Cephalopoda
(Molluscan Class)

Margot Forte

First Edition, 2012

ISBN 978-81-323-4101-7

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

Table of Contents

Chapter 1

Cephalopod

Cephalopods Temporal range: Devonian – Recent (Stem-groups from Cambrian)	

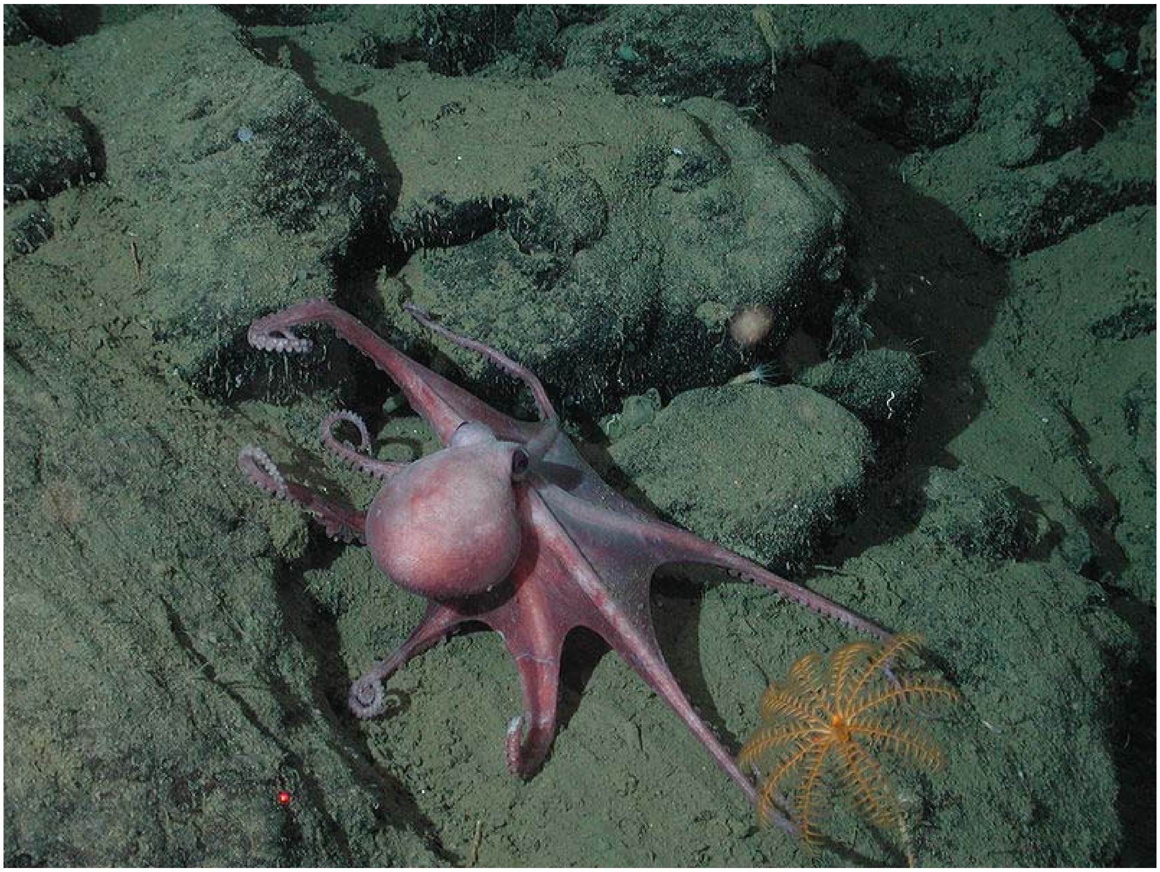
Bigfin reef squid (*Sepioteuthis lessoniana*)

Scientific classification [e]	
Kingdom:	Animalia
Phylum:	Mollusca
Class:	**Cephalopoda** Cuvier, 1797

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



Left: A pair of *Sepia officinalis* in shallow water
Right: *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

