to frighten away potential predators.



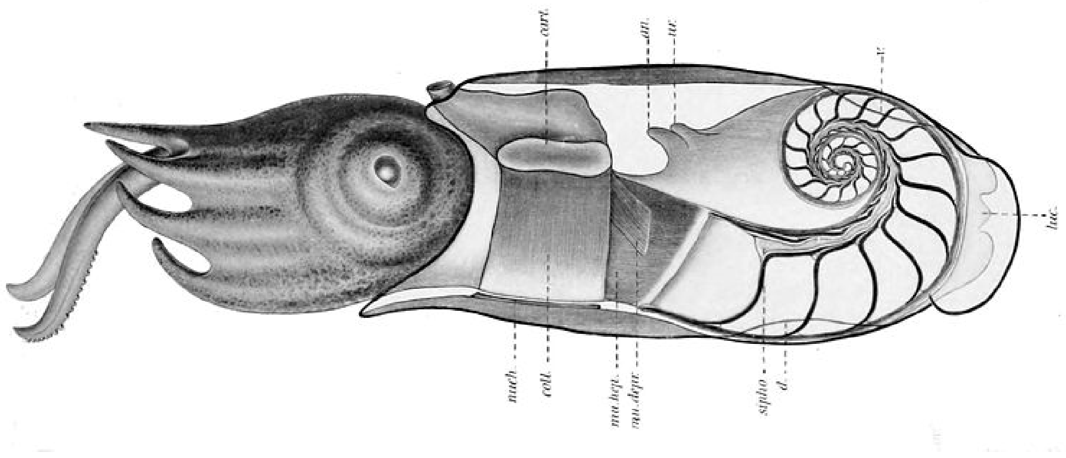
Nautilus belauensis seen from the front, showing the opening of the hyponome

Early cephalopods are thought to have produced jets by drawing their body into their shells, as *Nautilus* does today. *Nautilus* is also capable of creating a jet by undulations of its funnel; this slower flow of water is more suited to the extraction of oxygen from the water. The jet velocity in *Nautilus* is much slower than in coleoids, but less musculature and energy is involved in its production. Jet thrust in cephalopods is controlled primarily by the maximum diameter of the funnel orifice (or, perhaps, the average diameter of the funnel) and the diameter of the mantle cavity. Changes in the size of the orifice are used most at intermediate velocities. The absolute velocity achieved is limited by the cephalopod's requirement to inhale water for expulsion; this intake limits the maximum velocity to eight body-lengths per second, a speed which most cephalopods can attain after two funnel-blows. Water refills the cavity by entering not only through the orifices, but also though the funnel. To accommodate the rapid changes in water intake and expulsion, the orifices are highly flexible and can change their size by a factor of twenty; the funnel radius, conversely, changes only by a factor of around 1.5.

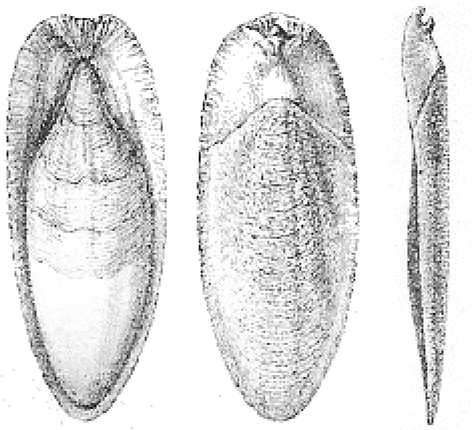
Some octopus species are also able to walk along the sea bed. Squids and cuttlefish can move short distances in any direction by rippling of a flap of muscle around the mantle.

While most cephalopods float (i.e. are neutrally buoyant or nearly so; in fact most cephalopods are about 2-3% denser than seawater), they achieve this in different ways. Some, such as *Nautilus*, allow gas to diffuse into the gap between the mantle and the shell; others allow purer water to ooze from their kidneys, forcing out denser salt water from the body cavity; others, like some fish, accumulate oils in the liver; and some octopuses have a gelatinous body with lighter chlorine ions replacing sulfate in the body chemistry.

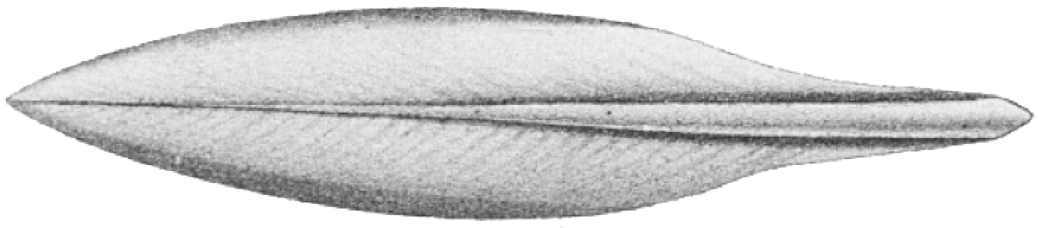
Shell



Cross section of *Spirula spirula*, showing the position of the shell inside the mantle



Cuttlebone of *Sepia officinalis*



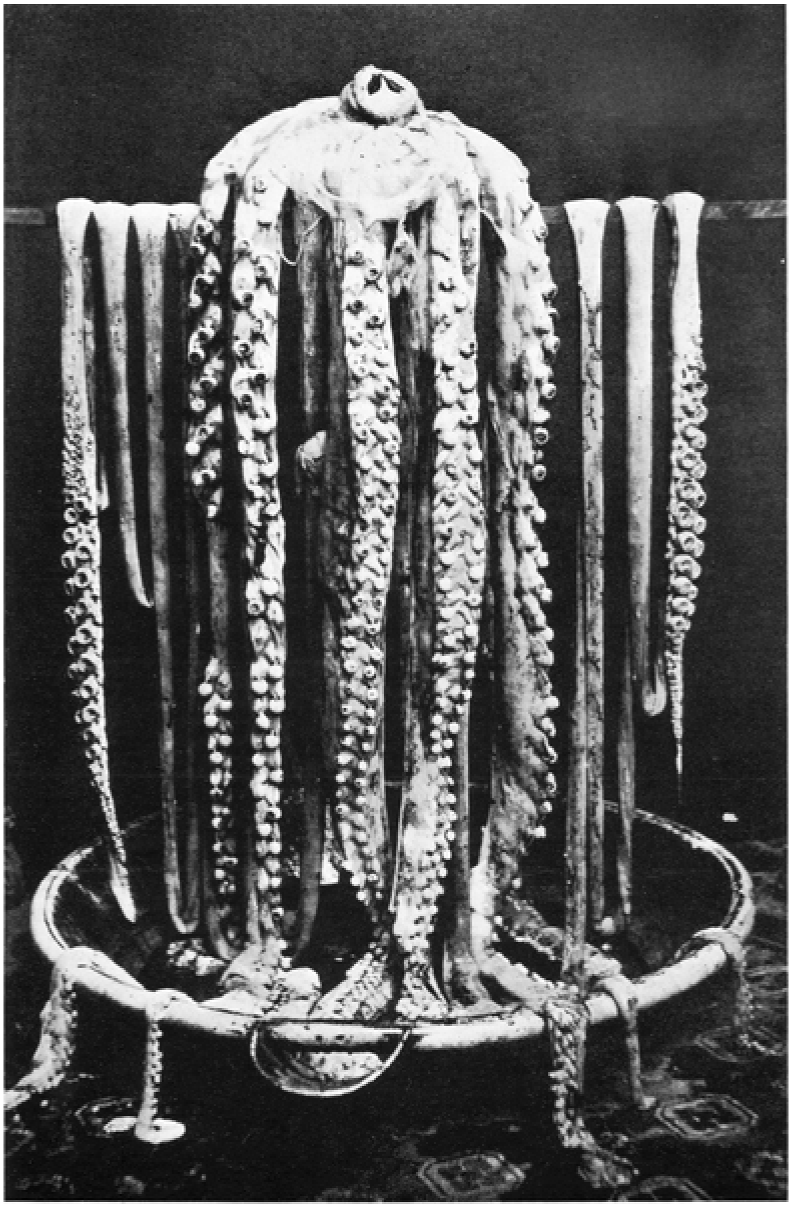
Gladius of *Sepioteuthis lessoniana*

Nautiluses are the only extant cephalopods with an external shell. However, all molluscan shells are formed from the ectoderm (outer layer of the embryo); in cuttlefish (*Sepia* spp.), for example, an invagination of the ectoderm forms during the embryonic period, resulting in a shell that is internal in the adult. The same is true of the chitinous gladius of squid and octopus. Cirrate octopuses have cartilaginous fin supports, which are sometimes referred to as a "shell vestige" or "gladius". The Incirrina have no vestige of an internal shell, and some squid also lack a gladius. Interestingly, the shelled coleoids do not form a clade or even a paraphyletic group. The *Spirula* shell begins as an organic structure, and is then very rapidly mineralized. Shells that are "lost" may be lost by resorption of the calcium carbonate component.

Females of the octopus genus *Argonauta* secrete a specialised paper-thin eggcase in which they reside, and this is popularly regarded as a "shell", although it is not attached to the body of the animal.

The largest group of shelled cephalopods, the ammonites, are extinct, but their shells are very common as fossils.

The deposition of carbonate, leading to a mineralized shell, appears to be related to the acidity of the organic shell matrix; shell-forming cephalopods have an acidic matrix, whereas the gladius of squid has a basic matrix.



Top: A giant squid found in Logy Bay, Newfoundland, in 1873. The two long feeding tentacles are visible on the extreme left and right.
Bottom: Detail of the tentacular club of *Abraliopsis morisi*

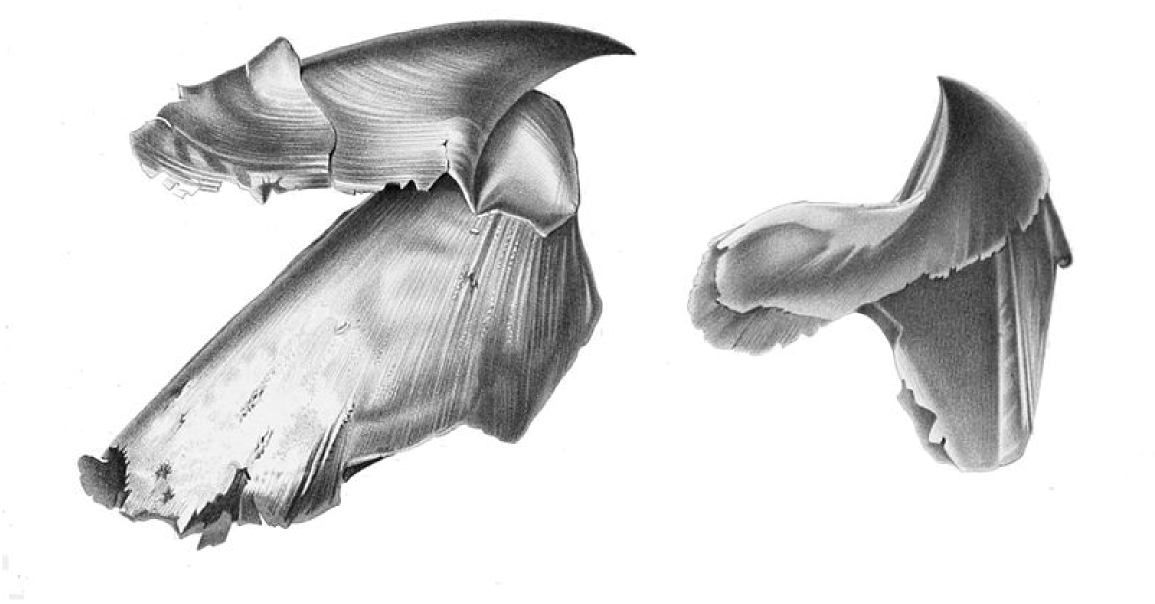
Head appendages

Cuttlefish and squid have five pairs of muscular appendages surrounding their mouths. The longer two, termed tentacles, are actively involved in capturing prey; they can lengthen rapidly (in as little as 15 milliseconds). In giant squid they may reach a length of 8 metres. They may terminate by broadening into a sucker-coated club. The shorter four pairs are termed arms, and are involved in holding and manipulating the captured organism. They too have suckers, on the side closest to the mouth; these help to hold onto the prey.

The tentacle consists of a thick central nerve cord (which must be thick to allow each sucker to be controlled independently) surrounded by circular and radial muscles. Because the volume of the tentacle remains constant, contracting the circular muscles decreases the radius and permits the rapid increase in length. Typically a 70% lengthening is achieved by decreasing the width by 23%.

The size of the tentacle is related to the size of the buccal cavity; larger, stronger tentacles can hold prey as small bites are taken from it; with more numerous, smaller tentacles, prey is swallowed whole, so the mouth cavity must be larger.

Feeding



The two-part beak of the giant squid, *Architeuthis* sp.

All living cephalopods have a two-part beak; most have a radula, although it is reduced in most octopus and absent altogether in *Spirula*. They feed by capturing prey with their tentacles, drawing it in to their mouth and taking bites from it. They have a mixture of toxic digestive juices, some of which are manufactured by symbiotic algae, which they eject from their salivary glands onto their captured prey held in their mouth. These juices separate the flesh of their prey from the bone or shell. The salivary gland has a small tooth at its end which can be poked into an organism to digest it from within.

The digestive gland itself is rather short. It has four elements, with food passing through the crop, stomach and caecum before entering the intestine. Most digestion, as well as the absorption of nutrients, occurs in the digestive gland, sometimes called the liver. Nutrients and waste materials are exchanged between the gut and the digestive gland through a pair of connections linking the gland to the junction of the stomach and caecum. Cells in the digestive gland directly release pigmented excretory chemicals into the lumen of the gut, which are then bound with mucus passed through the anus as long dark strings, ejected with the aid of exhaled water from the funnel.

Radula

Amphioctopus marginatus eating a crab

The cephalopod radula consists of multiple symmetrical rows of up to nine teeth – thirteen in fossil classes. The organ is reduced or even vestigial in certain octopus species and is absent in *Spirula*. The teeth may be homodont (i.e. similar in form across a row), heterodont (otherwise), or ctenodont (comb-like). Their height, width and number of cusps is variable between species. The pattern of teeth repeats, but each row may not be identical to the last; in the octopus, for instance, the sequence repeats every five rows.

Cephalopod radulae are known from fossil deposits dating back to the Ordovician. They are usually preserved within the cephalopod's body chamber, commonly in conjunction with the mandibles; but this need not always be the case; many radulae are preserved in a range of settings in the Mason Creek. Radulae are usually difficult to detect, even when they are preserved in fossils, as the rock must weather and crack in exactly the right fashion to expose them; for instance, radulae have only been found in nine of the 43 ammonite genera and they are rarer still in non-ammonoid forms: only three pre-Mesozoic species possess one.

Excretory system

Most cephalopods possess a single pair of large nephridia. Filtered nitrogenous waste is produced in the pericardial cavity of the branchial hearts, each of which is connected to a nephridium by a narrow canal. The canal delivers the excreta to a bladder-like renal sac, and also resorbs excess water from the filtrate. Several outgrowths of the lateral vena cava project into the renal sac, continuously inflating and deflating as the branchial hearts beat. This action helps to pump the secreted waste into the sacs, to be released into the mantle cavity through a pore.

Nautilus, unusually, possesses four nephridia, none of which are connected to the pericardial cavities.

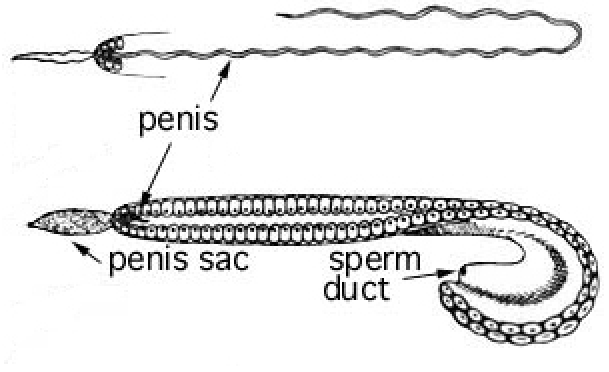
Ammonium

The handling of ammonia is thought to be important in shell formation in terrestrial molluscs, and in other nonmolluscan lineages.

Because protein (i.e. flesh) is a major constituent of the cephalopod diet, large amounts of ammonium are produced as waste. The main organs involved with the release of this excess ammonium are the gills.

The rate of this release is the lowest in the shelled cephalopods *Nautilus* and *Sepia*, probably as a result of their use of nitrogen to fill their shells with gas to produce buoyancy. Other cephalopods use ammonium in a similar way, storing the ions (as ammonium chloride) themselves to reduce their overall density and thus become more buoyant.

Reproduction and life cycle



Detail of the hectocotylus of *Ocythoe tuberculata*

Female *Argonauta argo* with eggcase and eggs

A dissected male specimen of *Onykia ingens*, showing a non-erect penis (the white tubular structure located below most of the other organs)

A specimen of the same species exhibiting elongation of the penis to 67 cm in length

With a few exceptions, Coleoidea live short lives with rapid growth. Most of the energy extracted from their food is used for growing. The penis in most male Coleoidea is a long and muscular end of the gonoduct used to transfer spermatophores to a modified arm called a hectocotylus. That, in turn, is used to transfer the spermatophores to the female. In species where the hectocotylus is missing, the penis is long and able to extend beyond the mantle cavity and transfers the spermatophores directly to the female. Deep water squid have the greatest known penis length relative to body size of all mobile animals, second in the entire animal kingdom only to certain sessile barnacles. Penis elongation in *Onykia ingens* may result in a penis that is as long as the mantle, head and arms combined.

Most cephalopods tend towards a semelparous reproduction strategy; they lay many small eggs in one batch and die afterwards. The Nautiloidea, on the other hand, stick to iteroparity; they produce a few large eggs in each batch and live for a long time.

External sexual characteristics are lacking in cephalopods, so cephalopods use colour communication. A courting male will approach a likely looking opposite number flashing his brightest colours, often in rippling displays. If the other cephalopod is female and receptive, her skin will change colour to become pale, and mating will occur. If the other cephalopod remains brightly coloured, it is taken as a warning.

The male has a sperm-carrying arm, known as the hectocotylous arm, with which to impregnate the female. In many cephalopods, mating occurs head to head and the male may simply transfer sperm to the female. Others may detach the sperm-carrying arm and leave it attached to the female. In the paper nautilus, this arm remains active and wriggling for some time, prompting the zoologists who discovered it to conclude it was some sort of worm-like parasite. It was duly given a genus name *Hectocotylus*, which held for some time until the mistake was discovered.

Nidamental glands are involved in the secretion of egg cases or the gelatinous substance comprising egg masses. The eggs may be brooded: female paper nautilus construct a shelter for the young, while Gonatiid squid carry a larva-laden membrane from the hooks on their arms. Other cephalopods deposit their young under rocks and aerate them with their tentacles hatching. Often, though, the eggs are left to their own devices; many squid lay sausage-like bunches of eggs in crevices or occasionally on the sea floor. Cuttlefish lay their eggs separately in cases and attach them to coral or algal fronds. Fossilised egg clutches show that ammonites also laid clutches of eggs.

Cephalopods are occasionally long-lived, especially in the deep water or polar forms, but most of the group live fast and die young, maturing rapidly to their adult size. Some may gain as much as 12% of their body mass each day. Most live for one to two years, reproducing and then dying shortly thereafter.

To free up resources for reproduction, many squid are known to resorb the muscle tissue of their mantle and tentacles, breaking down the tissue and using the energy contained therein to produce more gametes.

Egg cases laid by a female squid

Embryology

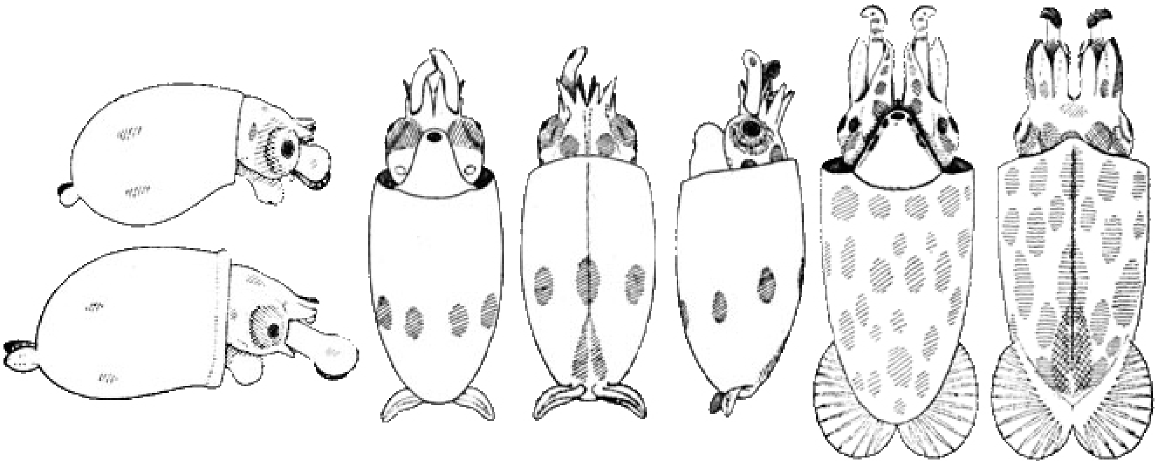
Unlike most other molluscs, cephalopods do not have a distinct larval stage. The fertilised ovum initially divides to produce a disc of germinal cells at one pole, with the yolk remaining at the opposite pole. The germinal disc grows to envelop and eventually absorb the yolk, forming the embryo. The tentacles and arms first appear at the hind part of the body, where the foot would be in other molluscs, and only later migrate towards the head.

The funnel of cephalopods develops on the top of their head, whereas the mouth develops on the opposite surface. The early embryological stages are reminiscent of ancestral gastropods and extant Monoplacophora.