Left: An octopus opening a container with a screw cap
Right: 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

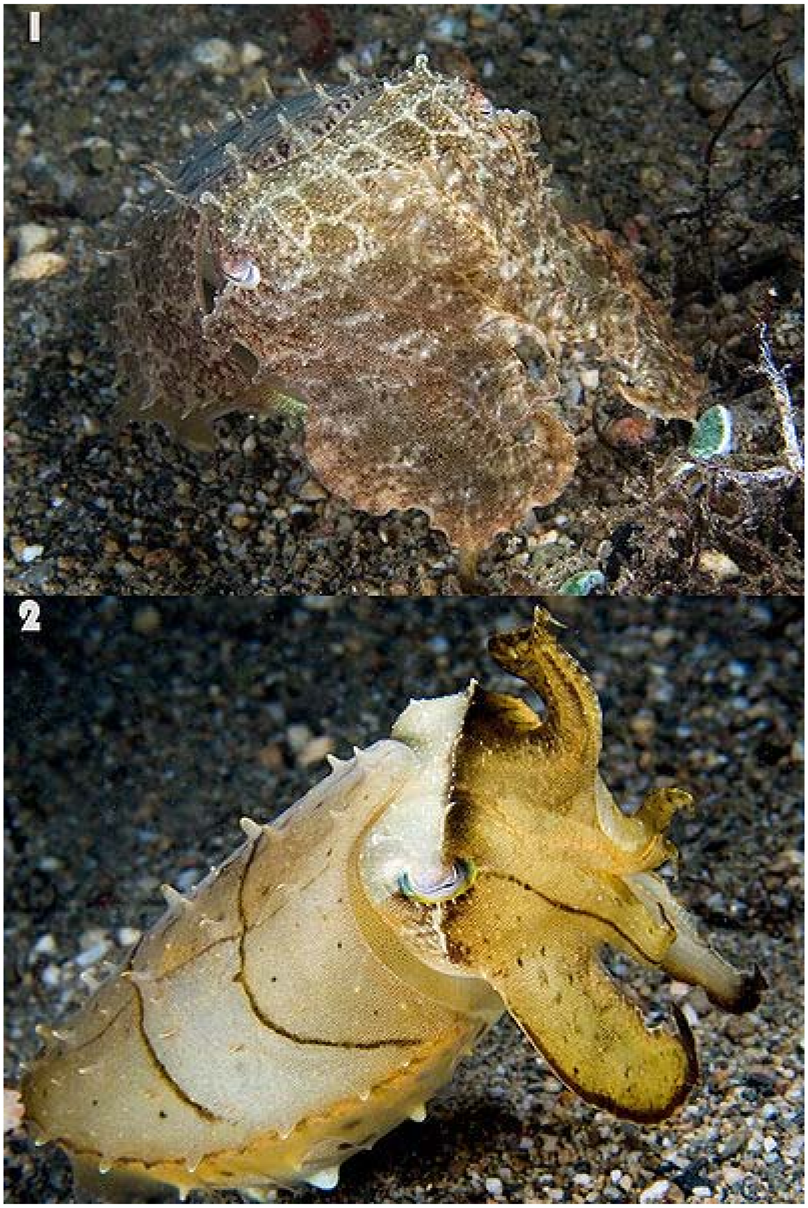
Most cephalopods rely on vision to detect predators and prey, and to communicate with one another. Consequently, cephalopod vision is acute: training experiments have shown that the common octopus can distinguish the brightness, size, shape, and horizontal or vertical orientation of objects. The morphological 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