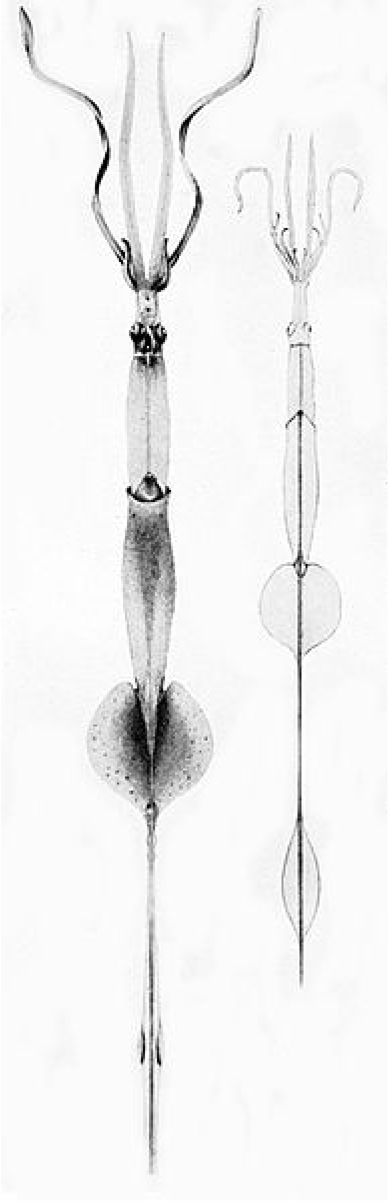
The shells develop from the ectoderm as an organic framework which is subsequently mineralised. In *Sepia*, which has an internal shell, the ectoderm forms an invagination whose pore is sealed off before this organic framework is deposited.

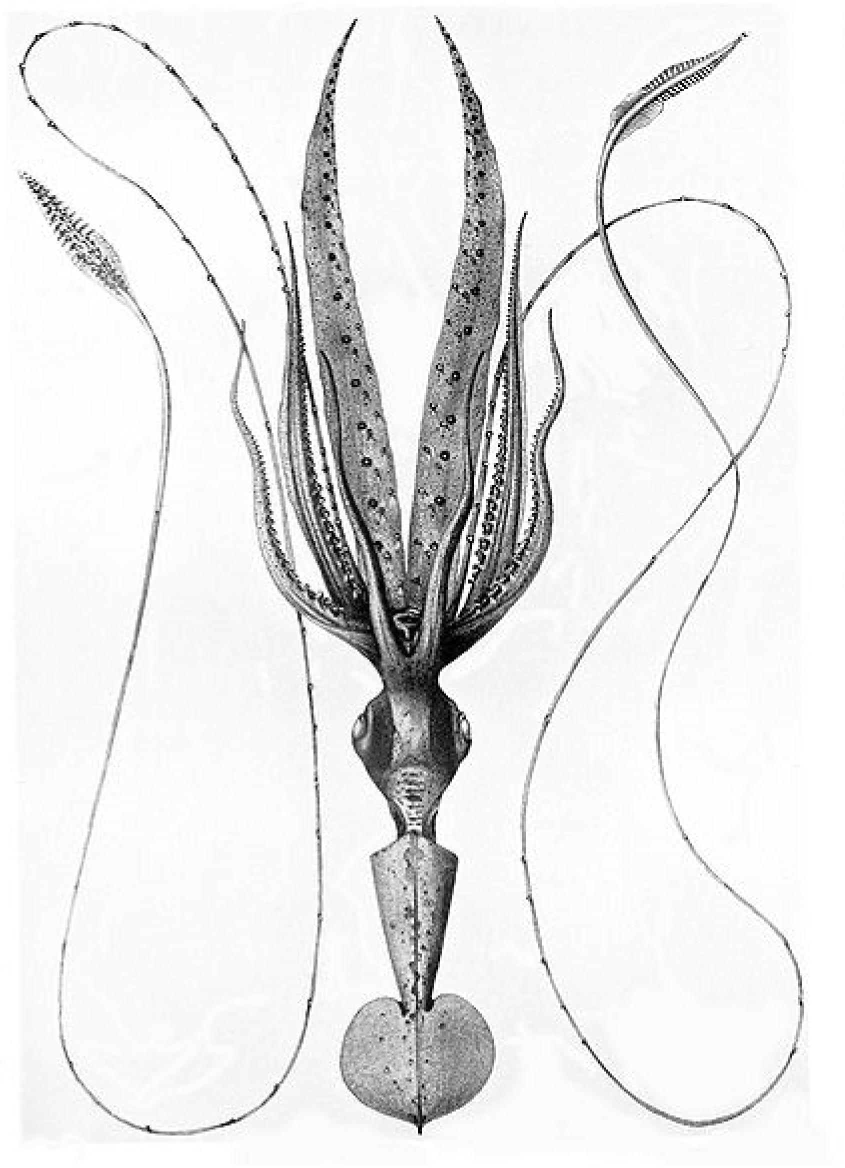
The gene *engrailed* is expressed first in the arms, funnel and optic vesicles, and is only later present in the tentacles and eyelids. It is expressed in embryonic stages 17–19 in all arm buds, and subsequently in the future-tentacles in stages 24–5, suggesting that it may serve a role in the differential development of tentacles. Sequential expression of Hox genes is also observed in cephalopod arms.

Development



Chtenopteryx sicula paralarvae. **Left:** Two very young paralarvae. The circular tentacular clubs bear approximately 20 irregularly arranged suckers. Two chromatophores are present on each side of the mantle. **Centre:** Ventral, dorsal and side views of a more advanced paralarva. An equatorial circulet of seven large yellow-brown chromatophores is present on the mantle. Posteriorly the expanded vanes of the gladius are visible in the dorsal view. **Right:** Ventral and dorsal views of a very advanced paralarva.





Top: Immature specimens of *Chiroteuthis veranyi*. In this paralarval form, known as the doratopsis stage, the pen is longer than the mantle and 'neck' combined

Bottom: A mature *Chiroteuthis veranyi*. This species has some of the longest tentacles in proportion to its size of any known cephalopod.

Cephalopod eggs span a large range of sizes, from 1 to 30 mm in diameter. The length of time before hatching is highly variable; smaller eggs in warmer waters are the fastest to hatch, and newborns can emerge after as little as a few days. Larger eggs in colder waters can develop for over a year before hatching.

The process from spawning to hatching follows a similar trajectory in all species, the main variable being the amount of yolk available to the young and when it is absorbed by the embryo.

Young do not pass through a larval stage, strictly speaking. They quickly learn how to hunt, using encounters with prey to refine their strategies.

Growth in juveniles is usually allometric, whilst adult growth is isometric.

Evolution

The traditional view of cephalopod evolution holds that they evolved in the Late Cambrian from a monoplacophoran-like ancestor with a curved, tapering shell, which was closely related to the gastropods (snails). The similarity of the early shelled cephalopod *Plectronoceras* to some gastropods was used in support of this view. The development of a siphuncle would have allowed the shells of these early forms to become gas-filled (thus buoyant) in order to support them and keep the shells upright while the animal crawled along the floor, and separated the true cephalopods from putative ancestors such as *Knightoconus*, which lacked a siphuncle. Neutral or positive buoyancy (i.e. the ability to float) would have come later, followed by swimming in the Plectronocerida and eventually jet propulsion in more derived cephalopods.

However, some morphological evidence is difficult to reconcile with this view, and the redescription of *Nectocaris pteryx*, which did not have a shell and appeared to possess jet propulsion in the manner of "derived" cephalopods, complicated the question of the order in which cephalopod features developed – provided *Nectocaris* is a cephalopod at all.

Early cephalopods were likely predators near the top of the food chain. They underwent pulses of diversification during the Ordovician period to become diverse and dominant in the Paleozoic and Mesozoic seas. In the Early Palaeozoic, their range was far more restricted than today; they were mainly constrained to sublittoral regions of shallow shelves of the low latitudes, and usually occur in association with thrombolites. A more pelagic habit was gradually adopted as the Ordovician progressed. Deep-water cephalopods, whilst rare, have been found in the Lower Ordovician - but only in high-latitude waters. The mid Ordovician saw the first cephalopods with septa strong enough to cope with the pressures associated with deeper water, and could inhabit depths greater than 100–200 m. The direction of shell coiling would prove to be crucial to the future success of the lineages; endogastric coiling would only permit large size to be attained with a straight shell, whereas exogastric coiling - initially rather rare - permitted the spirals familiar from the fossil record to develop, with their corresponding large size and diversity. (Endogastric mean the shell is curved so as the ventral or lower side is longitudinally concave (belly in); exogastric means the shell is curve so as the ventral side is longitudinally convex (belly out) allowing the funnel to be pointed backwards beneath the shell.)

An ammonitic ammonoid with the body chamber missing, showing the septal surface (especially at right) with its undulating lobes and saddles

The ancestors of coleoids (including most modern cephalopods) and the ancestors of the modern nautilus, had diverged by the Floian Age of the Early Ordovician Period, over 470 million years ago. The Bactritida, an Silurian–Triassic group of orthocones, are widely held to be paraphyletic to the coleoids and ammonoids – that is, the latter groups arose from within the Bactritida. An increase in the diversity of the coleoids and ammonoids is observed around the start of the Devonian period, and corresponds with a profound increase in fish diversity. This could represent the origin of the two derived groups.

Unlike most modern cephalopods, most ancient varieties had protective shells. These shells at first were conical but later developed into curved nautiloid shapes seen in modern nautilus species. Competitive pressure from fish is thought to have forced the shelled forms into deeper water, which provided an evolutionary pressure towards shell loss and gave rise to the modern coleoids, a change which led to greater metabolic costs associated with the loss of buoyancy, but which allowed them to recolonise shallow waters. However, some of the straight-shelled nautiloids evolved into belemnites, out of which some evolved into squid and cuttlefish. The loss of the shell may also have resulted from evolutionary pressure to increase manoeuvrability, resulting in a more fish-like habit.

Phylogeny

The internal phylogeny of the cephalopods is difficult to constrain; many molecular techniques have been adopted, but the results produced are conflicting. *Nautilus* tends to be considered an outgroup, with *Vampyroteuthis* forming an outgroup to other squid; however in one analysis the nautiloids, octopus and teuthids plot as a polytomy. Some molecular phylogenies do not recover the mineralized coleoids (*Spirula*, *Sepia*, and *Metasepia*) as a clade; however, others do recover this more parsimonious-seeming clade, with *Spirula* as a sister group to *Sepia* and *Metasepia* in a clade that had probably diverged before the end of the Triassic.

Molecular estimates for clade divergence vary. One 'statistically robust' estimate has *Nautilus* diverging from *Octopus* at 415 ± 24 million years ago.

Taxonomy

Chambered Nautilus (*Nautilus pompilius*)

Common Cuttlefish (*Sepia officinalis*)

Atlantic Bobtail (*Sepiola atlantica*)

Common Octopus (*Octopus vulgaris*)

European Squid (*Loligo vulgaris*)

The classification presented here, for recent cephalopods, follows largely from Current Classification of Recent Cephalopoda (May 2001), for fossil cephalopods takes from Arkell et al. 1957, Teichert and Moore 1964, Teichert 1988, and others. The three subclasses are traditional, corresponding to the three orders of cephalopods recognized by Bather.

Class Cephalopoda († indicates extinct groups)

- Subclass Nautiloidea: Fundamental ectocochliate cephalopods that provided the source for the Ammonoidea and Coleoidea.
    - Order † Plectronocerida: the ancestral cephalopods from the Cambrian Period
    - Order † Ellesmerocerida (500 to 470 Ma)
    - Order † Endocerida (485 to 430 Ma)
    - Order † Actinocerida (480 to 312 Ma)
    - Order † Discosorida (482 to 392 Ma)
    - Order † Pseudorthocerida (432 to 272 Ma)
    - Order † Tarphycerida (485 to 386 Ma)
    - Order † Oncocerida (478.5 to 324 Ma)

  - Order Nautilida (extant; 410.5 to 0 Ma)
  - Order † Orthocerida (482.5 to 211.5 Ma)
  - Order † Ascocerida (478 to 412 Ma)
  - Order † Bactritida (418.1 to 260.5 Ma)
- Subclass † Ammonoidea: Ammonites (479 to 65 Ma)
  - Order † Goniatitida (388.5 to 252 Ma)
  - Order † Ceratitida (254 to 200 Ma)
  - Order † Ammonitida (215 to 66 Ma)
- Subclass Coleoidea (410.0 Ma-Rec)
  - Cohort † Belemnoidea: Belemnites and kin
    - Genus † *Jeletzkya*
    - Order † Aulacocerida (265 to 183 Ma)
    - Order † Phragmoteuthida (189.6 to 183 Ma)
    - Order † Hematitida (339.4 to 318.1 Ma)
    - Order † Belemnitida (339.4 to 65.5 Ma)
    - Genus † *Belemnoteuthis* (189.6 to 183 Ma)
  - Cohort Neocoleoidea
    - Superorder Decapodiformes (also known as Decabrachia or Decembranchiata)
      - ?Order † Boletzkyida
      - Order Spirulida: Ram's Horn Squid
      - Order Sepiida: cuttlefish
      - Order Sepiolida: pygmy, bobtail and bottletail squid
      - Order Teuthida: squid
    - Superorder Octopodiformes (also known as Vampyropoda)
      - Family † Trachyteuthididae
      - Order Vampyromorphida: Vampire Squid
      - Order Octopoda: octopus

Other classifications differ, primarily in how the various decapod orders are related, and whether they should be orders or families.

Suprafamilial classification of the Treatise

This is the older classification that combines those found in parts K and L of the Treatise on Invertebrate Paleontology, which forms the basis for and is retained in large part by classifications that have come later.

Nautiloids in general, (Teichert and Moore 1964) Sequence as given.

> Subclass † Endoceratoidea. Not used by Flower, e.g. Flower and Kummel 1950, interjocerids included in the Endocerida.
> Order † Endocerida
> Order † Intejocerida
> Subclass † Actinoceratoidea Not used by Flower, ibid
> Order † Actinocerida

Subclass † Nautiloidea Nautiloidea in the restricted sense.
Order † Ellesmerocerida Plectronocerida subsequently split off as separate order.
Order † Orthocerida Includes orthocerids and pseudorthocerids
Order † Ascocerida
Order † Oncocerida
Order † Discosorida
Order † Tarphycerida
Order † Barrandeocerida A polyphyletic group now included in the Tarphycerida
Order Nautilida
Subclass † Bactritoidea
Order † Bactritida

Paleozoic Ammonoidea (Miller, Furnish, and Schindewolf, 1957)

Suborder † Anarcestina
Suborder † Clymeniina
Suborder † Goniatitina
Suborder † Prolecanitina

Mesozoic Ammonoidea (Arkel et al., 1957)

Suborder † Ceratitina
Suborder † Phylloceratina
Suborder † Lytoceratina
Suborder † Ammonitina

Subsequent revisions include the establishment of three Upper Cambrian orders, the Plectronocerida, Protactinocerida and Yanhecerida; separation of the pseudorthocerids as the Pseudorthocerida, and elevating orthoceritoids as the Subclass Orthoceratoidea.

Shevyrev classification

Shevyrev (2005) suggested a division into eight subclasses, mostly comprising the more diverse and numerous fossil forms, although this classification has been criticized as arbitrary.

Various species of ammonites

A fossilised belemnite

Holotype of *Ostenoteuthis siroi* from family Ostenoteuthidae

Class Cephalopoda

- Subclass † Ellesmeroceratoidea
    - Order † Plectronocerida (501 to 490 Ma)
    - Order † Protactinocerida
    - Order † Yanhecerida
    - Order † Ellesmerocerida (500 to 470 Ma)
- Subclass † Endoceratoidea (485 to 430 Ma)
    - Order † Endocerida (485 to 430 Ma)
    - Order † Intejocerida (485 to 480 Ma)
- Subclass † Actinoceratoidea
    - Order † Actinocerida (480 to 312 Ma)
- Subclass Nautiloidea (490.0 Ma- Rec)
    - Order † Bassleroceida (490 to 480 Ma)
    - Order † Tarphycerida (485 to 386 Ma)
    - Order † Lituitida (485 to 480 Ma)
    - Order † Discosorida (482 to 392 Ma)
    - Order † Oncocerida (478.5 to 324 Ma)
    - Order Nautilida (410.5 Ma-Rec)
- Subclass † Orthoceratoidea (482.5 to 211.5 Ma)
    - Order † Orthocerida (482.5 to 211.5 Ma)
    - Order † Ascocerida (478 to 412 Ma)
    - Order † Dissidocerida (479 to 457.5 Ma)
    - Order † Bajkalocerida

- Subclass † Bactritoidea (422 to 252 Ma)
- Subclass † Ammonoidea (410 to 66 Ma)
- Subclass Coleoidea (410.0 Ma-rec)

Cladistic classification

Pyritized fossil of *Vampyronassa rhodanica*, a vampyromorphid from the Lower Callovian (164.7 million years ago)

Another recent system divides all cephalopods into two clades. One includes nautilus and most fossil nautiloids. The other clade (Neocephalopoda or Angusteradulata) is closer to modern coleoids, and includes belemnoids, ammonoids, and many orthocerid families. There are also stem group cephalopods of the traditional Ellesmerocerida that belong to neither clade.

Monophyly of coeloids

The coeloids have been thought to possibly represent a polyphyletic group, although this has not been supported by the rising body of molecular data.

Post-mortem decay

After death, if undisturbed, cephalopods decay relatively quickly. Their muscle softens within a couple of days, and may swell; egg sacs can swell so much that they rip through the mantle. Subsequently, the organs shrink again; at this point the organism may start to break up into fragments. The eyes retain their size while the head shrinks around them. The gills may remain swollen at this point. After around a week, the carcass collapses in on itself and begins to disintegrate. The ink sac solidifies around this point. After a fortnight little is left but a blob with eyes, arms and ink sac visible. After a couple of months, these are only recognisable as flattened dark stains - although in some cases the eye lenses can remain intact for up to a year.

Chapter- 4

Chiton

Chiton Temporal range: Devonian–Recent	
 Lined chiton, *Tonicella lineata*. The anterior end of the animal is to the right	
Scientific classification	
Kingdom:	Animalia
Phylum:	Mollusca
Class:	**Polyplacophora** Blainville, 1816
Subclasses	
Neoloricata †Paleoloricata	

Chitons are small to large, primitive marine molluscs in the class **Polyplacophora**. There are 900 to 1,000 extant species of chitons in the class, which was formerly known as **Amphineura**.

These molluscs are also sometimes commonly known as **sea cradles** or "coat-of-mail shells". They are also sometimes referred to more formally as **loricates**, **polyplacophorans**, and rarely as **polyplacophores**.

Chitons have a dorsal shell which is composed of eight separate shell plates or valves. These plates overlap somewhat at the front and back edges, and yet the plates articulate well with one another. Because of this, although the plates provide good protection for impacts from above, they nonetheless permit the chiton to flex upward when needed for locomotion over uneven surfaces, and also the animal can slowly curl up into a ball when it is dislodged from the underlying surface. The shell plates are surrounded by a structure known as a girdle.

Habitat

Two individuals of *Acanthopleura granulata* on a rock at high tide level in Guadeloupe

Chitons live worldwide, in cold water and in the tropics. Most of them inhabit intertidal or subtidal zones and do not extend beyond the photic zone.

They live on hard surfaces, such as on or under rocks, or in rock crevices. Some species live quite high in the intertidal zone and are exposed to the air and light for long periods. Others live subtidally. A few species live in deep water, as deep as 6,000 metres (20,000 ft).

Chitons are exclusively and fully marine. This is in contrast to the bivalves which were able to adapt to brackish water and freshwater, and the gastropods which were able to make successful transitions to freshwater and terrestrial environments.

Morphology

Shell

All chitons bear a row of aragonitic shells, although in some species they are reduced or covered by the girdle tissue. The calcareous valves that chitons carry dorsally are protective, made wholly of aragonite, and variously colored, patterned, smooth or sculptured. The shell is divided into eight articulating calcareous (aragonite) valves embedded in the tough muscular girdle that surrounds the chiton's body. This arrangement allows chitons to roll into a protective ball when dislodged and to cling tightly to irregular surfaces.

Loose valves or plates of *Chiton tuberculatus* from the beachdrift on Nevis, West Indies. Head plates at the top, tail plates at the bottom

The most anterior plate is crescent shaped, and is known as the cephalic plate (sometimes called a "head plate", despite the absence of a complete head). The most posterior plate is known as the anal plate (sometimes called the "tail plate", although chitons do not have a tail.)

The front seven plates develop simultaneously, with the rear plate being added later in the developmental process. Growth lines are formed each winter. The inner layer of each of the six intermediate plates is produced anteriorly as an articulating flange. This is called the *articulamentum*. This inner layer may also be produced laterally in the form of notched *insertion plates*. These function as an attachment of the valve plates to the soft body. A similar series of insertion plates may be attached to the convex anterior border of the cephalic plate or the convex posterior border of the anal plate.

The sculpture of the valves is one of the taxonomic characteristics, along with the granulation or spinulation of the girdle

After a chiton dies, the individual valves which make up the 8-part shell come apart because the girdle is no longer holding them together, and then the plates sometimes wash up in beach drift. The individual shell plates from a chiton are sometimes known as "butterfly shells" because of their shape.

Girdle ornament

The girdle may be ornamented with scales or spicules which, like the shell plates, are mineralized with aragonite – although a different mineralization process operates in the spicules to in the teeth or shells (implying an independent evolutionary innovation). This process seems quite simple in comparison to other shelly tissue; the crystal structure of the deposited minerals closely resembles the disordered nature of crystals that form inorganically.

The protein component of the scales and sclerites is minuscule in comparison with other biomineralized structures, whereas the total proportion of matrix is *higher* than in mollusc shells. This implies that polysaccharides make up the bulk of the matrix. The girdle spines often bear length-parallel striations.

The wide form of girdle ornament suggests that it serves a secondary role; chitons can survive perfectly well without them. Camouflage or defence are two likely functions.

Internal anatomy

The girdle is often ornamented with spicules, bristles, hairy tufts, spikes, or snake-like scales. The majority of the body is a snail-like foot, but no head or other soft-parts beyond the girdle are visible from the dorsal side. The mantle cavity consists of a narrow channel on each side, lying between the body and the girdle. Water enters the cavity through openings either side of the mouth, then flows along the channel to a second, exhalant, opening close to the anus. Multiple gills hang down into the mantle cavity along part or all of the lateral pallial groove, each consisting of a central axis with a number of flattened filaments through which oxygen can be absorbed.

The heart has three chambers and is located towards the animal's hind end. Each of the two auricles collects blood from the gills on one side, while the muscular ventricle pumps blood through the aorta and round the body.

The excretory system consists of two nephridia, which connect to the pericardial cavity around the heart, and remove excreta through a pore that opens near the rear of the mantle cavity. The single gonad is located in front of the heart, and releases gametes through a pair of pores just in front of those used for excretion.

The underside of the gumboot chiton, *Cryptochiton stelleri*, showing the foot in the center, surrounded by the gills and mantle. The mouth is visible to the left in this image.

The mouth is located on the underside of the animal, and contains a tongue-like structure called a radula, which has numerous rows of 17 teeth each. The teeth are coated with magnetite, a hard ferric/ferrous oxide mineral. The radula is used to scrape microscopic algae off the substratum. The mouth cavity itself is lined with chitin and is associated with a pair of salivary glands. Two sacs open from the back of the mouth, one containing the radula, and the other containing a protrusible sensory **subradula** organ that is pressed against the substratum to taste for food.

Cilia pull the food through the mouth in a stream of mucus and through the oesophagus, where it is partially digested by enzymes from a pair of large pharyngeal glands. The oesophagus in turn opens into a stomach with where enzymes from a digestive gland complete the break down of the food. Nutrients are absorbed through the linings of the stomach and the first part of the intestine. The intestine is divided in two by a sphincter, with the latter part being highly coiled and functioning to compact the waste matter into faecal pellets. The anus opens just behind the foot.

Chitons lack a clearly demarcated head; their nervous system resembles a dispersed ladder. There are no true ganglia as there are in other molluscs, although there is a ring of dense neural tissue around the oesophagus. From this ring, nerves branch forwards to innervate the mouth and subradula, while two pairs of main nerve cords run back through the body. One pair, the pedal cords, innervate the foot, while the pallio-visceral cords innervate the mantle and remaining internal organs.

Some species bear an array of tentacles in front of the head.

Senses

The primary sense organs of chitons are the subradula organ and a large number of unique organs called aesthetes. The aesthetes consist of light sensitive cells just below the surface of the shell, although they are not capable of true vision. In some cases, however, they are modified to form ocelli, with a cluster of individual photoreceptor cells lying beneath a small lens. An individual chiton may have thousands of such ocelli

There is a relatively good fossil record of chiton shells, but ocelli are only present in those dating to 10 million years ago or younger; this would make the ocelli, whose precise function is unclear, the most recent eyes to evolve.

Although chitons lack osphradia, statocysts, and other sensory organs common to other molluscs, they do have numerous tactile nerve endings, especially on the girdle and within the mantle cavity.

However, chitons lack a cerebral ganglion.

Homing Ability

Several species of Chiton are known to exhibit homing behaviours, journeying to feed and then returning to the exact unique spot they previously inhabited. The specific method of how chitons can perform such behaviors has been investigated to some extent, however the reason remains unknown. Suggestions include the chitons remembering the topographic profile of the region, thus being able to guide themselves back to their home scar via a physical knowledge of the rocks and a visual input by their primitive eyes, The gastropod Nerita textilis is known to deposit mucus as it moves, which a chemoreceptive organ is able to detect and guide the snail back to its home site, It is unclear if chitons function in this manner. However, it is theorized that they may leave chemical cues along the rock surface and at the home scar which olfactory senses can detect and home in on. Furthermore, old trails may be detected, providing further stimulus for the Chiton to find its home, Also, chitons have teeth made of magnetite on their radula making them unique among animals. This means they have an exceptionally abrasive tongue with which to scrape food from rocks. These crystals are thought to be involved in magnetoreception, the ability to sense the polarity or the inclination of the Earth's magnetic field, and to be involved in navigation.

Culinary uses

Chitons are eaten in Tobago and were eaten by native Americans of the Pacific coasts of both North and South America. The *foot* of the chiton is prepared in a manner similar to abalone.

Life habits

Cryptoconchus porosus, a butterfly chiton, which has its valves completely covered by the mantle

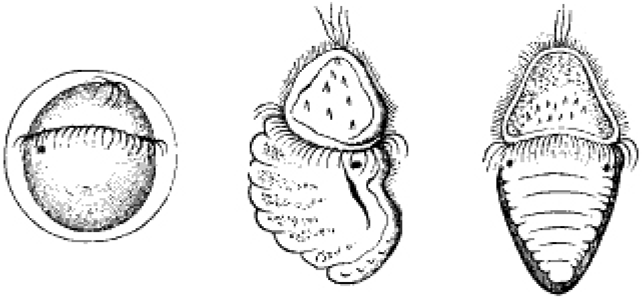
A chiton creeps along slowly on a muscular foot. They have considerable power of adhesion and can cling to rocks very powerfully, like a limpet.

Chitons are herbivorous grazers. They eat algae, bryozoans, diatoms and sometimes bacteria by scraping the rocky substrate with their well-developed radula.

A few species of chitons are predatory, such as the small western Pacific species *Placiphorella velata*. These predatory chitons have an enlarged anterior girdle. They catch other small invertebrates, such as shrimp and possibly even small fish, by holding the enlarged, hood-like front end of the girdle up off the surface, and then clamping down on unsuspecting, shelter-seeking prey.

Some chitons exhibit homing behavior, returning to the same spot for the daylight hours and roaming around at night to feed.

Reproduction and life cycle



Larvae of chitons: First image is the trochophore, second is in metamorphosis, third is an immature adult.

Chitons have separate sexes, and fertilisation is external. The male releases sperm into the water, while the female releases eggs either individually, or in a long string. In most cases, fertilisation takes placed either in the surrounding water, or in the mantle cavity of the female. Some species brood the eggs within the mantle cavity, and the species *Callistochiton viviparus* even retains them within the ovary and gives birth to live young, an example of ovoviviparity.

The eggs have a tough spiny coat, and usually hatch to release a free-swimming trochophore larva, typical of many other mollusc groups. In a few cases, the trochophore remains within the egg (and is then called *lecithotrophic* – deriving nutrition from yolk), which hatches to produce a miniature adult. Unlike most other molluscs, there is no intermediate stage, or veliger, between the trochophore and the adult. Instead, a segmented shell gland forms on one side of the larva, and a foot forms on the opposite side. When the larva is ready to become an adult, the body elongates, and the shell gland secretes the plates of the shell. Unlike the fully grown adult, the larva has a pair of simple eyes, although these may remain for some time in the immature adult.

Predators

Animals which prey on chitons include humans, seagulls, seastars, crabs, lobster and fish.

The largest species

The largest chiton (up to 33 cm in length) is the brick-red gumboot chiton of the Pacific Northwest. In this species the valves are completely internal.

Evolutionary origins

Chitons have a relatively good fossil record, stretching back 400 million years to the Devonian. Before this, some organisms have been interpreted (tentatively) as stem-group polyplacophora; the record of polyplacophora stretches back to the Ordovician.

Separate plates from *Matthevia*, a Late Cambrian polyplacophoran from the Hellnmaria Member of the Notch Peak Limestone, Steamboat Pass, southern House Range, Utah. The US one cent coin is 19 mm in diameter

Kimberella and *Wiwaxia* of the Precambrian and Cambrian may be related to ancestral polyplacophora. *Matthevia* is a Late Cambrian polyplacophoran preserved as individual pointed valves, and sometimes considered to be a chiton, although it can at best be a stem-group member of the group. Based on this and co-occurring fossils, one plausible hypothesis for the origin of polyplacophora has that they formed when an aberrant monoplacophoran was born with multiple centres of calcification, rather than the usual one. Selection quickly acted on the resultant conical shells to form them to overlap into protective armour; their original cones are homologous to the tips of the plates of modern chitons.

The chitons evolved from multiplacophora during the palaeozoic, with their relatively conserved modern-day body plan being fixed by the mesozoic.

History of the scientific investigation of chitons

Chitons were first studied by Carolus Linnaeus in 1758. Since his description of the first four species, chitons have been variously classified. They were called **Cyclobranchians** ("round arm") in the early 19th century, and then grouped with the aplacophorans in the subphylum **Amphineura** in 1876. The class **Polyplacophora** was named by J. E. Gray in 1821.

Etymology

The English name "chiton" originates from the Latin word chitōn, which means "mollusc", and in turn is derived from the Greek word "khitōn", meaning tunic (which also is the source of the word chitin). The Greek word "khitōn" can be traced to the Central Semitic word "*kittan", which is from the Akkadian words "kitû" or "kita'um", meaning flax or linen, and originally the Sumerian word "gada" or "gida".

The Greek-derived name Polyplacophora comes from the words poly- (many), plako- (tablet), and -phoros (bearing), a reference to the chiton's eight shell plates.

Taxonomy

Most classification schemes in use today are based, at least in part, on Pilsbry's Manual of Conchology (1892–1894), extended and revised by Kaas and Van Belle (1985–1990).

Since chitons were first described by Linnaeus (1758) there have been extensive taxonomic studies at the species level. However, the taxonomic classification at higher levels in the group has remained somewhat unsettled.

The most recent classification (Sirenko 2006) is based not only on shell morphology, as usual, but also other important features including aesthetes, girdle, radula, gills, glands, egg hull projections and spermatozoids. It includes all the living and extinct genera of chitons.

This system is now generally accepted.

Class Polyplacophora Gray, 1821

- Subclass Paleoloricata Bergenhayn, 1955
    - Order Chelodida Bergenhayn, 1943
            - Family Chelodidae Bergenhayn, 1943
                - *Chelodes* Davidson et King, 1874
                - *Euchelodes* Marek, 1962
                - *Calceochiton* Flower, 1968
    - Order Septemchitonida Bergenhayn, 1955
    - Family Gotlandochitonidae Bergenhayn, 1955
        - *Gotlandochiton* Bergenhayn, 1955
    - Family Helminthochitonidae Van Belle, 1975
        - *Kindbladochiton* Van Belle, 1975
        - *Diadelochiton* Hoare, 2000
        - *Helminthochiton* Salter in Griffith et M'Coy, 1846
        - *Echinochiton* Pojeta, Eernisse, Hoare et Henderson, 2003
    - Family Septemchitonidae Bergenhayn, 1955
        - *Septemchiton* Bergenhayn, 1955
        - *Paleochiton* A. G. Smith, 1964
        - *Thairoplax* Cherns, 1998

Subclass Loricata Shumacher, 1817

- Order Lepidopleurida Thiele, 1910
    - Suborder Cymatochitonina Sirenko et Starobogatov, 1977
        - Family Acutichitonidae Hoare, Mapes et Atwater, 1983
            - *Acutichiton* Hoare, Sturgeon et Hoare, 1972
            - *Elachychiton* Hoare, Sturgeon et Hoare, 1972
            - *Harpidochiton* Hoare et Cook, 2000
            - *Arcochiton* Hoare, Sturgeon et Hoare, 1972
            - *Kraterochiton* Hoare, 2000
            - *Soleachiton* Hoare, Sturgeon et Hoare, 1972
            - *Asketochiton* Hoare et Sabattini, 2000

- Family Cymatochitonidae Sirenko et Starobogatov, 1977

    - *Cymatochiton* Dall, 1882
    - *Compsochiton* Hoare et Cook, 2000

- Family Gryphochitonidae Pilsbry, 1900

    - *Gryphochiton* Gray, 1847

- Family Lekiskochitonidae Smith et Hoare, 1987

    - *Lekiskochiton* Hoare et Smith, 1984

- Family Permochitonidae Sirenko et Starobogatov, 1977

    - *Permochiton* Iredale et Hull, 1926

Suborder Lepidopleurina Thiele, 1910

    - Family Ferreiraellidae Dell' Angelo et Palazzi, 1991
        - *Glaphurochiton* Raymond, 1910
        - *?Pyknochiton* Hoare, 2000
        - *?Hadrochiton* Hoare, 2000
        - *Ferreiraella* Sirenko, 1988

- Family Glyptochitonidae Starobogatov et Sirenko, 1975

    - *Glyptochiton* Konninck, 1883

- Family Leptochitonidae Dall, 1889

    - *Colapterochiton* Hoare et Mapes, 1985
    - *Coryssochiton* DeBrock, Hoare et Mapes, 1984
    - *Proleptochiton* Sirenko et Starobogatov, 1977
    - *Schematochiton* Hoare, 2002
    - *Pterochiton* (Carpenter MS) Dall, 1882
    - *Leptochiton* Gray, 1847
    - *Parachiton* Thiele, 1909
    - *Terenochiton* Iredale, 1914
    - *Trachypleura* Jaeckel, 1900
    - *Pseudoischnochiton* Ashby, 1930
    - *Lepidopleurus* Risso, 1826
    - *Hanleyella* Sirenko, 1973

- Family Camptochitonidae Sirenko, 1997

    - *Camptochiton* DeBrock, Hoare et Mapes, 1984
    - *Pedanochiton* DeBrock, Hoare et Mapes, 1984
    - *Euleptochiton* Hoare et Mapes, 1985
    - *Pileochiton* DeBrock, Hoare et Mapes, 1984
    - *Chauliochiton* Hoare et Smith, 1984
    - *Stegochiton* Hoare et Smith, 1984

- Family Nierstraszellidae Sirenko, 1992

    - *Nierstraszella* Sirenko, 1992

- Family Mesochitonidae Dell’ Angelo et Palazzi, 1989

    - *Mesochiton* Van Belle, 1975
    - *Pterygochiton* Rochebrune, 1883

- Family Protochitonidae Ashby, 1925

    - *Protochiton* Ashby, 1925
    - *Deshayesiella* (Carpenter MS) Dall, 1879
    - *Oldroydia* Dall, 1894

        - Family Hanleyidae Bergenhayn, 1955
            - *Hanleya* Gray, 1857
            - *Hemiarthrum* Dall, 1876

- Order Chitonida Thiele, 1910

    - Suborder Chitonina Thiele, 1910
    - Superfamily Chitonoidea Rafinesque, 1815
        - Family Ochmazochitonidae Hoare et Smith, 1984
            - *Ochmazochiton* Hoare et Smith, 1984
        - Family Ischnochitonidae Dall, 1889
            - *Ischnochiton* Gray, 1847
            - *Stenochiton* H. Adams et Angas, 1864
            - *Stenoplax* (Carpenter MS) Dall, 1879
            - *Lepidozona* Pilsbry, 1892
            - *Stenosemus* Middendorff, 1847
            - *Subterenochiton* Iredale et Hull, 1924
            - *Thermochiton* Saito et Okutani, 1990
            - *Connexochiton* Kaas, 1979
            - *Tonicina* Thiele, 1906

- Family Callistoplacidae Pilsbry, 1893

    - *Ischnoplax* Dall, 1879
    - *Callistochiton* Carpenter MS, Dall, 1879
    - *Callistoplax* Dall, 1882
    - *Ceratozona* Dall, 1882
    - *Calloplax* Thiele, 1909

- Family Chaetopleuridae Plate, 1899

    - *Chaetopleura* Shuttleworth, 1853
    - *Dinoplax* Carpenter MS, Dall, 1882

- Family Loricidae Iredale et Hull, 1923

  - *Lorica* H. et A. Adams, 1852
  - *Loricella* Pilsbry, 1893
  - *Oochiton* Ashby, 1929

- Family Callochitonidae Plate, 1901

  - *Callochiton* Gray, 1847
  - *Eudoxochiton* Shuttleworth, 1853
  - *Vermichiton* Kaas, 1979

- Family Chitonidae Rafinesque, 1815

  - Subfamily Chitoninae Rafinesque, 1815
  - *Chiton* Linnaeus, 1758
  - *Amaurochiton* Thiele, 1893
  - *Radsia* Gray, 1847
  - *Sypharochiton* Thiele, 1893
  - *Nodiplax* Beu, 1967
  - *Rhyssoplax* Thiele, 1893
  - *Teguloaplax* Iredale & Hull, 1926
  - *Mucrosquama* Iredale, 1893
  - Subfamily Toniciinae Pilsbry, 1893
  - *Tonicia* Gray, 1847
  - *Onithochiton* Gray, 1847
  - Subfamily Acanthopleurinae Dall, 1889
  - *Acanthopleura* Guilding, 1829
  - *Liolophura* Pilsbry, 1893
  - *Enoplochiton* Gray, 1847
  - *Squamopleura* Nierstrasz, 1905

  - - Superfamily Schizochitonoidea Dall, 1889
  - Family Schizochitonidae Dall, 1889
    - *Incissiochiton* Van Belle, 1985
    - *Schizochiton* Gray, 1847

- Suborder Acanthochitonina Bergenhayn, 1930

  - Family Mopalioidea Dall, 1889

- Family Tonicellidae Simroth, 1894
- Subfamily Tonicellinae Simroth, 1894

  - *Lepidochitona* Gray, 1821
  - *Particulazona* Kaas, 1993
  - *Boreochiton* Sars, 1878
  - *Tonicella* Carpenter, 1873

  - *Nuttallina* (Carpenter MS) Dall, 1871
  - *Spongioradsia* Pilsbry, 1894
  - *Oligochiton* Berry, 1922

- Subfamily Juvenichitoninae Sirenko, 1975

  - *Juvenichiton* Sirenko, 1975
  - *Micichiton* Sirenko, 1975
  - *Nanichiton* Sirenko, 1975

- Family Schizoplacidae Bergenhayn, 1955

  - *Schizoplax* Dall, 1878

- Family Mopaliidae Dall, 1889
- Subfamily Heterochitoninae Van Belle, 1978

  - *Heterochiton* Fucini, 1912
  - *Allochiton* Fucini, 1912

- Subfamily Mopaliinae Dall, 1889

  - *Aerilamma* Hull, 1924
  - *Guildingia* Pilsbry, 1893
  - *Frembleya* H. Adams, 1866
  - *Diaphoroplax* Iredale, 1914
  - *Plaxiphora* Gray, 1847
  - *Placiphorina* Kaas & Van Belle, 1994
  - *Nuttallochiton* Plate, 1899
  - *Mopalia* Gray, 1847
  - *Maorichiton* Iredale, 1914
  - *Placiphorella* (Carpenter MS) Dall, 1879
  - *Katharina* Gray, 1847
  - *Amicula* Gray, 1847

        - Superfamily Cryptoplacoidea H. et A. Adams, 1858
        - Family Acanthochitonidae Pilsbry, 1893
        - Subfamily Acanthochitoninae Pilsbry, 1893
          - *Acanthochitona* Gray, 1921
          - *Craspedochiton* Shuttleworth, 1853
          - *Spongiochiton* (Carpenter MS) Dall, 1882
          - *Notoplax* H. Adams, 1861
          - *Pseudotonicia* Ashby, 1928
          - *Bassethullia* Pilsbry, 1928
          - *Americhiton* Watters, 1990
          - *Choneplax* (Carpenter MS) Dall, 1882

        - *Cryptoconchus* (de Blainville MS) Burrow, 1815
    - Subfamily Cryptochitoninae Pilsbry, 1893
        - *Cryptochiton* Middendorff, 1847
    - Family Hemiarthridae Sirenko, 1997
        - *Hemiarthrum* Carpenter in Dall, 1876
        - *Weedingia* Kaas, 1988
    - Family Choriplacidae Ashby, 1928
        - *Choriplax* Pilsbry, 1894
    - Family Cryptoplacidae H. et A. Adams, 1858
        - *Cryptoplax* de Blainville, 1818

- *Incertae sedis*

    - Family Scanochitonidae Bergenhayn, 1955
        - *Scanochiton* Bergenhayn, 1955
    - Family Olingechitonidae Starobogatov et Sirenko, 1977
        - *Olingechiton* Bergenhayn, 1943
    - Family Haeggochitonidae Sirenko et Starobogatov, 1977
        - *Haeggochiton* Bergenhayn, 1955
    - Family Ivoechitonidae Sirenko et Starobogatov, 1977
        - *Ivoechiton* Bergenhayn, 1955

Chapter- 5

Gastropoda

Gastropod
Temporal range: Late Cambrian–Recent

Air-breathing land gastropod *Helix pomatia*, the Roman snail

Scientific classification

Kingdom:	Animalia
Phylum:	Mollusca
Class:	**Gastropoda** Cuvier, 1795

Clades

"*Paleozoic uncertain* ..."
"*Basal taxa* ..."
clade Patellogastropoda
clade Vetigastropoda
clade Cocculiniformia
clade Neritimorpha
clade Caenogastropoda
clade Heterobranchia

The **Gastropoda** or **gastropods** are a large taxonomic class within the molluscs, a group of animals that are more commonly known as **snails and slugs**. The class includes snails and slugs of all kinds and all sizes: huge numbers of marine snails and sea slugs, as well as freshwater snails and freshwater limpets, and the terrestrial (land) snails and slugs. The class Gastropoda contains a vast total of named species, second only to the insects in overall number. The fossil history of this class goes all the way back to the Late Cambrian. There are 611 families of gastropods, of which 202 families are extinct, being found only in the fossil record.

Gastropoda (previously known as **univalves** and sometimes spelled Gasteropoda) are a major part of the phylum Mollusca and are the most highly diversified class in the phylum, with 60,000 to 80,000 living snail and slug species. The anatomy, behavior, feeding and reproductive adaptations of gastropods vary very significantly from one clade or group to another. Therefore, it is difficult or impossible to make more than a few general statements that are valid for all gastropods.

The class Gastropoda has an extraordinary diversification of habitats. Representatives live in gardens, in woodland, in deserts, and on mountains; in small ditches, great rivers and lakes; in estuaries, mudflats, the rocky intertidal, the sandy subtidal, in the abyssal depths of the oceans including the hydrothermal vents, and numerous other ecological niches, including parasitic ones.