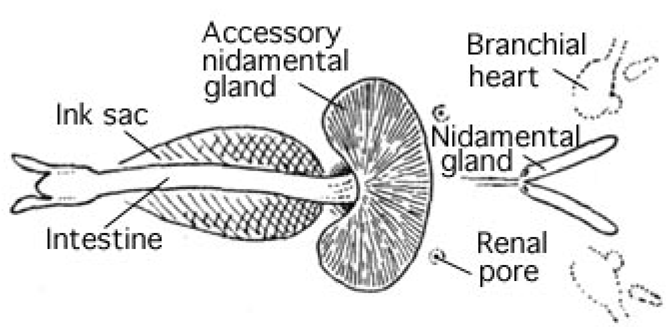
Colouration can be changed in milliseconds as they adapt to their environment, and the pigment cells are expandable by muscular contraction. Colouration is typically more pronounced in near-shore species than those living in the open ocean, whose functions tend to be restricted to camouflage by breaking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

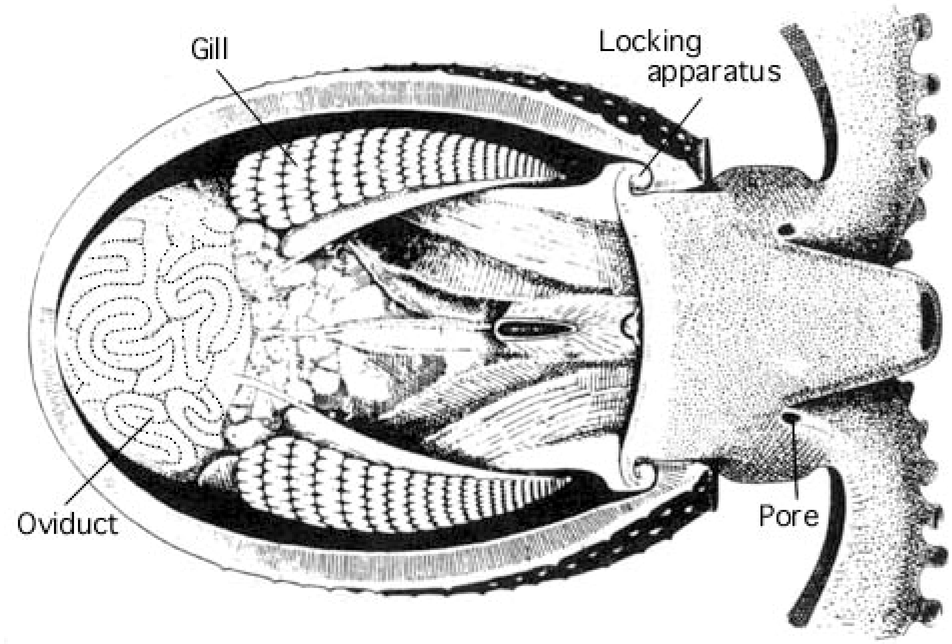
Ink

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

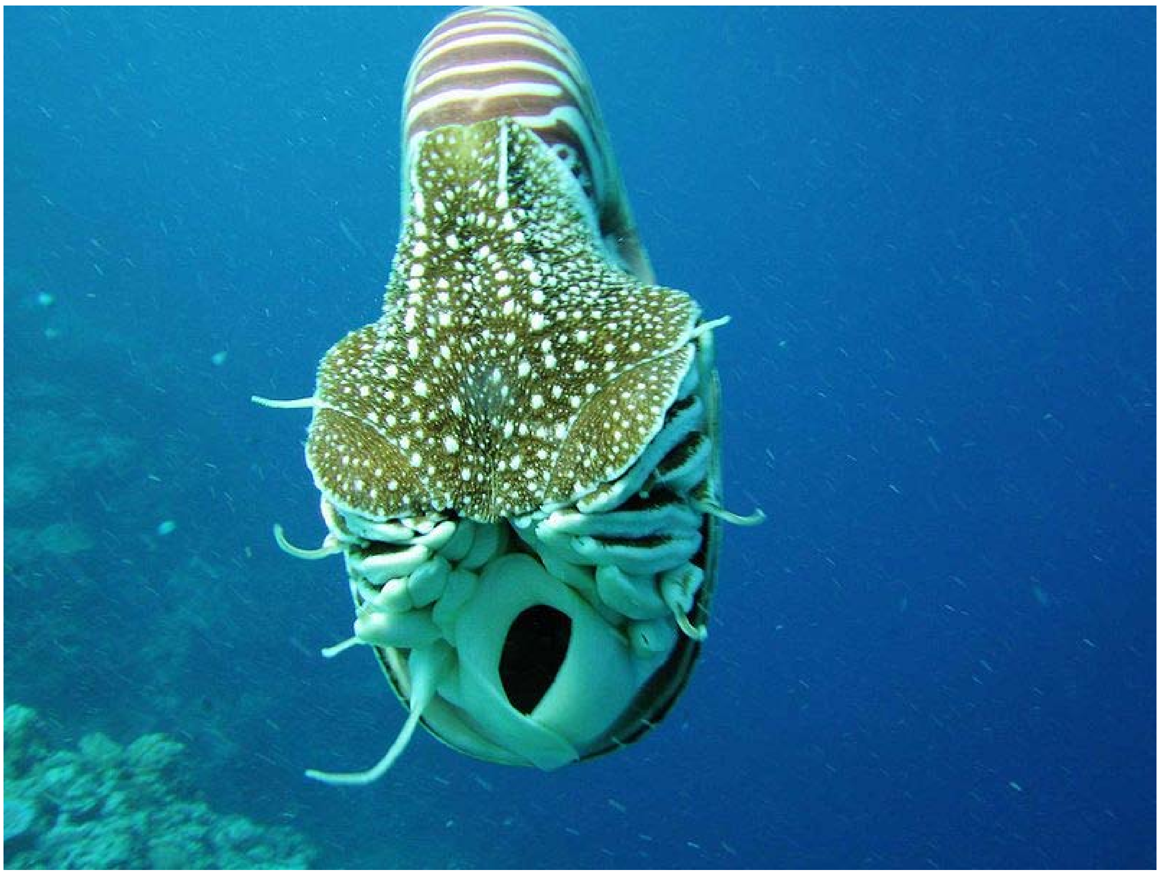