Although the name "snail" can be, and often is, applied to all the members of this class, commonly this word means only those species with an external shell large enough that the soft parts can withdraw completely into it. Those gastropods without a shell, and those with only a very reduced or internal shell, are usually known as slugs.

The marine shelled species of gastropod include edible species such as abalone, conches, periwinkles, whelks, and numerous other sea snails that produce seashells which are coiled in the adult stage, even though in some cases the coiling may not be very visible, for example in cowries. There are also a number of families of species such as all the various limpets, where the shell is coiled only in the larval stage, and is a simple conical structure after that.

Etymology

The word "gastropod" is derived from the Ancient Greek words *γαστήρ (gastér,* stem: *gastr-)* "stomach", and *πούς (poús,* stem: *pod-)* "foot", hence stomach-foot. This is an anthropomorphic name, based on the fact that to humans it appears as if snails and slugs crawl on their bellies. In reality, snails and slugs have their stomach, the rest of their digestive system and all the rest of their viscera in a hump on the opposite, dorsal side of the body. In most gastropods this visceral hump is covered by, and contained within, the shell.

In the scientific literature, gastropods were described under the vernacular (French) name "gasteropodes" by Georges Cuvier in 1795. The name was later Latinized.

The earlier name *univalve* means "one valve", and contrasts with *bivalve* ("two valves").

Diversity

At all taxonomic levels, gastropods are second only to the insects in terms of their diversity.

Gastropods form the class of molluscs with the greatest numbers. However the estimated total number of gastropod species varies widely, depending on the cited sources. The number of gastropod species can be deduced from estimates of the number of described species of Mollusca with accepted names: about 85,000 (minimum 50,000, maximum 120,000). But an estimate of the total number of Mollusca, including undescribed species, is about 240,000 species. The estimate of 85,000 molluscs includes 24,000 described species of terrestrial gastropods.

Different estimations (from different sources) for aquatic gastropods give about 30,000 species of marine gastropods and about 5,000 species of freshwater and brackish gastropods. Total number of recent species of freshwater snails is about 4,000.

The number of prehistoric (fossil) species of gastropods is at least 15,000 species.

Habitat

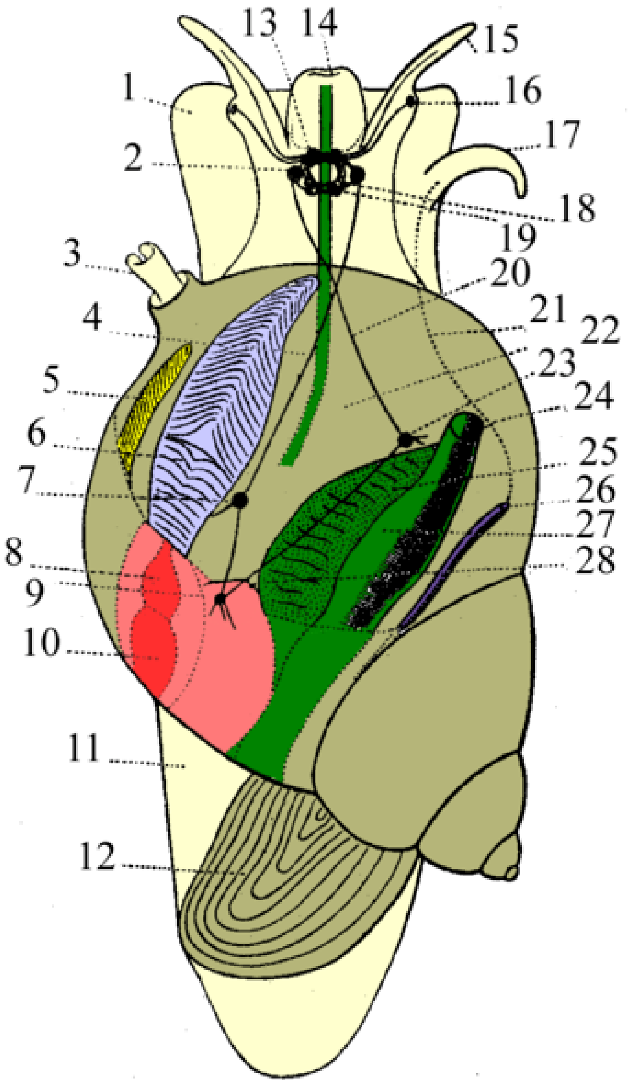
Some of the more familiar and better-known gastropods are terrestrial (the land snails and slugs) and some live in freshwater, but more than two thirds of all named species live in a marine environment.

Gastropods have a worldwide distribution from the near Arctic and Antarctic zones to the tropics. They have become adapted to almost every kind of existence on earth, having colonized every medium available except the air.

In habitats where there is not enough calcium carbonate to build a really solid shell, such as on some acidic soils on land, there are still various species of slugs, and also some snails with a thin translucent shell, mostly or entirely composed of the protein conchiolin.

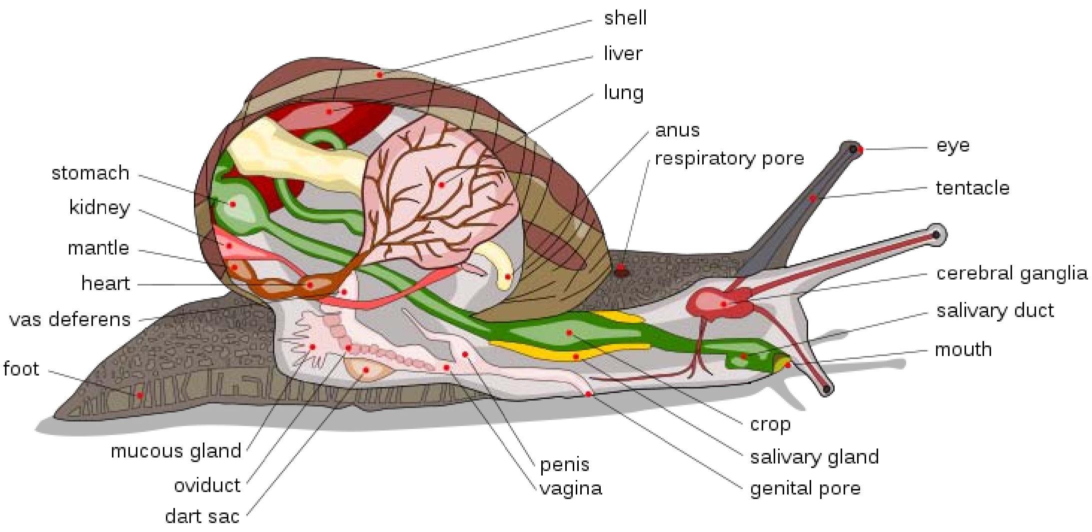
Snails such as *Sphincterochila boissieri* and *Xerocrassa seetzeni* have adapted to desert conditions, other snails have adapted to an existence in ditches, near deepwater hydrothermal vents, the pounding surf of rocky shores, caves, and many other diverse areas.

Anatomy



The anatomy of an aquatic snail with a gill, a male prosobranch gastropod. Note that much of this anatomy does not apply to gastropods in other clades.
Light yellow - body
Brown - shell and operculum
Green - digestive system
Light purple - gills
Yellow - osphradium
Red - heart
Pink -
Dark violet -
1. foot
2. cerebral ganglion
3. pneumostome
4. upper commissura

5. osphradium
6. gills
7. pleural ganglion
8. atrium of heart
9. visceral ganglion
10. ventricle
11. foot
12. operculum
13. brain
14. mouth
15. tentacle (chemosensory, 2 or 4)
16. eye
17. penis (everted, normally internal)
18. esophageal nerve ring
19. pedal ganglion
20. lower commissura
21. vas deferens
22. pallial cavity / mantle cavity / respiratory cavity
23. parietal ganglion
24. anus
25. hepatopancreas
26. gonad
27. rectum
28. nephridium



The anatomy of a common air-breathing land snail such as *Helix aspersa*. Note that much of this anatomy does not apply to gastropods in other clades or groups.

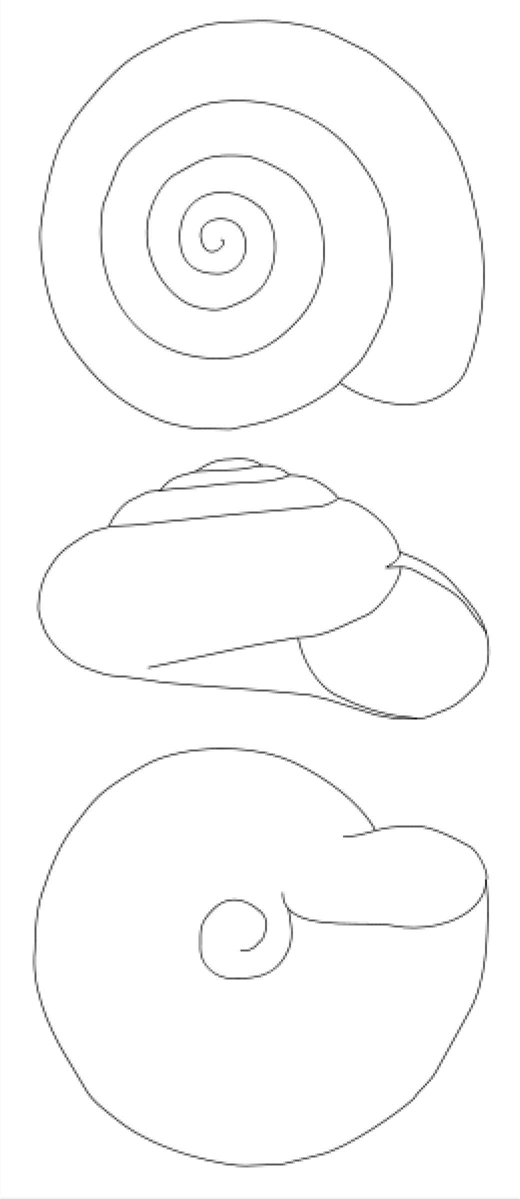
Snails are distinguished by an anatomical process known as torsion, where the visceral mass of the animal rotates 180° to one side during development, such that the anus is situated more or less above the head. This process is unrelated to the coiling of the shell, which is a separate phenomenon. Torsion is present in all gastropods, but the opisthobranch gastropods are secondarily de-torted to various degrees.

Torsion occurs in two mechanistic stages. The first is muscular, and the second is mutagenetic. The effects of torsion are primarily physiological - the organism develops an asymmetrical nature with the majority of growth occurring on the left side. This leads to the loss of right-paired appendages (e.g. ctenidia (comb-like respiratory apparatus), gonads, nephridia, etc.). Furthermore, the anus becomes redirected to the same space as the head. This is speculated to have some evolutionary function, as prior to torsion, when retracting into the shell, first the posterior end would get pulled in, and then the anterior. Now, the front can be retracted more easily, perhaps suggesting a defensive purpose.

However, this "rotation hypothesis" is being challenged by the "asymmetry hypothesis" in which the gastropod mantle cavity originated from one side only of a bilateral set of mantle cavities.

Gastropods typically have a well-defined head with two or four sensory tentacles with eyes, and a ventral foot, which gives them their name (Greek *gaster*, stomach, and *poda*, feet). The foremost division of the foot is called the **propodium**. Its function is to push away sediment as the snail crawls. The larval shell of a gastropod is called a protoconch.

The shell



The shell of *Zonitoides nitidus*, a small land snail, has dextral coiling, which is typical (but not universal) in gastropod shells.
Upper image: dorsal view of the shell, showing the apex
Central image: lateral view showing the spire and aperture of the shell
Lower image: basal view showing the umbilicus

Most shelled gastropods have a one piece shell, typically coiled or spiraled. This coiled shell usually opens on the right-hand side (as viewed with the shell apex pointing upward). Numerous species have an operculum, which in many species acts as a trapdoor to close the shell. This is usually made of a horn-like material, but in some molluscs it is calcareous. In the land slugs, the shell is reduced or absent, and the body is streamlined.

Body wall

Some sea slugs are very brightly colored. This serves either as a warning, when they are poisonous or contain stinging cells, or to camouflage them on the brightly-colored hydroids, sponges and seaweeds on which many of the species are found.

Lateral outgrowths on the body of nudibranchs are called cerata. These contain a part of digestive gland, which is called the diverticula.

Digestive system

The radula of a gastropod is usually adapted to the food that a species eats. The simplest gastropods are the limpets and abalones, herbivores that use their hard radula to rasp at seaweeds on rocks.

Many marine gastropods are burrowers, and have a siphon that extends out from the mantle edge. Sometimes the shell has a siphonal canal to accommodate this structure. A siphon enables the animal to draw water into their mantle cavity and over the gill. They use the siphon primarily to "taste" the water to detect prey from a distance. Gastropods with siphons tend to be either predators or scavengers.

Respiratory system

Almost all marine gastropods breathe with a gill, but many freshwater species, and the majority of terrestrial species, have a pallial lung. Gastropods with a lung belong to one group with common descent, the Pulmonata, however, gastropods with gills are paraphyletic. The respiratory protein in almost all gastropods is hemocyanin, but a pulmonate family Planorbidae have hemoglobin as respiratory protein.

In one large group of sea slugs, the gills are arranged as a rosette of feathery plumes on their backs, which gives rise to their other name, nudibranchs. Some nudibranchs have smooth or warty backs and have no visible gill mechanism, such that respiration may likely take place directly through the skin.

Circulatory system

Gastropods have open circulatory system and the transport fluid is hemolymph. Hemocyanin is present in the hemolymph as the respiratory pigment.

Excretory system

The primary organs of excretion in gastropods are nephridia, which produce either ammonia or uric acid as a waste product. The nephridium also plays an important role in maintaining water balance in freshwater and terrestrial species. Additional organs of excretion, at least in some species, include pericardial glands in the body cavity, and digestive glands opening into the stomach.

Sensory organs and nervous system

The upper pair of tentacles on the head of *Helix pomatia* have eye spots, but the main sensory organs of the snail are sensory receptors for olfaction, situated in the epithelium of the tentacles.

Sensory organs of gastropods include olfactory organs, eyes, statocysts and mechanoreceptors. Gastropods have no hearing.

In terrestrial gastropods (land snails and slugs), the olfactory organs, located on the tips of the 4 tentacles, are the most important sensory organ, The chemosensory organs of opisthobranch marine gastropods are called rhinophores.

The majority of gastropods have simple visual organs, eye spots, that are situated either at the tip of the tentacles or the base of the tentacles. However "eyes" in gastropods range from these simple ocelli which cannot process an image being only able to distinguish light and dark, to more complex pit eyes, and even to lens eyes. In land snails and slugs, vision is not the most important sense, because they are mainly nocturnal animals.

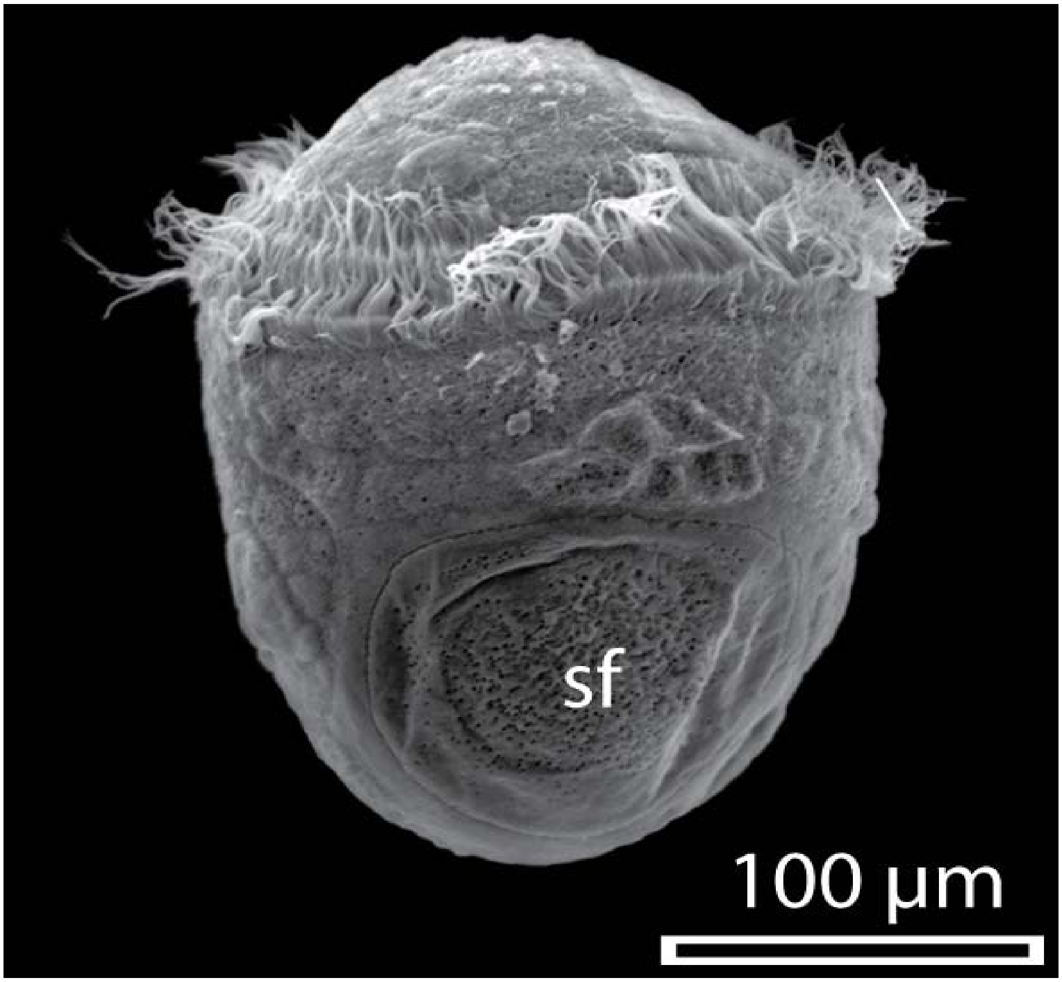
The nervous system of gastropods includes the peripheral nervous system and the central nervous system. The central nervous system consist of ganglia connected by nerve cells. It includes paired ganglia: the cerebral ganglia, pedal ganglia, osphradial ganglia, pleural ganglia, parietal ganglia and the visceral ganglia. There are sometimes also buccal ganglia.

Reproductive system

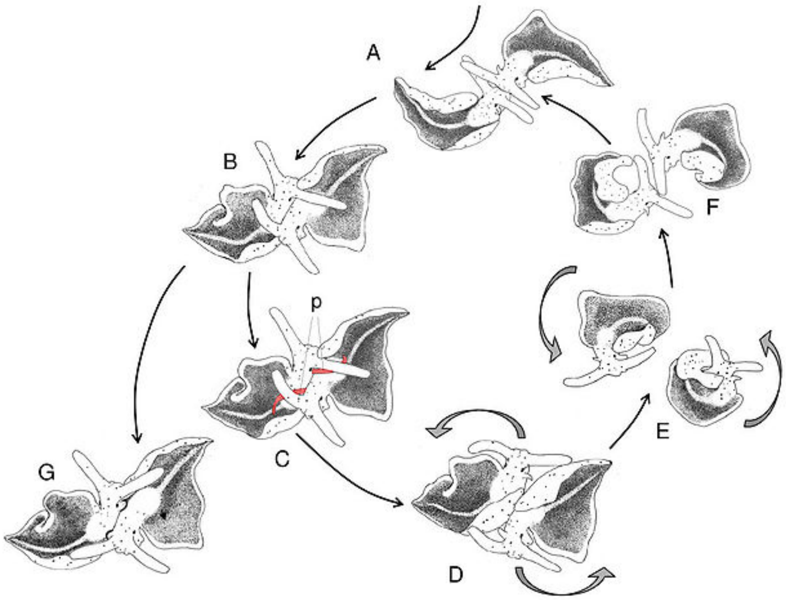
Courtship is a part of mating behavior in some gastropods including some of the Helicidae. Again, in some land snails, an unusual feature of the reproductive system of gastropods is the presence and utilization of love darts.

In many marine gastropods other than the opisthobranchs, there are separate sexes; most land gastropods however are hermaphrodites.

Life cycle



A 9-hour-old trochophore of *Haliotis asinina*
sf - shell field



Mating behaviour of *Elysia timida*

The main aspects of the life cycle of gastropods include:

- Egg laying and the eggs of gastropods
- The Embryonic development of gastropods
- The larvae or larval stadium: some gastropods may be trochophore and/or veliger
- Estivation and hibernation (each of these are present in some gastropods only)
- The growth of gastropods
- Courtship of gastropods and mating of gastropods: fertilisation is internal or external according to the species. External fertilisation is common in marine gastropods.

Feeding behavior

Marine gastropods include some that are herbivores, detritus feeders, predatory carnivores, scavengers, parasites, and also a few ciliary feeders, in which the radula is reduced or absent. In some species that have evolved into endoparasites, such as *Parenteroxenos doglieli*, many of the standard gastropod features are strongly reduced or absent.

A few sea slugs are herbivores and some are carnivores. Many have distinct dietary preferences and regularly occur in close association with their food species.

Some predatory carnivorous gastropods include, for example: Cone shells, *Testacella*, *Daudebardia*, Ghost slug and others.

Genetics

Gastropods exhibit an important degree of variation in mt gene organization when compared to other animals. Main events of gene rearrangement occurred at the origin of Patellogastropoda and Heterobranchia, whereas fewer changes occurred between the ancestors of Vetigastropoda (only tRNAs D, C and N) and Caenogastropoda (a large single inversion, and translocations of the tRNAs D and N). Within Heterobranchia, gene order seems to be relatively conserved and gene rearrangements are mostly related with transposition of tRNA genes.

Geological history

Fossil gastropod and attached mytilid bivalves on a Jurassic limestone bedding plane of the Matmor Formation in southern Israel.

Helix aspersa: a European pulmonate land snail that has been accidentally introduced in many countries tlroughout the world.