Cephalopods exchange gasses with the seawater by forcing water through their gills, which are attached to the roof of the organism. Water enters the mantle cavity on the outside of the gills, and the entrance of the mantle cavity closes. When the mantle contracts, water is forced through the gills, which 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.



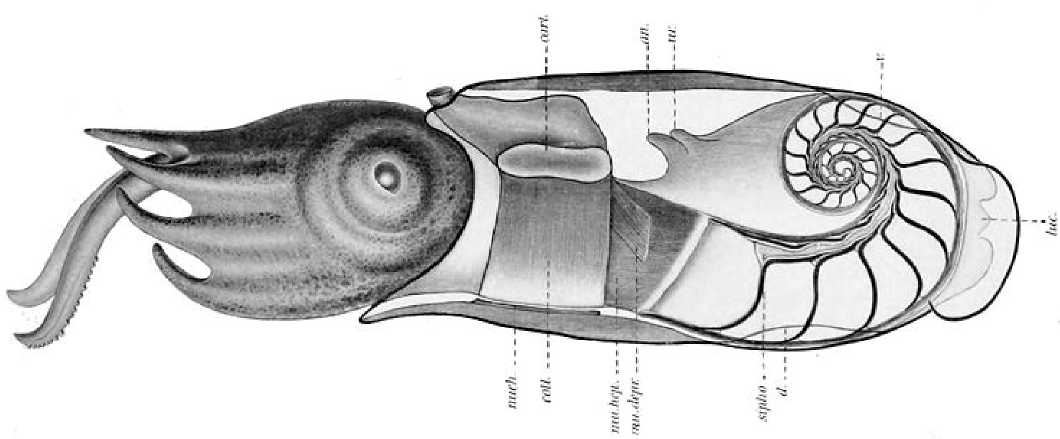
Nautilus belauensis seen from the front, showing the opening of the hyponome

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.