The first gastropods were exclusively marine, with the earliest representatives of the group appearing in the Late Cambrian (*Chippewaella*, *Strepsodiscus*). Early Cambrian forms like *Helcionella* and *Scenella* are no longer considered gastropods, and the tiny coiled *Aldanella* of earliest Cambrian time is probably not even a mollusk. By the Ordovician period the gastropods were a varied group present in a range of aquatic habitats. Commonly, fossil gastropods from the rocks of the early Palaeozoic era are too poorly preserved for accurate identification. Still, the Silurian genus *Poleumita* contains fiftean identified species. Fossil gastropods were less common during the Palaeozoic era than bivalves.

Most of the gastropods of the Palaeozoic era belong to primitive groups, a few of which still survive today. By the Carboniferous period many of the shapes we see in living gastropods can be matched in the fossil record, but despite these similarities in appearance the majority of these older forms are not directly related to living forms. It was during the Mesozoic era that the ancestors of many of the living gastropods evolved.

One of the earliest known terrestrial (land-dwelling) gastropods is *Maturipupa*, which is found in the Coal Measures of the Carboniferous period in Europe, but relatives of the modern land snails are rare before the Cretaceous period, when the familiar *Helix* first appeared.

Cepaea nemoralis: another European pulmonate land snail, which has been introduced to many other countries

In rocks of the Mesozoic era, gastropods are slightly more common as fossils, their shells are often well preserved. Their fossils occur in ancient beds deposited in both freshwater and marine environments. The "Purbeck Marble" of the Jurassic period and the "Sussex Marble" of the early Cretaceous period, which both occur in southern England, are limestones containing the tightly packed remains of the pond snail *Viviparus*.

Rocks of the Cenozoic era yield very large numbers of gastropod fossils, many of these fossils being closely related to modern living forms. The diversity of the gastropods increased markedly at the beginning of this era, along with that of the bivalves.

Certain trail-like markings preserved in ancient sedimentary rocks are thought to have been made by gastropods crawling over the soft mud and sand. Although these trails are of debatable origin, some of them do resemble the trails made by living gastropods today.

Gastropod fossils may sometimes be confused with ammonites or other shelled cephalopods. An example of this is *Bellerophon* from the limestones of the Carboniferous period in Europe, the shell of which is planispirally coiled and can be mistaken for the shell of a cephalopod.

Gastropods are one of the groups that record the changes in fauna caused by the advance and retreat of the Ice Sheets during the Pleistocene epoch.

Taxonomy

A group of fossil *Turritella cingulifera* from the Pliocene of Cyprus

The taxonomy of the Gastropoda is under constant revision, and more and more of the old taxonomy is being abandoned as the results of DNA studies slowly become clearer. Nevertheless a few of the older terms such as "opisthobranch" and "prosobranch" are still sometimes used in a descriptive way.

The taxonomy of the Gastropoda as shown in various texts can differ in major ways, and on-going revisions of the higher taxonomic levels are to be expected in the near future.

In the older classification there were four subclasses:

- Opisthobranchia (gills to the right and behind the heart).
- Gymnomorpha (no shell)
- Prosobranchia (gills in front of the heart).
- Pulmonata (with a lung instead of gills)

According to newer insights based on DNA sequencing, the taxonomy of the Gastropoda must be rewritten in terms of strictly monophyletic groups. Integrating these findings into a working taxonomy will continue to be a challenge in coming years. At present, it is impossible to give a classification of the Gastropoda that has consistent ranks and also reflects current usage.

Convergent evolution, which appears to exist at especially high frequency in the Gastropoda class, may account for the observed differences between the phylogenies, which are obtained from morphological data and more recent gene sequences studies.

Bouchet & Rocroi (2005) made changes in systematics, resulting in a taxonomy that is a step closer to the evolutionary history of the phylum.

This classification system is based partly on the older systems of classification and partly on new cladistic research. In the past, the taxonomy of gastropods was largely based on phenetic morphological characters of the taxa. The recent advances are more based on molecular characters through research of DNA and RNA. This has made the taxonomical ranks and their hierarchy controversial. The debate about these issues is not likely to end soon.

In this taxonomy, Bouchet, Rocroi *et al.* have used **unranked** clades for taxa above the rank of superfamily (replacing the ranks suborder, order, superorder and subclass), while using the traditional Linnaean approach for all taxa below the rank of superfamily. Whenever monophyly has not been tested, or is known to be paraphyletic or polyphyletic, the term "group" or "informal group" has been used. The classification of families into subfamilies is often not well resolved, and should be regarded as the best possible hypothesis.

In 2004 Brian Simison and David R. Lindberg showed possible diphyletic origins of the Gastropoda based on mitochondrial gene order and amino acid sequence analyses of complete genes.

Chapter- 6

Monoplacophora and Rostroconchia

Monoplacophora

Monoplacophorans Temporal range: early Cambrian–mid Devonian	
	
Neopilina sp. Head region is on the right.	
Scientific classification	
Kingdom:	Animalia
Phylum:	Mollusca
(unranked):	**Monoplacophora** Odhner, 1940
Included taxa	
†Archinacelloidea †Maikhanellidae †Pelagiellida Tergomya	

Monoplacophora, meaning "bearing one plate", is a polyphyletic class of mollusks with a cap-like shell, living on the bottom of deep sea. Extant representatives were unknown until 1952; previously they were known only from the fossil record.

Definition

Discussion about monoplacophorans is made difficult by the slippery definition of the taxon; some authors take it to refer to all non-gastropod molluscs with a single shell, or all single-shelled molluscs with serially-repeated units; whereas other workers restrict the definition to cap-shaped forms, excluding spiral and other shapes of shell. The inclusion of the gastropod-like Bellerophontoidea within the group is also contentious.

One attempt to resolve this confusion was to separate out the predominantly coiled helcionelloids from the traditional, cap-like tergomyans, this latter group containing extant Tryblidiids.

Habitat

Extant monoplacophorans live in deeper waters (175 m & deeper). Cambrian forms predominately lived in shallow seas, whereas later Paleozoic forms are more commonly found and in deeper waters with soft, muddy sea floors.

Phylogenetic position

In 2006 a molecular study on *Laevipilina antarctica* suggested that Monoplacophora and Polyplacophora form a well-supported clade with the researched Neopilina closest to the chitons. The two classes in this new clade, with the proposed name Serialia, all show a variable number of serially repeated gills and eight sets of dorsoventral pedal retractor muscles.

This study contradicts the fossil evidence, which suggests that the Monoplacophora are the sister group to the remainder of the conchiferans, and that the cephalopods (squid and octopus) arose from within the monoplacophoran lineage. However, some authors dispute this view and do not necessarily see modern monoplacophora as related to their fossil ancestors.

The fossil record does indicate that the ancestral mollusc was monoplacophoran-like and that the polyplacophora arose from within the monoplacophora – not the other way round; this could be reconciled if a secondary loss of shells caused a monoplacophoran body form to reappear secondarily. This is plausible: modern monoplacophorans are not closely related to vent-dwelling representatives from the Silurian, at least.

Cambrian monoplacophoran *Knightoconus antarcticus* is thought to be an ancestor to the cephalopods.

Fossil species

Families:

Tryblidiida

- Tryblidiidae von Zittel, 1899

ordo ?

- family ?
    - *Knightoconus*
        - *Knightoconus antarcticus*

The taxonomy of the Gastropoda by Bouchet & Rocroi, 2005 also contains Paleozoic molluscs of uncertain systematic position. It is not known whether these were gastropods or monoplacophorans.

Rostroconchia

Rostroconchia **Temporal range: Cambrian–Permian**	
Scientific classification	
Kingdom:	Animalia
Phylum:	Mollusca
Class:	**Rostroconchia**

The **Rostroconchia** is a class of extinct mollusks dating from the early Cambrian to the late Permian. They were initially thought to be bivalves, but were later given their own class. They have a single shell in their larval stage, and the adult typically has a single, pseudo-bivalved shell enclosing the mantle and muscular foot. The anterior part of the shell probably pointed downward and had a gap from which the foot could probably emerge. **Rostroconchs** probably lived a sedentary semi-infaunal lifestyle. There were probably more than 1,000 species of members of this class.

Approximately 3 dozen genera and an even greater number of species have been described. Generally, rostroconchs are small, less than two centimeters in length, but larger forms, found in United States Devonian limestones, can grow to a length of 15 cm.

Morphology and Lifestyle

Externally, rostroconchs look much like bivalves and rostroconchs probably had an extendable muscular foot, indicated by a prominent anterior gape in the rostroconch's shell. It seems, however, that the internal anatomy and morphology of the foot were closer to that of the scaphopods.

Rostroconchs began their life as a small, bilaterally symmetrical, univalved protoconch planktonic larva. The bilateral shell grew into two valves as the rostroconch entered adulthood. Adult rostroconchs differ from bivalves because they have no functional hinge. unlike the shell of a bivalve, which was able to move or articulate, the shell layers of a rostroconch—the layers of rigid calcite—continue across the whole dorsal area of the rostroconch. In this way, the rostroconch shell is more like a taco shell than a clam shell. The two valves would have been rigidly fixed in place, and would have to have been broken periodically to allow the rostroconch shell to grow.

The posterior of the shell contains a flattened tube that is called the rostrum. The rostroconch to have burrowed itself into the sediment anterior first and the rostrum was above the sediment used possibly as a water filtration system.

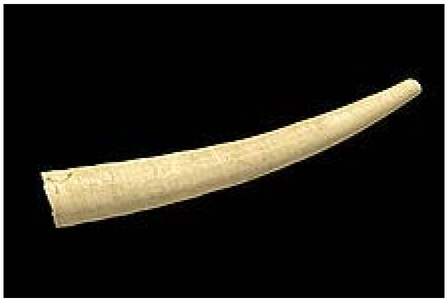
Evolutionary History

Heraultipegma is the earliest, very primitive, rostroconch genus dating from the Late Terreneuvian. True Rostroconchs appeared during the Ordovician, heavily competing with the bivalves until their decline in the end-early Ordovician turnover.

Early, primitive rostroconchs such as *Ribeiroia* had a hinge in which all shell layers covered the dorsal region resulting in a very rigid shell. In *Conocardium*, a more advanced rostroconch, the outer shell layers do not cross the entire margin, suggesting independent steps towards the bivalve flexible hinge.

Chapter- 7

Tusk Shell

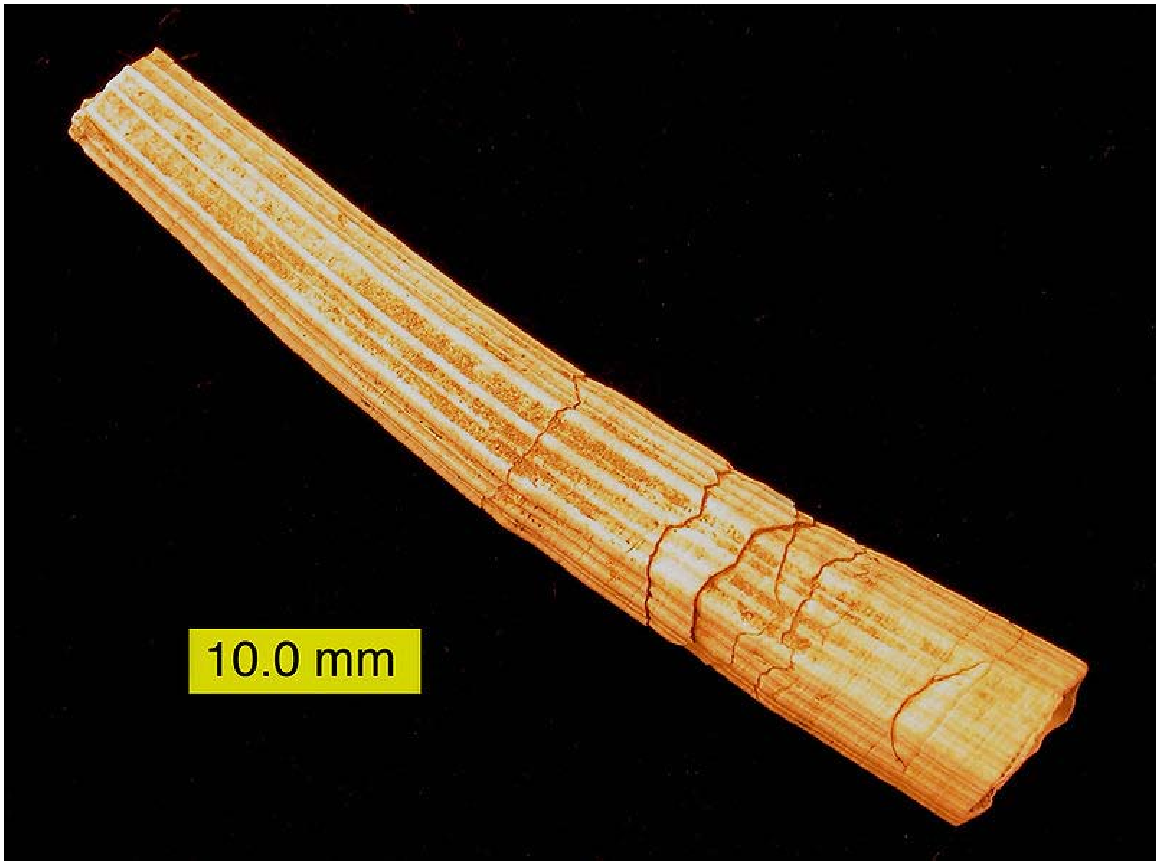
Tusk shells Temporal range: Mississippian–Recent	
	
A shell of the scaphopod *Antalis vulgaris* from France	
Scientific classification	
Kingdom:	Animalia
Phylum:	Mollusca
Class:	**Scaphopoda** Bronn, 1862
Orders	
Dentaliida Gadilida	

The **tusk shells** or **scaphopods** are a class of shelled marine mollusks. The scientific name of this class is **Scaphopoda**, meaning "shovel-footed". Shells of species within this class range from about 0.5 to 15 cm in length. Members of the Order Dentaliida are generally significantly larger than those of the Order Gadilida.

These molluscs live on soft substrates offshore (usually not intertidally). Because of this subtidal habitat and the small size of most species, many beachcombers are unfamiliar with them; their shells are usually not nearly as common or as easily visible in the beach drift as the shells of sea snails and clams.

Molecular data suggests that the scaphopods are a sister group to the cephalopods, although higher-level molluscan phylogeny remains somewhat unresolved.

Shell description



A fossil *Dentalium* shell from the Pliocene of Cyprus

The aragonitic shells of scaphopods are conical and curved in a planispiral way, and they are usually whitish in color. Because of these characters, the shell somewhat resembles a miniature elephant's tusk, hence the common name tusk shell. However, unlike an elephant's tusk, the shells of these molluscs are hollow and open at both ends; the opening at the larger end is the main or anterior aperture of the shell. The smaller opening is known as the apical aperture. Some tusk shells are minute, and most are 4 to 6 centimetres (1.6 to 2.4 in) long; however, a few species reach 15 centimetres (5.9 in) in length.

The scaphopod shell bears a prominent cross-lamellar layer, and has a bioeroded tip.

Habitat and distribution

Tusk shells live in seafloor sediment where they feed on detritus, foraminiferans and microscopic animals.

Classification

The group is composed of a two subtaxa, the Dentaliida (which may be paraphyletic) and the monophyletic Gadilida. The differences between the two orders is subtle and hinges on details of the radula and shell.

Anatomy of the soft parts

The mantle of a scaphopod is entirely within the shell. The foot extends from the larger end of the shell, and is used to burrow through the substrate. The scaphopod positions itself head down in the substrate, with the apical end of the shell (at the rear of the animal's body) projecting up into the water.

Water enters the mantle cavity through the apical aperture, and is wafted along the body surface by cilia. There are no gills; the entire surface of the mantle cavity absorbs oxygen from the water. Unlike most other molluscs, there is no continuous flow of water with a separate exhalant stream. Instead, dexoygenated water is expelled rapidly back through the apical aperture through muscular action once every ten to twelve minutes.

A number of minute tentacles around the foot, called **captacula**, sift through the sediment and latch onto bits of food, which they then convey to the mouth. The mouth has a grinding radula that breaks the bit into smaller pieces for digestion. The remainder of the digestive system consists of an oesophagus, stomach, and intestine. A digestive gland secretes enzymes into the stomach, but, unlike some other molluscs, does not digest the food directly itself. The anus opens on the underside of the animal, roughly in the middle of the mantle cavity.

The scaphopod vascular system is rudimentary, lacking both heart and blood vessels; the blood is held in sinuses throughout the body cavity, and is pumped through the body by the rhythmic action of the foot. Metabolic waste is excreted through a pair of nephridia close to the anus.

The nervous system is generally similar to that of gastropods. One pair each of cerebral and pleural ganglia lie close to the oesophagus, and effectively form the animal's brain. A separate set of pedal ganglia lie in the foot, and a pair of visceral ganglia are set further back in the body. Scaphopods have no eyes, or other distinct sensory organs.

Reproduction and development

Scaphopods have separate sexes, and external fertilisation. They have a single gonad occupying much of the posterior part of the body, and shed their gametes into the water through the nephridium.

Once fertilised, the eggs hatch into a free-living trochophore larva, which develops into a veliger larva that more closely resembles the adult, but lacks the extreme elongation of the adult body.

Fossil record

There is a good fossil record of scaphopods from the Mississippian onwards, making them the youngest molluscan class; but the origin of the group remains contentious.

The Ordovician *Rhytiodentalium kentuckyensis* has been interpreted as an early antecedent of the scaphopods, implying an evolutionary succession from ribeirioid rostroconch molluscs such as *Pinnocaris*. However, a competing hypothesis suggests a Devonian/Carboniferous origin from a non-mineralized ancestor, or from a more derived, Devonian, conocardioid rostroconch.

As such they were the most recent of all molluscan classes to evolve. They are most closely related to the extinct molluscan class Rostroconchia.

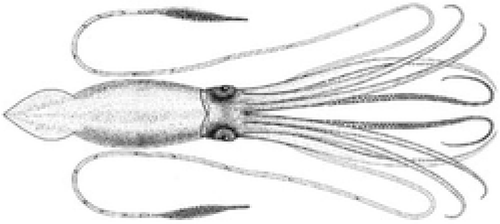
Human use

The shells of *Dentalium hexagonum*, a scaphopod mollusc, were strung on thread and used by the natives of the Pacific Northwest as shell money. *Dentalium* shells were also used to make belts and headdresses by the Natufian culture of the Middle East, and are a possible indicator of early social stratification.

Chapter- 8

Giant Squid

Giant squid



Giant squid, *Architeuthis* sp., modified from an illustration by A.E. Verrill, 1880.

Scientific classification

Kingdom:	Animalia
Phylum:	Mollusca
Class:	Cephalopoda
Subclass:	Coleoidea
Order:	Teuthida
Suborder:	Oegopsina
Family:	**Architeuthidae** Pfeffer, 1900
Genus:	***Architeuthis*** Steenstrup *in* Harting, 1860

Species

- *Architeuthis dux* Steenstrup, 1857
- ?*Architeuthis hartingii* Verrill, 1875
- ?*Architeuthis japonica* Pfeffer, 1912
- ?*Architeuthis kirkii* Robson, 1887
- ?*Architeuthis martensi* (Hilgendorf, 1880)
- ?*Architeuthis physeteris* (Joubin, 1900)

- ?*Architeuthis sanctipauli* (Velain, 1877)
- ?*Architeuthis stockii* (Kirk, 1882)

Synonyms

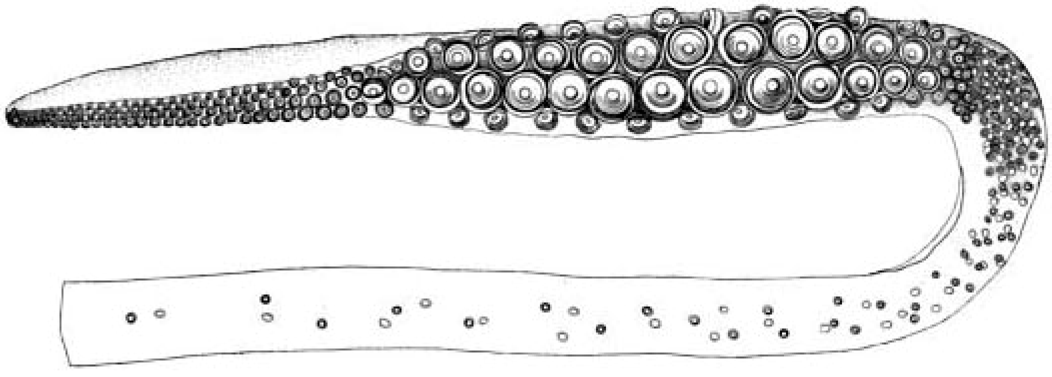
- *Architeuthus* Steenstrup, 1857
- *Dinoteuthis* More, 1875
- *Dubioteuthis* Joubin, 1900
- *Megaloteuthis* Kent, 1874
- *Megateuthis* Hilgendorf *in* Carus, 1880
- *Megateuthus* Hilgendorf, 1880
- *Mouchezis* Velain, 1877
- *Plectoteuthis* Owen, 1881
- *Steenstrupia* Kirk, 1882

The **giant squid** (genus: ***Architeuthis***) is a deep-ocean dwelling squid in the family **Architeuthidae**, represented by as many as eight species. Giant squid can grow to a tremendous size: recent estimates put the maximum size at 13 metres (43 ft) for females and 10 metres (33 ft) for males from caudal fin to the tip of the two long tentacles (second only to the colossal squid at an estimated 14 metres (46 ft), one of the largest living organisms). The mantle is about 2 metres (6.6 ft) long (more for females, less for males), and the length of the squid excluding its tentacles is about 5 metres (16 ft). There have been claims reported of specimens of 20 metres (66 ft) or more, but no animals of such size have been scientifically documented.

On September 30, 2004, researchers from the National Science Museum of Japan and the Ogasawara Whale Watching Association took the first images of a live giant squid in its natural habitat. Several of the 556 photographs were released a year later. The same team successfully filmed a live adult giant squid for the first time on December 4, 2006.