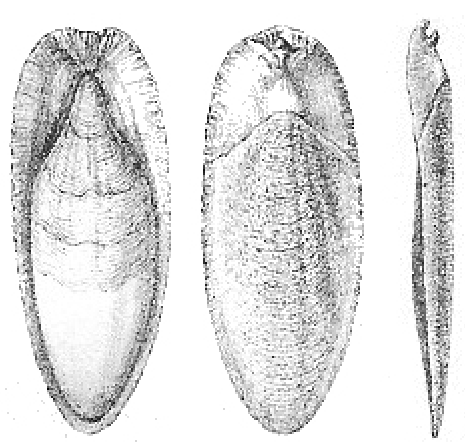
Some octopus species are also able to walk along the sea bed. Squids and cuttlefish can move short distances in any direction by rippling of a flap of muscle around the mantle.

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.

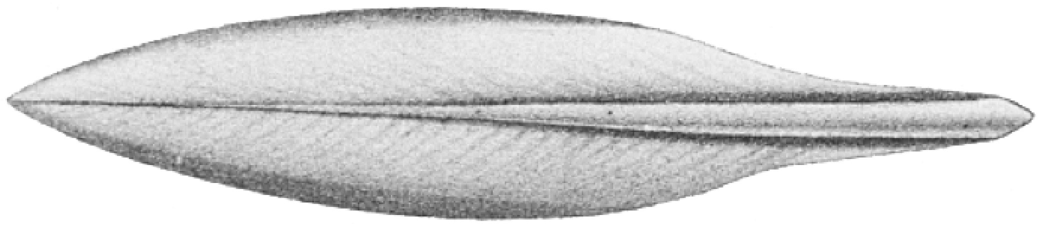
Shell



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



Cuttlebone of *Sepia officinalis*



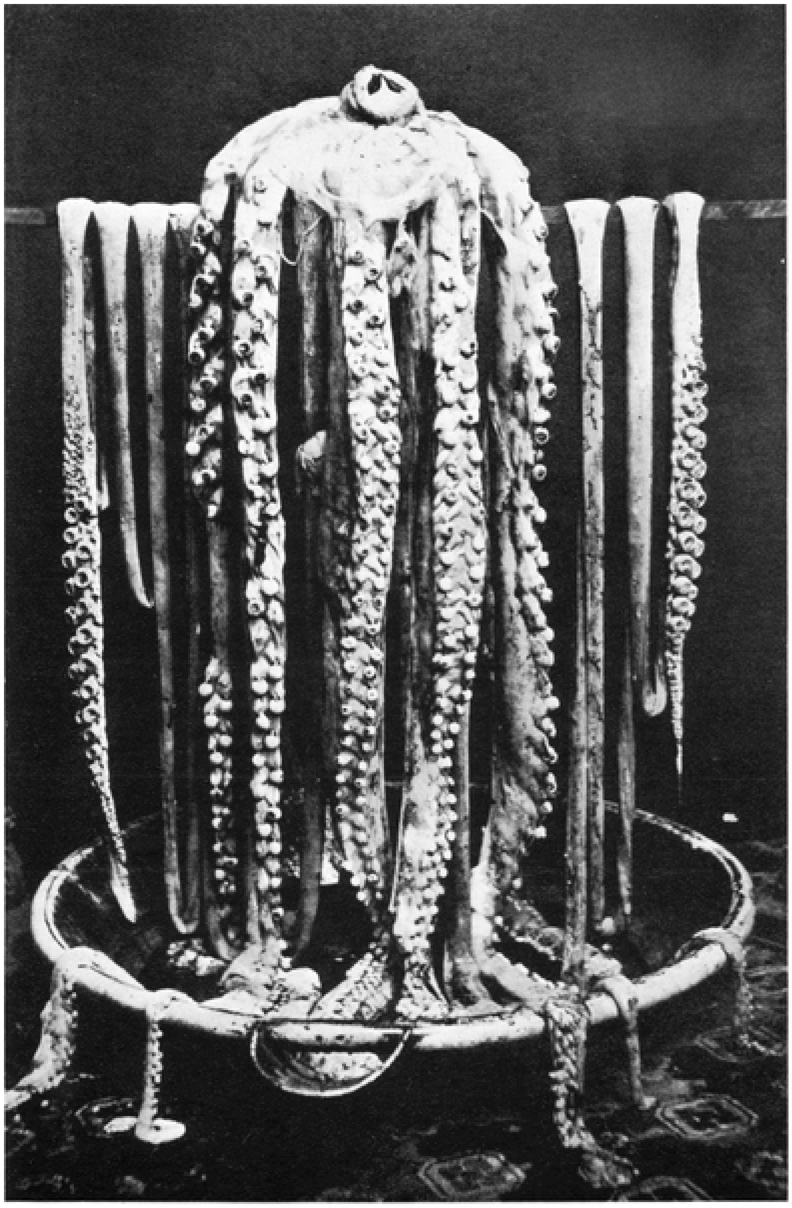