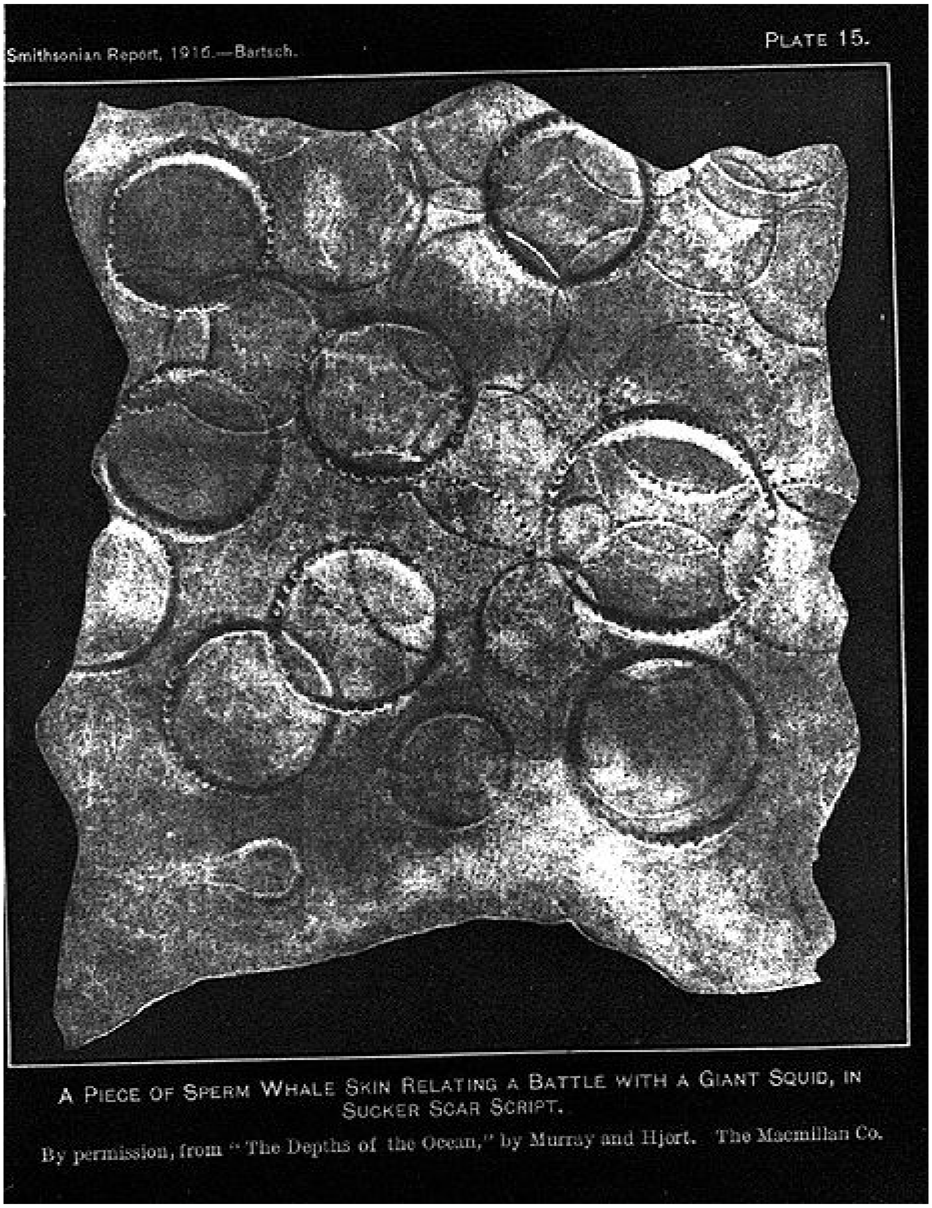
Morphology and anatomy

Like all squid, a giant squid has a mantle (torso), eight arms, and two longer tentacles (the longest known tentacles of any cephalopod). The arms and tentacles account for much of the squid's great length, making giant squid much lighter than their chief predators, sperm whales. Scientifically documented specimens have masses of hundreds, rather than thousands, of kilograms.



Tentacular club of *Architeuthis*

The inside surfaces of the arms and tentacles are lined with hundreds of sub-spherical suction cups, 2 to 5 centimetres (0.79 to 2.0 in) in diameter, each mounted on a stalk. The circumference of these suckers is lined with sharp, finely serrated rings of chitin. The perforation of these teeth and the suction of the cups serve to attach the squid to its prey. It is common to find circular scars from the suckers on or close to the head of sperm whales that have attacked giant squid. Each arm and tentacle is divided into three regions — carpus ("wrist"), manus ("hand") and dactylus ("finger"). The carpus has a dense cluster of cups, in six or seven irregular, transverse rows. The manus is broader, close to the end of the arm, and has enlarged suckers in two medial rows. The dactylus is the tip. The bases of all the arms and tentacles are arranged in a circle surrounding the animal's single parrot-like beak, as in other cephalopods.



Smithsonian Report, 1916.—Bartsch.

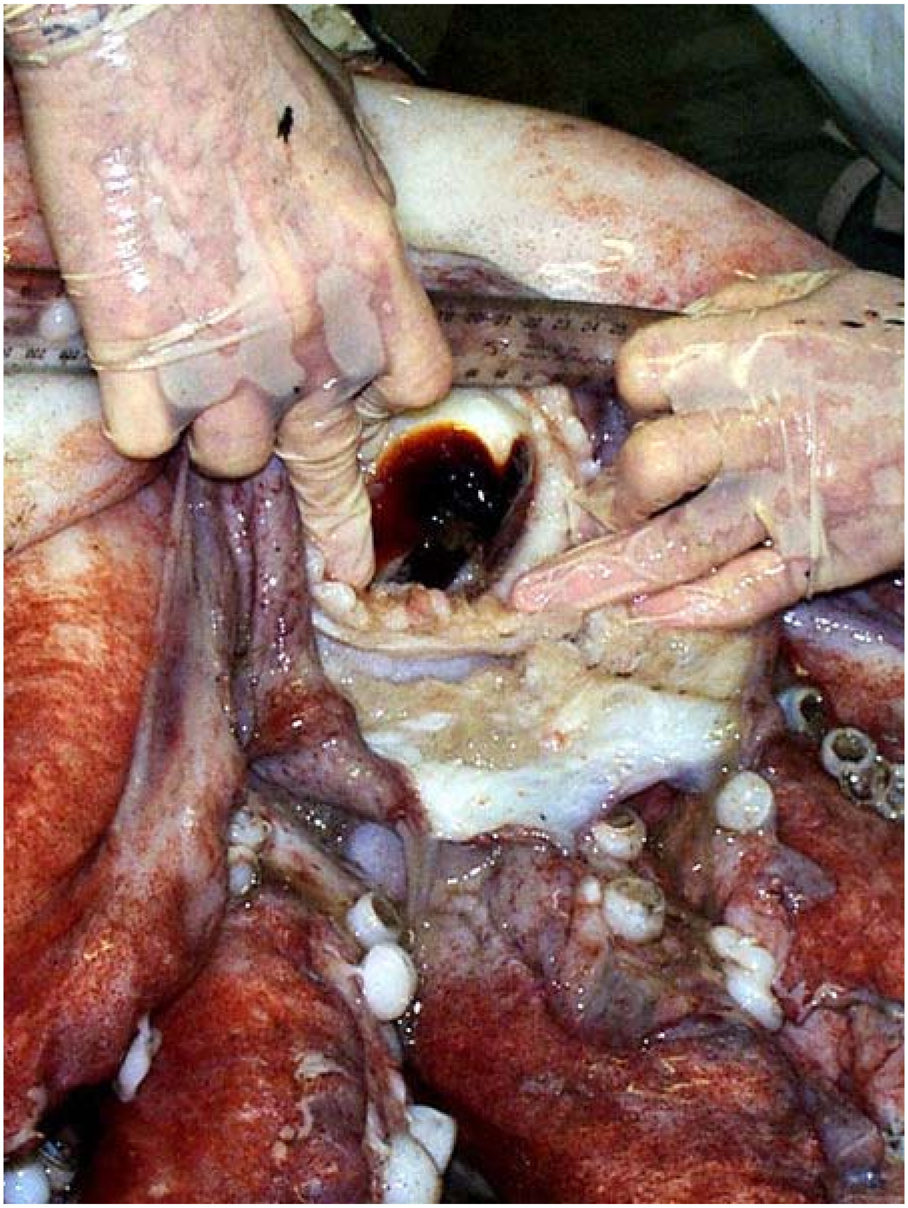
PLATE 15.

A PIECE OF SPERM WHALE SKIN RELATING A BATTLE WITH A GIANT SQUID, IN SUCKER SCAR SCRIPT.

By permission, from "The Depths of the Ocean," by Murray and Hjort. The Macmillan Co.

A portion of Sperm Whale skin with giant squid sucker scars

Giant squid have small fins at the rear of the mantle used for locomotion. Like other cephalopods, giant squid are propelled by jet — by pushing water through its mantle cavity through the funnel, in gentle, rhythmic pulses. They can also move quickly by expanding the cavity to fill it with water, then contracting muscles to jet water through the funnel. Giant squid breathe using two large gills inside the mantle cavity. The circulatory system is closed, which is a distinct characteristic of cephalopods. Like other squid, they contain dark ink used to deter predators.



The beak of a giant squid, surrounded by the buccal mass

Giant squid have a sophisticated nervous system and complex brain, attracting great interest from scientists. They also have the largest eyes of any living creature except perhaps colossal squid — over 30 centimetres (1 ft) in diameter. Large eyes can better detect light (including bioluminescent light), which is scarce in deep water. It is thought the giant squid cannot see colour, but they can probably discern small differences in tone, which is important in the low-light conditions of the deep ocean.

Giant squid and some other large squid species maintain neutral buoyancy in seawater through an ammonium chloride solution which flows throughout their body and is lighter than seawater. This differs from the method of flotation used by fish, which involves a gas-filled swim bladder. The solution tastes somewhat like salmiakki and makes giant squid unattractive for general human consumption.

Like all cephalopods, giant squid have organs called statocysts to sense their orientation and motion in water. The age of a giant squid can be determined by "growth rings" in the statocyst's "statolith", similar to determining the age of a tree by counting its rings. Much of what is known about giant squid age is based on estimates of the growth rings and from undigested beaks found in the stomachs of sperm whales.

Size

The giant squid is the second largest mollusc and the second largest of all extant invertebrates. It is only exceeded in size by the Colossal Squid, *Mesonychoteuthis hamiltoni*, which may have a mantle nearly twice as long. Several extinct cephalopods, such as the Cretaceous vampyromorphid *Tusoteuthis*, the Cretaceous coleoid *Yezoteuthis*, and the Ordovician nautiloid *Cameroceras* may have grown even larger.

Giant squid size, particularly total length, has often been misreported and exaggerated. Reports of specimens reaching and even exceeding 20 metres (66 ft) in length are widespread, but no animals approaching this size have been scientifically documented. According to giant squid expert Dr. Steve O'Shea, such lengths were likely achieved by greatly stretching the two tentacles like elastic bands.

A giant squid specimen measuring over 4 metres (13 ft) without its two long feeding tentacles

Based on the examination of 130 specimens and of beaks found inside sperm whales, giant squid's mantles are not known to exceed 2.25 metres (7.4 ft) in length. Including the head and arms, but excluding the tentacles, the length very rarely exceeds 5 metres (16 ft). Maximum total length, when measured relaxed *post mortem*, is estimated at 13 metres (43 ft) for females and 10 metres (33 ft) for males from caudal fin to the tip of the two long tentacles. Giant squid exhibit reverse sexual dimorphism. Maximum weight is estimated at 275 kilograms (610 lb) for females and 150 kilograms (330 lb) for males.

Reproductive cycle

Little is known about the reproductive cycle of giant squid. It is thought that they reach sexual maturity at about 3 years; males reach sexual maturity at a smaller size than females. Females produce large quantities of eggs, sometimes more than 5 kilograms (11 lb), that average 0.5 to 1.4 millimetres (0.020 to 0.055 in) long and 0.3 to 0.7 millimetre (0.012 to 0.028 in) wide. Females have a single median ovary in the rear end of the mantle cavity and paired convoluted oviducts where mature eggs pass exiting through the oviducal glands, then through the nidamental glands. As in other squid, these glands produce a gelatinous material used to keep the eggs together once they are laid.

In males, as with most other cephalopods, the single, posterior testis produces sperm that move into a complex system of glands that manufacture the spermatophores. These are stored in the elongate sac, or Needham's sac, that terminates in the penis from which they are expelled during mating. The penis is prehensile, over 90 centimeters long, and extends from inside the mantle.

How the sperm is transferred to the egg mass is much debated, as giant squid lack the hectocotylus used for reproduction in many other cephalopods. It may be transferred in sacs of spermatophores, called spermatangia, which the male injects into the female's arms. This is suggested by a female specimen recently found in Tasmania, having a small subsidiary tendril attached to the base of each arm.

Post-larval juveniles have been discovered in surface waters off New Zealand, and there are plans to capture more and maintain them in an aquarium to learn more about the creature.

Ecology

Feeding

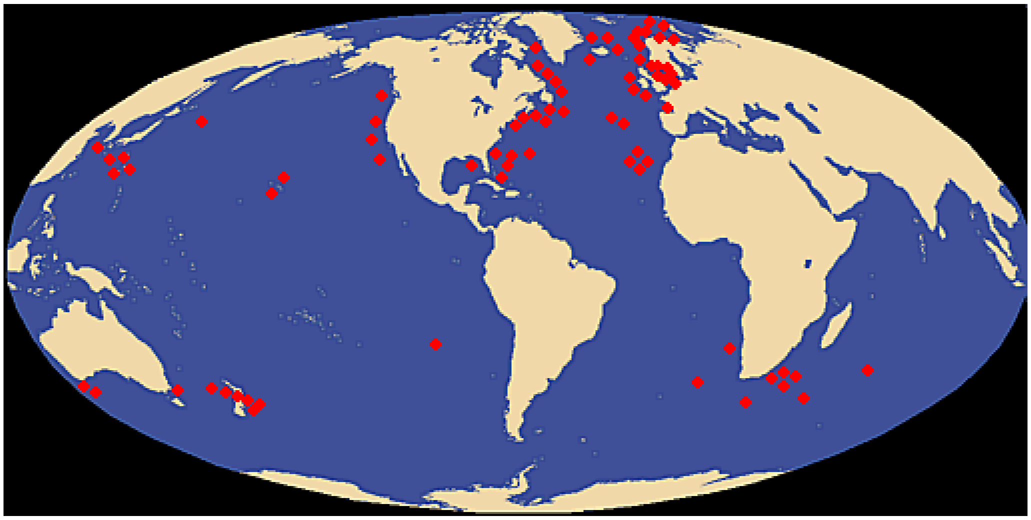
The fabled underwater encounter between the sperm whale and giant squid, from a diorama at the American Museum of Natural History

Recent studies show that giant squid feed on deep-sea fish and other squid species. They catch prey using the two tentacles, gripping it with serrated sucker rings on the ends. Then they bring it toward the powerful beak, and shred it with the radula (tongue with small, file-like teeth) before it reaches the esophagus. They are believed to be solitary hunters, as only individual giant squid have been caught in fishing nets. Although the majority of giant squid caught by trawl in New Zealand waters have been associated with the local hoki (*Macruronus novaezelandiae*) fishery, the fish themselves do not feature in the squid's diet. This suggests that giant squid and hoki prey on the same animals.

Predators

Adult giant squids' only known predators are sperm whales. It has also been suggested that pilot whales may feed on giant squid. Juveniles are preyed on by deep sea sharks and fishes. Because sperm whales are skilled at locating giant squid, scientists have tried to observe them to study the squid.

Range and habitat



Worldwide giant squid distribution based on recovered specimens

Giant squid are very widespread, occurring in all of the world's oceans. They are usually found near continental and island slopes from the North Atlantic Ocean, especially Newfoundland, Norway, the northern British Isles, and the oceanic islands of the Azores and Madeira, to the South Atlantic around southern Africa, the North Pacific around Japan, and the southwestern Pacific around New Zealand and Australia. Specimens are rare in tropical and polar latitudes.

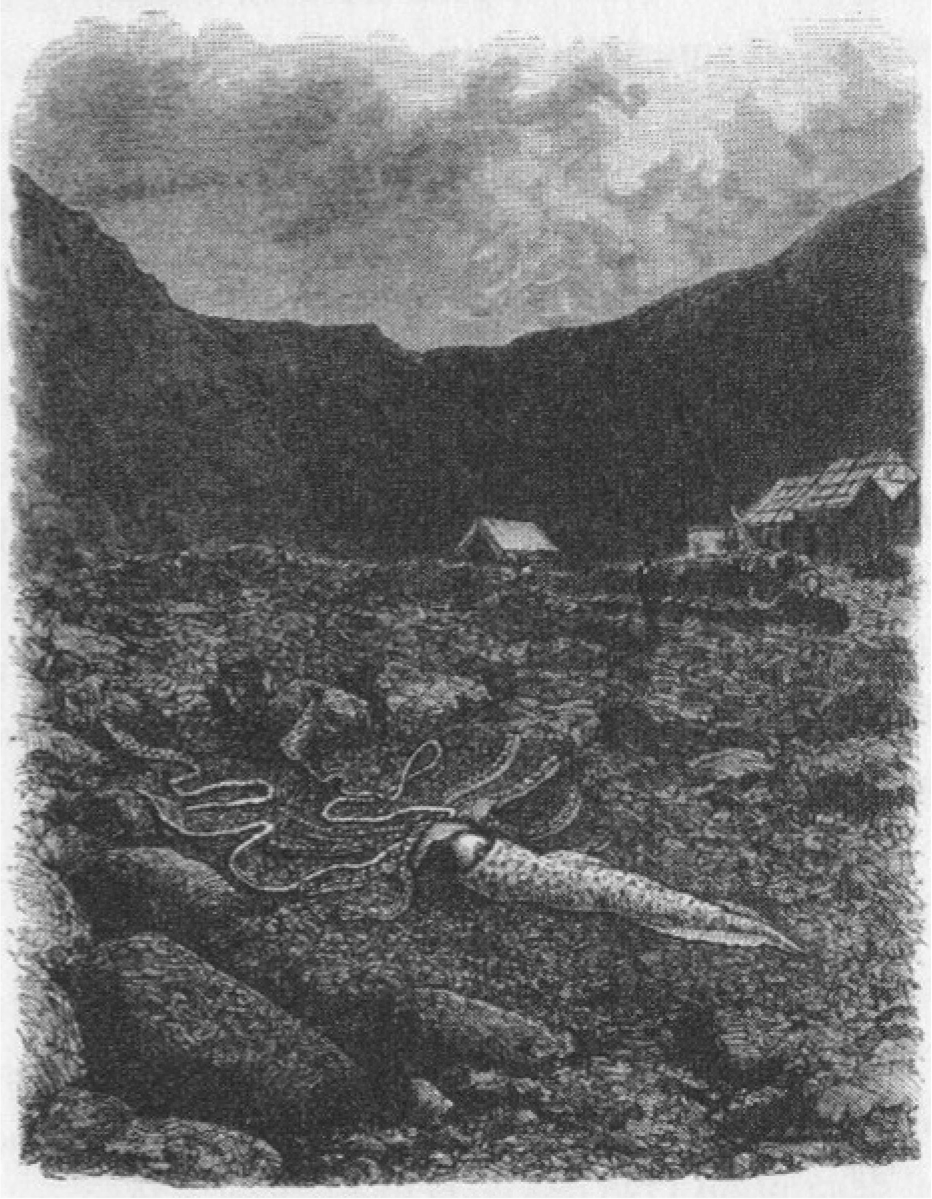
The vertical distribution of giant squid is incompletely known, but data from trawled specimens and sperm whale diving behaviour suggests it spans a large range of depths, possibly 300–1000 m.

Species

The taxonomy of the giant squid, as with many cephalopod genera, has not been resolved. Lumpers and splitters may propose as many as eight species or as few as one. The broadest list is:

- *Architeuthis dux*, "Atlantic Giant Squid"
- *Architeuthis hartingii*
- *Architeuthis japonica*
- *Architeuthis kirkii*
- *Architeuthis martensi*, "North Pacific Giant Squid"
- *Architeuthis physeteris*
- *Architeuthis sanctipauli*, "Southern Giant Squid"

- *Architeuthis stockii*



Architeuthis sanctipauli was described in 1877 based on a specimen found washed ashore in Île Saint-Paul three years earlier

It is probable that not all of these are distinct species. No genetic or physical basis for distinguishing between them has been proposed, as evidenced by the placenames — of location of specimen capture — used to describe several of them. The rarity of observations of specimens and the extreme difficulty of observing them alive, tracking their movements, or studying their mating habits militates against a complete understanding.

In the 1984 *FAO Species Catalogue of the Cephalopods of the World*, C.F.E. Roper, M.J. Sweeney and C.F. Nauen wrote:

"Many species have been named in the sole genus of the family Architeuthidae, but they are so inadequately described and poorly understood that the systematics of the group is thoroughly confused."

Kir Nazimovich Nesis (1982) considered that only three species were likely to be valid.

In 1991, Frederick Aldrich of the Memorial University of Newfoundland wrote:

"I reject the concept of 20 separate species, and until that issue is resolved, I choose to place them all in synonymy with *Architeuthis dux* Steenstrup."

In a letter to Richard Ellis dated June 18, 1996, Martina Roeleveld of the South African Museum wrote:

"So far, I have seen nothing to suggest that there might be more than one species of *Architeuthis*."