Gladius of *Sepioteuthis lessoniana*

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.



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

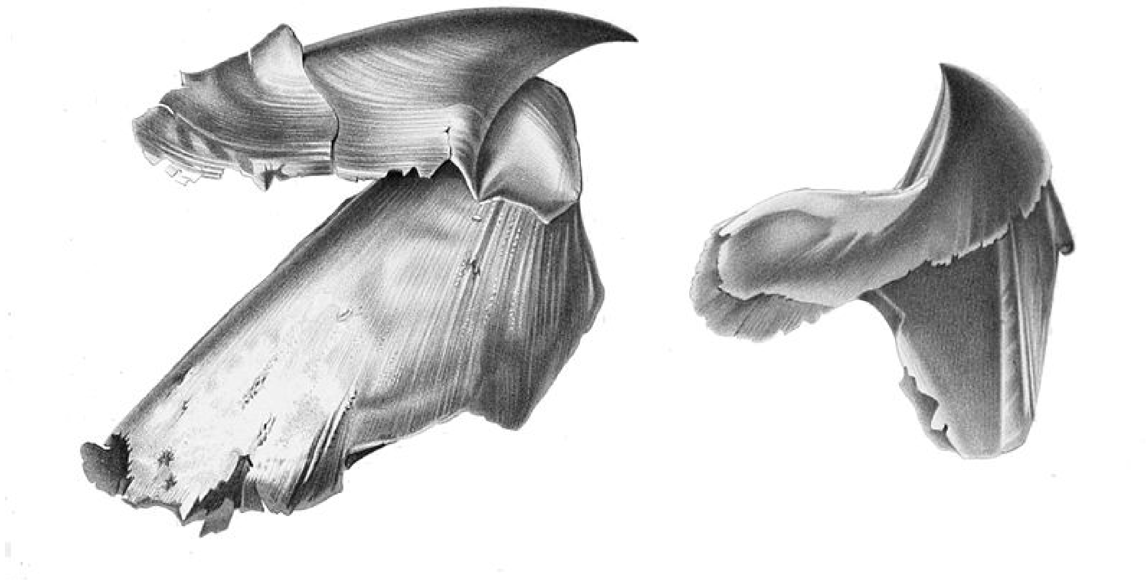
Head appendages

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

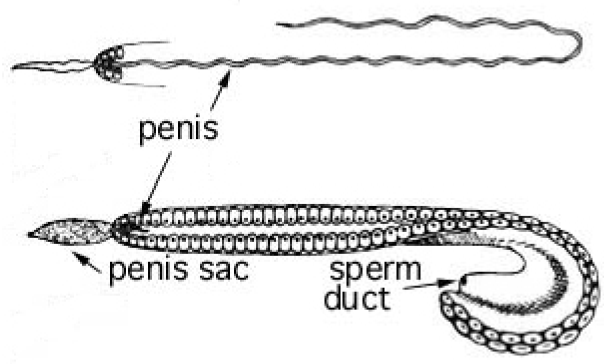
The handling of ammonia is thought to be important in shell formation in terrestrial molluscs, and in other nonmolluscan lineages.