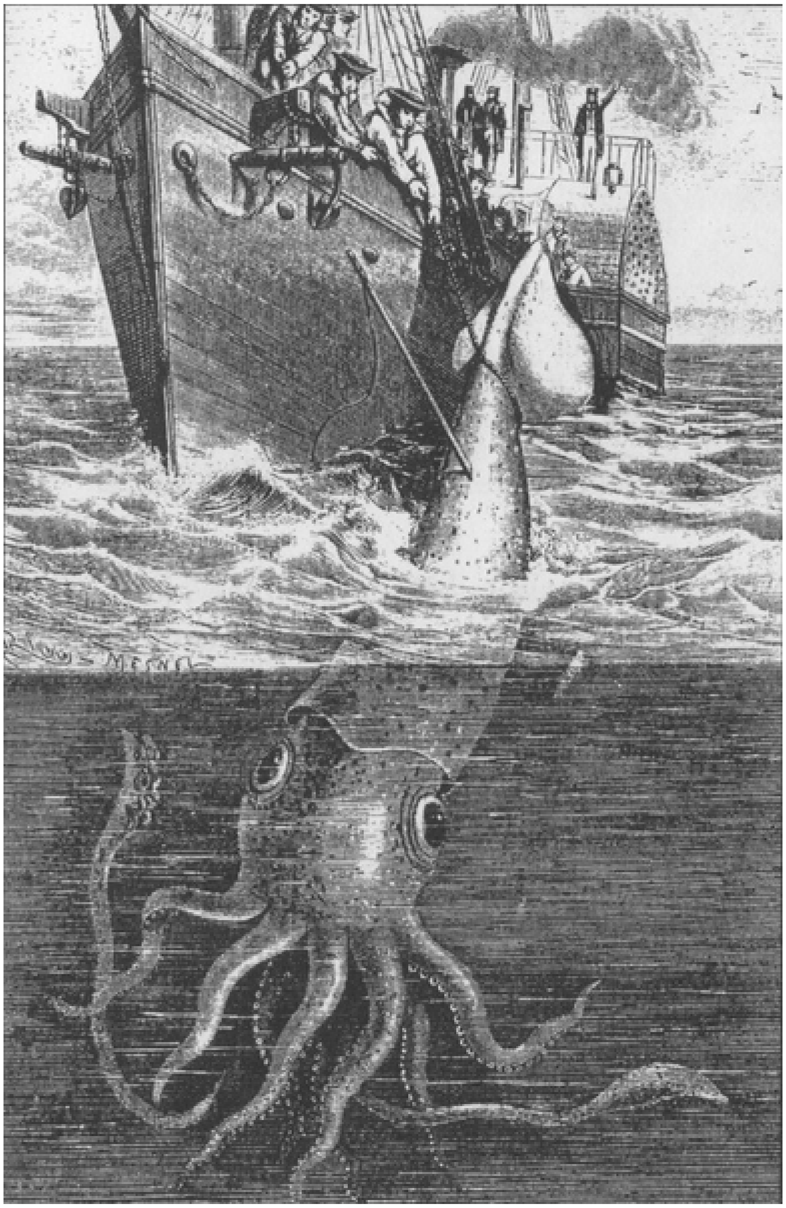
In *Cephalopods: A World Guide* (2000), Mark Norman writes the following:

"The number of species of giant squid is not known although the general consensus amongst researchers is that there are at least three species, one in the Atlantic Ocean (*Architeuthis dux*), one in the Southern Ocean (*A. sanctipauli*) and at least one in the northern Pacific Ocean (*A. martensi*)."

Timeline

Aristotle, who lived in the fourth century B.C., already described a large squid, which he called *teuthus*, distinguishing it from the smaller squid, the *teuthis*. He mentions that "of the calamaries the so-called teuthus is much bigger than the teuthis; for teuthi [plural of *teuthus*] have been found as much as five ells long."

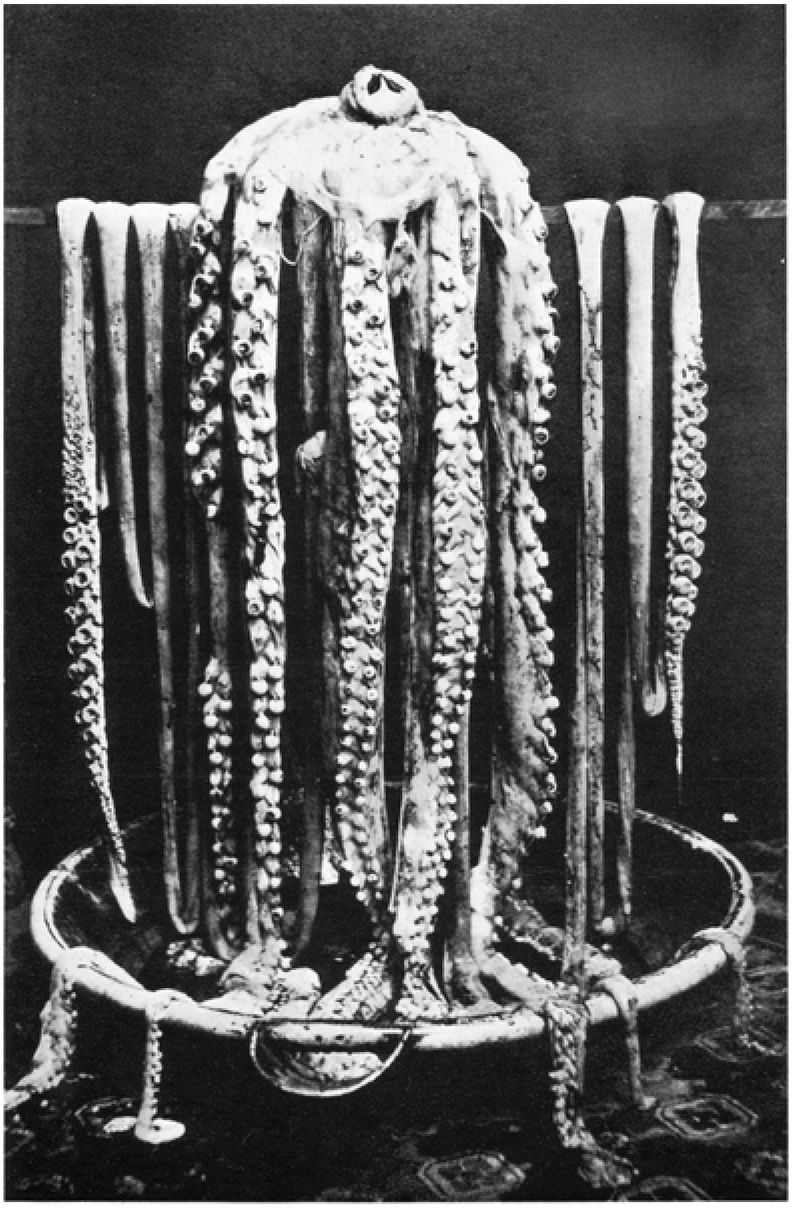
Pliny the Elder, living in the first century A.D., also described a gigantic squid in his *Natural History*, with the head "as big as a cask", arms 30 feet (9.1 m) long, and carcass weighing 700 pounds (320 kg).



The *Alecton* attempts to capture a giant squid in 1861

Tales of giant squid have been common among mariners since ancient times, and may have led to the Norse legend of the kraken, a tentacled sea monster as large as an island capable of engulfing and sinking any ship. Japetus Steenstrup, the describer of *Architeuthis*, suggested a giant squid was the species described as a sea monk to the Danish king Christian III *c*.1550. The Lusca of the Caribbean and Scylla in Greek mythology may also derive from giant squid sightings. Eyewitness accounts of other sea monsters like the sea serpent are also thought to be mistaken interpretations of giant squid.

Steenstrup wrote a number of papers on giant squid in the 1850s. He first used the term "*Architeuthus*" (this was the spelling he chose) in a paper in 1857. A portion of a giant squid was secured by the French gunboat *Alecton* in 1861 leading to wider recognition of the genus in the scientific community. From 1870 to 1880, many squid were stranded on the shores of Newfoundland. For example, a specimen washed ashore in Thimble Tickle Bay, Newfoundland on November 2, 1878; its mantle was reported to be 6.1 metres (20 ft) long, with one tentacle 10.7 metres (35 ft) long, and it was estimated as weighing 2.2 tonnes. In 1873, a squid "attacked" a minister and a young boy in a dory in Bell Island, Newfoundland. Many strandings also occurred in New Zealand during the late 19th century.



Giant squid from Logy Bay, Newfoundland in Reverend Moses Harvey's bathtub, November/December, 1873

Although strandings continue to occur sporadically throughout the world, none have been as frequent as those at Newfoundland and New Zealand in the 19th century. It is not known why giant squid become stranded on shore, but it may be because the distribution of deep, cold water where squid live is temporarily altered. Many scientists who have studied squid mass strandings believe that they are cyclical and predictable. The length of time between strandings is not known, but was proposed to be 90 years by *Architeuthis* specialist Frederick Aldrich. Aldrich used this value to correctly predict a relatively small stranding that occurred between 1964 and 1966.

In 2004, another giant squid, later named "Archie", was caught off the coast of the Falkland Islands by a trawler. It was 8.62 metres (28.3 ft) long and was sent to the Natural History Museum in London to be studied and preserved. It was put on display on March 1, 2006 at the Darwin Centre. The find of such a large, complete specimen is very rare, as most specimens are in a poor condition, having washed up dead on beaches or been retrieved from the stomach of dead sperm whales.

Researchers undertook a painstaking process to preserve the body. It was transported to England on ice aboard the trawler; then it was defrosted, which took about four days. The major difficulty was that thawing the thick mantle took much longer than the tentacles. To prevent the tentacles from rotting, scientists covered them in ice packs, and bathed the mantle in water. Then they injected the squid with a formol-saline solution to prevent rotting. The creature is now on show in a 9 metres (30 ft) long glass tank at the Darwin Centre of the Natural History Museum.

The giant squid specimen preserved in a block of ice at the Melbourne Aquarium

In December 2005, the Melbourne Aquarium in Australia paid A$100,000 for the intact body of a giant squid, preserved in a giant block of ice, which had been caught by fishermen off the coast of New Zealand's South Island that year.

The number of known giant squid specimens was close to 600 in 2004, and new ones are reported each year. The search for a live *Architeuthis* specimen includes attempts to find live young, including larvae. The larvae closely resemble those of *Nototodarus* and

Onykia, but are distinguished by the shape of the mantle attachment to the head, the tentacle suckers, and the beaks.

Images and video of live animals

The giant squid was one of the last extant megafauna to never have been photographed alive, either in the wild or in captivity. Marine biologist and author Richard Ellis described it as "the most elusive image in natural history".

In 1993, an image purporting to show a diver with a live giant squid (identified as *Architeuthis dux*) was published in the book *European Seashells*. However, the animal in this photograph was a sick or dying *Onykia robusta*, not a giant squid.

The first footage of live larval giant squid ever captured on film was in 2001. The footage was shown on *Chasing Giants: On the Trail of the Giant Squid* on the Discovery Channel.

First images of live adult

The specimen from Goshiki beach is seen here tied with a rope. The delicate skin is only partially intact. Muscular constriction around the squid's eye obscures much of its surface in this image.

The first image of a live mature giant squid was taken on January 15, 2002, on Goshiki beach, Amino Cho, Kyoto Prefecture, Japan. The animal, which measured about 2 metres (6.6 ft) in mantle length and 4 metres (13 ft) in total length, was found near the water's surface. It was captured and tied to a quay, where it died overnight. The specimen was identified by Koutarou Tsuchiya of the Tokyo University of Fisheries. It is on display at the National Science Museum of Japan.

First observations in the wild

The first photographs of a live giant squid in its natural habitat were taken on September 30, 2004, by Tsunemi Kubodera (National Science Museum of Japan) and Kyoichi Mori (Ogasawara Whale Watching Association). Their teams had worked together for nearly two years to accomplish this. They used a five-ton fishing boat and only two crew members. The images were created on their third trip to a known sperm whale hunting ground 970 kilometres (600 mi) south of Tokyo, where they had dropped a 900-metre (3,000 ft) line baited with squid and shrimp. The line also held a camera and a flash. After over 20 tries that day, an 8-metre (26 ft) giant squid attacked the lure and snagged its tentacle. The camera took over 500 photos before the squid managed to break free after four hours. The squid's 5.5-metre (18 ft) tentacle remained attached to the lure. Later DNA tests confirmed the animal as a giant squid.

One of the series of images of a live giant squid taken by Kubodera and Mori in 2004

On September 27, 2005, Kubodera and Mori released the photographs to the world. The photo sequence, taken at a depth of 900 metres (3,000 ft) off Japan's Ogasawara Islands, shows the squid homing in on the baited line and enveloping it in "a ball of tentacles." The researchers were able to locate the likely general location of giant squid by closely tailing the movements of sperm whales. According to Kubodera, "we knew that they fed on the squid, and we knew when and how deep they dived, so we used them to lead us to the squid." Kubodera and Mori reported their observations in the journal *Proceedings of the Royal Society*.

Among other things, the observations demonstrate actual hunting behaviors of adult *Architeuthis*, a subject on which there had been much speculation. The photographs showed an aggressive hunting pattern by the baited squid, leading to it impaling a tentacle on the bait ball's hooks. This may disprove the theory that the giant squid is a drifter which eats whatever floats by, rarely moving so as to conserve energy. It seems that the species has a much more belligerent feeding technique.

First video of live adult

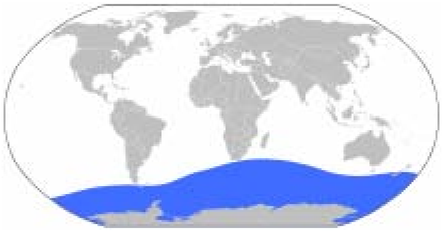
On December 4, 2006, an adult giant squid was finally caught on video near the Ogasawara Islands, 1,000 kilometres (620 mi) south of Tokyo, by researchers from the National Science Museum of Japan led by Tsunemi Kubodera. It was a small female about 3.5 metres (11 ft) long and weighing 50 kilograms (110 lb). The bait used by the scientists initially attracted a medium-sized squid measuring around 55 centimetres (22 in), which in turn attracted the giant squid. It was pulled aboard the research vessel but died in the process.

Chapter- 9

Colossal Squid

Colossal Squid	
	
Scientific classification	
Kingdom:	Animalia
Phylum:	Mollusca
Class:	Cephalopoda
Order:	Teuthida
Family:	Cranchiidae
Subfamily:	Taoniinae
Genus:	***Mesonychoteuthis*** Robson, 1925
Species:	***M. hamiltoni***
Binomial name	
Mesonychoteuthis hamiltoni	

Robson, 1925



Global range of *M. hamiltoni*

The **Colossal Squid** (*Mesonychoteuthis hamiltoni*, from Greek *mesos* (middle), *nychus* (claw), and *teuthis* (squid)), sometimes called the **Antarctic** or **Giant Cranch Squid**, is believed to be the largest squid species in terms of mass. It is the only known member of the genus ***Mesonychoteuthis***. Though it is known from only a few specimens, current estimates put its maximum size at 12–14 metres (39–46 feet) long, based on analysis of smaller and immature specimens, making it the largest known invertebrate.

Morphology

Unlike the giant squid, whose arms and tentacles only have suckers lined with small teeth, the Colossal Squid's limbs are also equipped with sharp hooks: some swiveling, others three-pointed. Its body is wider and stouter, and therefore heavier, than that of the giant squid. Colossal Squids are believed to have a longer mantle than giant squids, although their tentacles are shorter.

The squid exhibits abyssal gigantism. The beak of *Mesonychoteuthis hamiltoni* is the largest known of any squid, exceeding that of *Architeuthis* (giant squid) in size and in robustness. The Colossal Squid also has the largest eyes documented in the animal kingdom.

Distribution

The squid's known range extends thousands of miles northward from Antarctica to southern South America, southern South Africa, and the southern tip of New Zealand, making it primarily an inhabitant of the entire circumantarctic Southern Ocean.

Ecology and life history

While little is known about the life of this creature, it is believed to feed on prey such as chaetognatha, large fish like the Patagonian toothfish and other squid in the deep ocean using bioluminescence. The Colossal Squid is thought to have a slow metabolic rate, requiring only around 30 g of prey daily. Estimates of its energetic demands suggest that it is a slow-moving ambush predator, using its large eyes primarily for predator detection rather than active hunting.

Based on capture depths of a few specimens, as well as beaks found in sperm whale stomachs, the adult squid ranges at least to a depth of 2200 metres, while juveniles can go as deep as 1000 metres. It is believed to be sexually dimorphic, with mature females generally being much larger than mature males, as is common in many species of invertebrates.

The squid's method of reproduction has not been observed, although some data on their reproduction can be inferred from anatomy. Since males lack an organ called a hectocotylus (a tentacle used in other cephalopods to transfer a spermatophore to the female), they probably use a penis instead, which would be used to directly implant sperm into females.

Many sperm whales carry scars on their backs believed to be caused by the hooks of Colossal Squid. Colossal Squid are a major prey item for Antarctic sperm whales feeding in the Southern Ocean; 14% of the squid beaks found in the stomachs of these sperm whales are those of the Colossal Squid, which indicates that Colossal Squid make up 77% of the biomass consumed by these whales. Many other animals also feed on this squid, including beaked whales (such as the bottlenose whales), pilot whales, southern elephant seals, Patagonian toothfish, sleeper sharks (*Somniosus* cf. *microcephalus*), and albatrosses (e.g., the Wandering and Sooty albatrosses). However, beaks from mature adults have only been recovered from those animals large enough to take such prey (i.e., sperm whales and sleeper sharks), while the remaining predators are limited to eating juveniles or young adults.

Timeline

- 1925 – Species was first discovered in the form of two tentacles found in the stomach of a sperm whale.
- 1981 – A Russian trawler in the Ross Sea, off the coast of Antarctica, caught a large squid with a total length of 4 metres (13 ft), which was later identified as an immature female of *Mesonychoteuthis hamiltoni*.
- 2003 – A complete specimen of a subadult female was found near the surface with a total length of 6 m (20 ft) and a mantle length of 2.5 m (8 ft).
- 2005 – A specimen was captured at a depth of 1625 m while taking a toothfish from a longline off South Georgia Island. Although the mantle was not brought aboard, the mantle length was estimated at over 2.5 m, and the tentacles measured 230 cm. The animal is thought to have weighed between 150 and 200 kg.
- 2007 – The largest recorded specimen was captured by a New Zealand fishing boat off Antarctica. It was initially estimated to measure 10 m (33 ft) in length and weigh 450 kg (992 lb). The squid was taken back to New Zealand for scientific study. A study on the specimen later showed that its actual weight was 495 kg (1,091 lb), but that it only measured 4.2 m (14 ft) in total length as a result of the tentacles shrinking *post mortem*.

Largest known specimen

This specimen, caught in early 2007, is the largest cephalopod ever recorded. Here it is shown in its live state during capture, with the delicate red skin still intact and the mantle characteristically inflated.

On February 22, 2007, it was announced by authorities in New Zealand that the largest known Colossal Squid had been captured. The specimen weighed 495 kg (1,091 lb) and was initially estimated to measure 10 m (33 ft) in total length. Fishermen on the vessel *San Aspiring*, owned by the Sanford seafood company, caught the animal in the freezing Antarctic waters of the Ross Sea. It was brought to the surface as it fed on an Antarctic toothfish that had been caught off a long line. It would not let go of its prey and could not be removed from the line by the fishermen, so they decided to catch it instead. They managed to envelop it in a net, hauled it aboard and froze it. The specimen eclipsed the previous largest find in 2003 by about 195 kilograms (430 lb), although it is still considerably smaller than some estimates have predicted. The specimen was frozen in a cubic metre of water and transported to the Museum of New Zealand Te Papa Tongarewa, New Zealand's national museum. Media reports suggested that scientists at the museum were considering using a giant microwave to defrost the squid because defrosting the squid at room temperatures would take days and it would be likely for the outside to rot while the core remained frozen. However, they later opted for the more conventional approach of thawing the specimen in a bath of salt water. After thawing, the squid measured only 4.2 m (14 ft) in total length, with the tentacles having shrunk significantly. Although initially thought to be a male, closer inspection of the specimen showed it to be a female.

Defrosting and dissection, April-May 2008

Thawing and dissection of the specimen took place at the Museum of New Zealand Te Papa Tongarewa under the direction of senior biologist Chris Paulin, with technician Mark Fenwick, Dutch marine biologist and toxicologist Olaf Blaauw, AUT biologist Dr Steve O'Shea, Dr Tsunemi Kubodera, and AUT biologist Kat Bolstad.

Parts of the specimen have been examined:

- The beak is considerably smaller than some found in the stomachs of sperm whales, suggesting there are Colossal Squid much larger than this one.
- The eye is 27 cm (10.63 in) wide, with a lens 12 cm across. This is the largest eye of any known animal. These measurements are of the partly collapsed specimen: when living the eye was probably 30 to 40 cm (12 to 16 in) across.
- Inspection of the specimen with an endoscope revealed ovaries containing thousands of eggs.

Exhibition

The specimen on display at the Museum of New Zealand Te Papa Tongarewa

The Museum of New Zealand Te Papa Tongarewa is displaying this specimen in an exhibition which opened on December 13, 2008. A website on the squid specimen is also available.

Chapter- 10

Octopus

Octopus

The Common Octopus, *Octopus vulgaris*.

Scientific classification

Kingdom:	Animalia
Phylum:	Mollusca
Class:	Cephalopoda
Superorder:	Octopodiformes
Order:	**Octopoda** Leach, 1818

Suborders

- Cirrina
- Incirrina

Synonyms

- Octopoida
  Leach, 1817

The **octopus** is a cephalopod mollusc of the order **Octopoda**. Octopuses have two eyes and four pairs of arms, and like other cephalopods they are bilaterally symmetric. An octopus has a hard beak, with its mouth at the center point of the arms. Octopuses have no internal or external skeleton (although some species have a vestigial remnant of a shell inside their mantle), allowing them to squeeze through tight places. Octopuses are among the most intelligent and behaviorally flexible of all invertebrates.

The octopus inhabits many diverse regions of the ocean, including coral reefs, pelagic waters, and the ocean floor. They have numerous strategies for defending themselves against predators, including the expulsion of ink, the use of camouflage and deimatic displays, their ability to jet quickly through the water, and their ability to hide. An octopus trails its eight arms behind it as it swims. All octopuses are venomous, but only one group, the blue-ringed octopuses, is known to be deadly to humans.

There are around 300 recognized octopus species, which is over one-third of the total number of known cephalopod species. The term *octopus* may also be used to refer only to those creatures in the genus *Octopus*.

Biology

A Common Octopus (*Octopus vulgaris*)

Octopuses are characterized by their eight arms, usually bearing suction cups. The arms of octopuses are often distinguished from the pair of feeding tentacles found in squid and cuttlefish. Both types of limbs are muscular hydrostats. Unlike most other cephalopods, the majority of octopuses – those in the suborder most commonly known, Incirrina – have almost entirely soft bodies with no internal skeleton. They have neither a protective outer shell like the nautilus, nor any vestige of an internal shell or bones, like cuttlefish or squid. A beak, similar in shape to a parrot's beak, is the only hard part of their body. This enables them to squeeze through very narrow slits between underwater rocks, which is very helpful when they are fleeing from morays or other predatory fish. The octopuses in the less familiar Cirrina suborder have two fins and an internal shell, generally reducing their ability to squeeze into small spaces. These cirrate species are often free-swimming and live in deep-water habitats, while incirrate octopus species are found in reefs and other shallower seafloor habitats.

An octopus moving between tide pools during low tide

Octopuses have a relatively short life expectancy, and some species live for as little as six months. Larger species, such as the North Pacific Giant Octopus, may live for up to five years under suitable circumstances. However, reproduction is a cause of death: males can only live for a few months after mating, and females die shortly after their eggs hatch. They neglect to eat during the (roughly) one month period spent taking care of their unhatched eggs, but they do not die of starvation. Endocrine secretions from the two optic glands are the cause of genetically programmed death (and if these glands are surgically removed, the octopus may live many months beyond reproduction, until she finally starves).

Grimpoteuthis discoveryi, a finned octopus of the suborder Cirrina

Octopuses have three hearts. Two branchial hearts pump blood through each of the two gills, while the third pumps blood through the body. Octopus blood contains the copper-rich protein hemocyanin for transporting oxygen. Although less efficient under normal conditions than the iron-rich hemoglobin of vertebrates, in cold conditions with low oxygen pressure, hemocyanin oxygen transportation is more efficient than hemoglobin oxygen transportation. The hemocyanin is dissolved in the plasma instead of being carried within red blood cells and gives the blood a bluish color. Octopuses draw water into their mantle cavity where it passes through its gills. As mollusks, octopuses have gills that are finely divided and vascularized outgrowths of either the outer or the inner body surface.

Intelligence

Octopuses are highly intelligent, likely more so than any other order of invertebrates. The exact extent of their intelligence and learning capability is much debated among biologists, but maze and problem-solving experiments have shown that they show evidence of a memory system that can store both short- and long-term memory. It is not known precisely what contribution learning makes to adult octopus behavior. Young octopuses learn almost no behaviors from their parents, with whom they have very little contact.

An octopus opening a container with a screw cap

An octopus has a highly complex nervous system, only part of which is localized in its brain. Two-thirds of an octopus's neurons are found in the nerve cords of its arms, which have limited functional autonomy. Octopus arms show a variety of complex reflex actions that persist even when they have no input from the brain. Unlike vertebrates, the complex motor skills of octopuses are not organized in their brain using an internal somatotopic map of its body, as is the motor system in vertebrates Some octopuses, such as the mimic octopus, will move their arms in ways that emulate the shape and movements of other sea creatures.

In laboratory experiments, octopuses can be readily trained to distinguish between different shapes and patterns. They have been reported to practice observational learning, although the validity of these findings is widely contested on a number of grounds. Octopuses have also been observed in what some have described as play: repeatedly releasing bottles or toys into a circular current in their aquariums and then catching them. Octopuses often break out of their aquariums and sometimes into others in search of food. They have even boarded fishing boats and opened holds to eat crabs.

In some countries, octopuses are on the list of experimental animals on which surgery may not be performed without anesthesia. In the UK, cephalopods such as octopuses are regarded as *honorary vertebrates* under the Animals (Scientific Procedures) Act 1986 and other cruelty to animals legislation, extending to them protections not normally afforded to invertebrates.

The octopus is the only invertebrate which has been shown to use tools. At least four specimens of the Veined Octopus (*Amphioctopus marginatus*) have been witnessed retrieving discarded coconut shells, manipulating them, and then reassembling them to use as shelter. This discovery was documented in the journal *Current Biology* and has also been caught on video.

Defense

Greater Blue-ringed Octopus (*Hapalochlaena lunulata*)

An octopus's main (primary) defense is to hide, either not to be seen at all, or not to be detected as an octopus. Octopuses have several secondary defenses (defenses they use once they have been seen by a predator). The most common secondary defense is fast escape. Other defenses include the use of ink sacs, camouflage, and autotomising limbs.

Most octopuses can eject a thick blackish ink in a large cloud to aid in escaping from predators. The main coloring agent of the ink is melanin, which is the same chemical that gives humans their hair and skin color. This ink cloud is thought to reduce the efficiency of olfactory organs, which would aid an octopus's evasion from predators that employ smell for hunting, such as sharks. Ink clouds of some species might serve as pseudomorphs, or decoys that the predator attacks instead.

Amphioctopus marginatus travels with shells it has collected for protection

An octopus's camouflage is aided by certain specialized skin cells which can change the apparent color, opacity, and reflectiveness of the epidermis. Chromatophores contain yellow, orange, red, brown, or black pigments; most species have three of these colors, while some have two or four. Other color-changing cells are reflective iridophores, and leucophores (white). This color-changing ability can also be used to communicate with or warn other octopuses. The very venomous blue-ringed octopus becomes bright yellow with blue rings when it is provoked. Octopuses can use muscles in the skin to change the texture of their mantle to achieve a greater camouflage. In some species the mantle can take on the spiky appearance of seaweed, or the scraggly, bumpy texture of a rock, among other disguises. However in some species skin anatomy is limited to relatively patternless shades of one color, and limited skin texture. It is thought that octopuses that are day-active and/or live in complex habitats such as coral reefs have evolved more complex skin than their nocturnal and/or sand-dwelling relatives.

When under attack, some octopuses can perform arm autotomy, in a similar manner to the way skinks and other lizards detach their tails. The crawling arm serves as a distraction to would-be predators.

A few species, such as the Mimic Octopus, have a fourth defense mechanism. They can combine their highly flexible bodies with their color changing ability to accurately mimic other, more dangerous animals such as lionfish, sea snakes, and eels.

Reproduction

When octopuses reproduce, males use a specialized arm called a hectocotylus to insert spermatophores (packets of sperm) into the female's mantle cavity. The hectocotylus in benthic octopuses is usually the third right arm. Males die within a few months of mating. In some species, the female octopus can keep the sperm alive inside her for weeks until her eggs are mature. After they have been fertilized, the female lays about 200,000 eggs (this figure dramatically varies between families, genera, species and also individuals). The female hangs these eggs in strings from the ceiling of her lair, or individually attaches them to the substrate depending on the species. The female cares for the eggs, guarding them against predators, and gently blowing currents of water over them so that they get enough oxygen. The female does not hunt during the roughly one-month period spent taking care of the unhatched eggs and may ingest some of her own arms for sustenance. At around the time the eggs hatch, the mother leaves the lair and is too weak to defend herself from predators like cod, often succumbing to their attacks. The young larval octopuses spend a period of time drifting in clouds of plankton, where they feed on copepods, larval crabs and larval starfish until they are ready to descend to the ocean bottom, where the cycle repeats. This is a dangerous time for the larval octopuses; in the plankton cloud they are vulnerable to plankton eaters. In some deeper dwelling species, the young do not go through this period.

Sensation

Eye of *Octopus vulgaris*

Octopuses have keen eyesight. Octopuses, like other cephalopods, can distinguish the polarization of light. Color vision appears to vary from species to species, being present in *Octopus aegina* but absent in *Octopus vulgaris*. Attached to the brain are two special organs, called statocysts, that allow the octopus to sense the orientation of its body relative to horizontal. An autonomic response keeps the octopus's eyes oriented so that the pupil slit is always horizontal.

Octopuses also have an excellent sense of touch. An octopus's suction cups are equipped with chemoreceptors so that the octopus can taste what it is touching. The arms contain tension sensors so that the octopus knows whether its arms are stretched out. However, the octopus has a very poor proprioceptive sense. The tension receptors are not sufficient for the octopus brain to determine the position of the octopus's body or arms. (It is not clear that the octopus brain would be capable of processing the large amount of information that this would require; the flexibility of an octopus's arms is much greater than that of the limbs of vertebrates, which devote large areas of cerebral cortex to the processing of proprioceptive inputs.) As a result, the octopus does not possess stereognosis; that is, it does not form a mental image of the overall shape of the object it is handling. It can detect local texture variations, but cannot integrate the information into a larger picture.

The neurological autonomy of the arms means that the octopus has great difficulty learning about the detailed effects of its motions. The brain may issue a high-level command to the arms, but the nerve cords in the arms execute the details. There is no neurological path for the brain to receive feedback about just how its command was executed by the arms; the only way it knows just what motions were made is by observing the arms visually.

Octopuses appear to have limited hearing.

Octopuses swim headfirst, with arms trailing behind

Locomotion

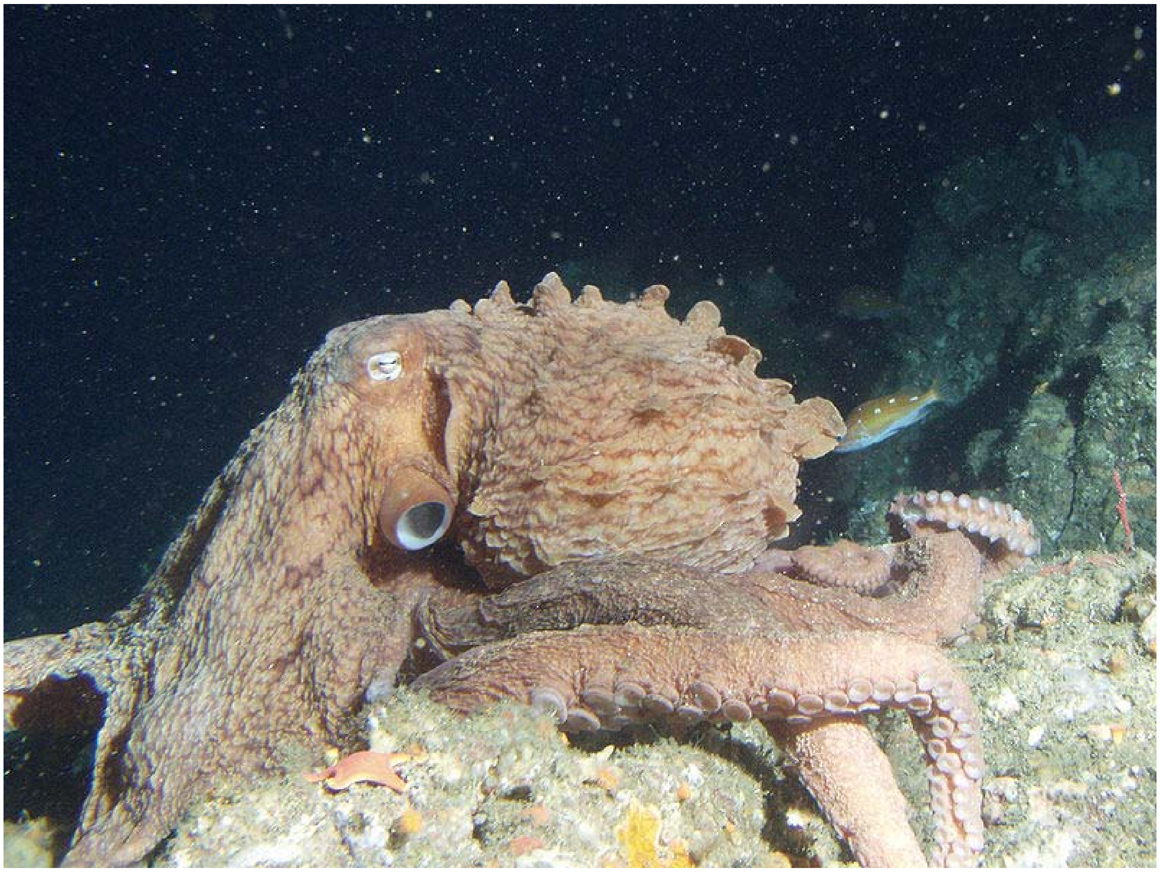
An octopus in its natural habitat

Octopuses move about by crawling or swimming. Their main means of slow travel is crawling, with some swimming. Jet propulsion is their fastest means of locomotion, followed by swimming and walking.

They crawl by walking on their arms, usually on many at once, on both solid and soft surfaces, while supported in water. In 2005 it was reported that some octopuses (*Adopus aculeatus* and *Amphioctopus marginatus* under current taxonomy) can walk on two arms, while at the same time resembling plant matter. This form of locomotion allows these octopuses to move quickly away from a potential predator while possibly not triggering that predator's search image for octopus (food).

Octopuses swim by expelling a jet of water from a contractile mantle, and aiming it via a muscular siphon.

Size



An adult North Pacific Giant Octopus, *Enteroctopus dofleini*

The North Pacific Giant Octopus, *Enteroctopus dofleini*, is often cited as the largest octopus species. Adults usually weigh around 15 kg (33 lb), with an arm span of up to 4.3 m (14 ft). The largest specimen of this species to be scientifically documented was an animal with a live mass of 71 kg (156.5 lb). The alternative contender is the Seven-arm Octopus, *Haliphron atlanticus*, based on a 61 kg (134 lb) carcass estimated to have a live mass of 75 kg (165 lb). However, there are a number of questionable size records that would suggest *E. dofleini* is the largest of all octopus species by a considerable margin; one such record is of a specimen weighing 272 kg (600 lb) and having an arm span of 9 m (30 ft).

Terminology

The term octopus is from Greek ὀκτάπους (*oktapous*), "eight-footed",. Currently, *octopuses* is the most common form in both the US and the UK; *octopodes* is rare, and *octopi* is often objectionable.

The plural form *octopi* is often described as a hypercorrection. The *Oxford English Dictionary* (2008 Draft Revision) lists *octopuses*, *octopi* and *octopodes* (in that order); it labels *octopodes* "rare", although the correct Greek plural form, and notes that *octopi* derives from the "apprehension" that *octōpūs* is a second declension Latin noun, though it is not. It is a Latinization of Greek third-declension masculine *oktṓpous* (ὀκτώπους, 'eight-foot'), plural *oktṓpodes* (ὀκτώποδες). If the word were native to Latin, it would be *octōpēs*, plural *octōpedes*, after the pattern of *pēs* ('foot'), plural *pedēs*, analogous to "centipede". The actual Latin word for octopus and other similar species is *polypus*, from Greek *polýpous* (πολύπους, 'many-foot'); usually the inaccurate plural *polypī* is used instead of *polypodēs*.

In modern Greek, the word is *khtapódi* (χταπόδι), plural *khtapódia* (χταπόδια), from Medieval *oktapódion* (ὀκταπόδιον), equivalent to Classical *oktápous* (ὀκτάπους), variant of *oktṓpous*.

Chambers 21st Century Dictionary and the *Compact Oxford Dictionary* list only *octopuses*, although the latter notes that *octopodes* is "still occasionally used"; the British National Corpus has 29 instances of *octopuses*, 11 of *octopi* and 4 of *octopodes*. *Merriam-Webster 11th Collegiate Dictionary* lists *octopuses* and *octopi*, in that order; *Webster's New World College Dictionary* lists *octopuses*, *octopi* and *octopodes* (in that order).

Fowler's Modern English Usage states that "the only acceptable plural in English is *octopuses,*" and that *octopi* is misconceived and *octopodes* pedantic.

The term *octopod* (plural *octopods* or *octopodes*) is taken from the taxonomic order Octopoda but has no classical equivalent. The collective form *octopus* is usually reserved for animals consumed for food.

In mythology

The Hawaiian creation myth relates that the present cosmos is only the last of a series, having arisen in stages from the wreck of the previous universe. In this account, the octopus is the lone survivor of the previous, alien universe.

In literature

The octopus has a significant role in Victor Hugo's book *Travailleurs de la mer* (*Toilers of the Sea*).

As a metaphor

Due to having numerous tentacles that emanate from a common center, the octopus is often used as a metaphor for a group or organziation which is perceived as being powerful, manipulative or bent on domination. Use of this terminology is invariably negative and employed by the opponents of the groups or institutions so described.

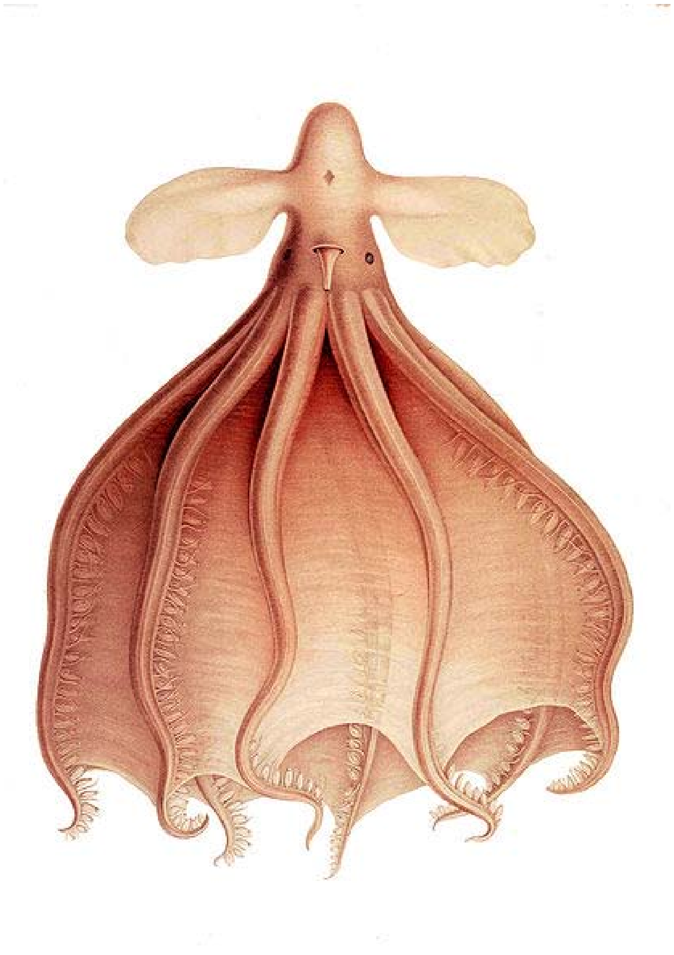
As pets

Though octopuses can be difficult to keep in captivity, some people keep them as pets. Octopuses often escape even from supposedly secure tanks, due to their problem-solving skills, mobility and lack of rigid structure.

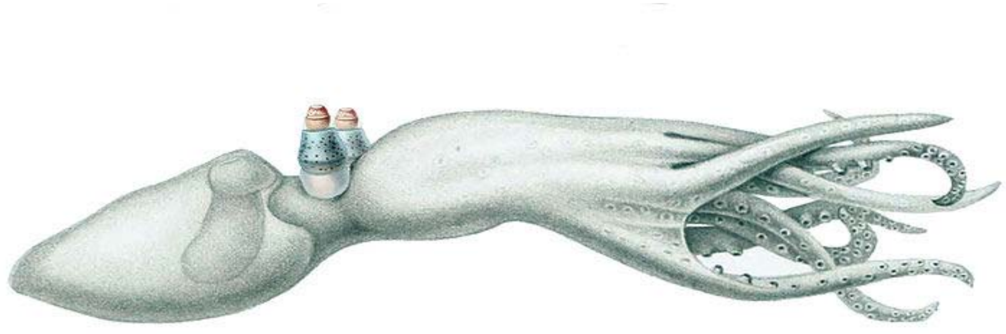
The variation in size and life span among octopus species makes it difficult to know how long a new specimen can naturally be expected to live. That is, a small octopus may be just born or may be an adult, depending on its species. By selecting a well-known species, such as the California Two-spot Octopus, one can choose a small octopus (around the size of a tennis ball) and be confident that it is young with a full life ahead of it.

Octopuses are also quite strong for their size. Octopuses kept as pets have been known to open the covers of their aquariums and survive for a time in the air in order to get to a nearby feeder tank and gorge themselves on the fish there. Large octopuses have also been known to catch and kill some species of sharks.

Classification



Cirrothauma murrayi



Amphitretus pelagicus

Class CEPHALOPODA

- Subclass Nautiloidea: nautilus
- Subclass Coleoidea
    - Superorder Decapodiformes: squid, cuttlefish
    - Superorder Octopodiformes
        - Family †Trachyteuthididae (*incertae sedis*)
        - Order Vampyromorphida: Vampire Squid
        - **Order Octopoda**
            - Genus †*Keuppia* (*incertae sedis*)
            - Genus †*Palaeoctopus* (*incertae sedis*)
            - Genus †*Paleocirroteuthis* (*incertae sedis*)
            - Genus †*Pohlsepia* (*incertae sedis*)
            - Genus †*Proteroctopus* (*incertae sedis*)
            - Genus †*Styletoctopus* (*incertae sedis*)
            - Suborder Cirrina: finned deep-sea octopus
                - Family Opisthoteuthidae: umbrella octopus
                - Family Cirroteuthidae
                - Family Stauroteuthidae
            - Suborder Incirrina
                - Family Amphitretidae: telescope octopus
                - Family Bolitaenidae: gelatinous octopus
                - Family Octopodidae: benthic octopus
                - Family Vitreledonellidae: Glass Octopus
                - Superfamily Argonautoida
                    - Family Alloposidae: Seven-arm Octopus
                    - Family Argonautidae: argonauts
                    - Family Ocythoidae: Tuberculate Pelagic Octopus
                    - Family Tremoctopodidae: blanket octopus