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

Female *Argonauta argo* with eggcase and eggs



Detail of the hectocotylus of *Ocythoe tuberculata*

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

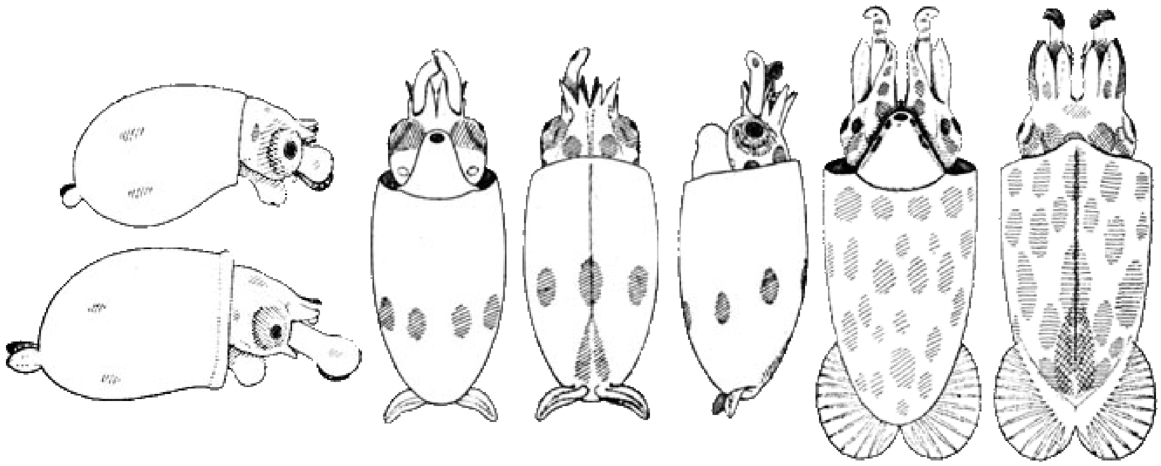
Unlike most other molluscs, cephalopods do not have a distinct larval stage. The fertilised ovum initially divides to produce a disc of germinal cells at one pole, with the yolk remaining at the opposite pole. The germinal disc grows to envelop and eventually absorb the yolk, forming the embryo. The 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.

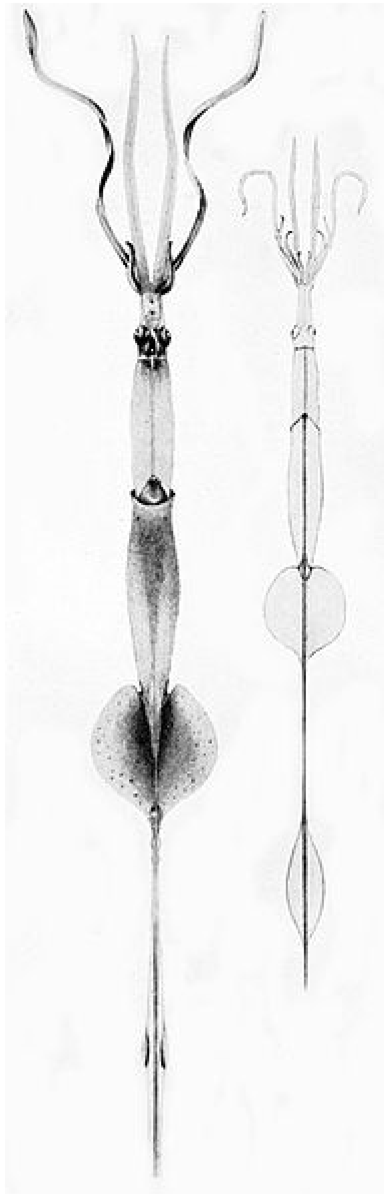
The shells develop from the ectoderm as an organic framework which is subsequently mineralised. In *Sepia*, which has an internal shell, the ectoderm forms an invagination whose pore is sealed off before this organic framework is deposited.

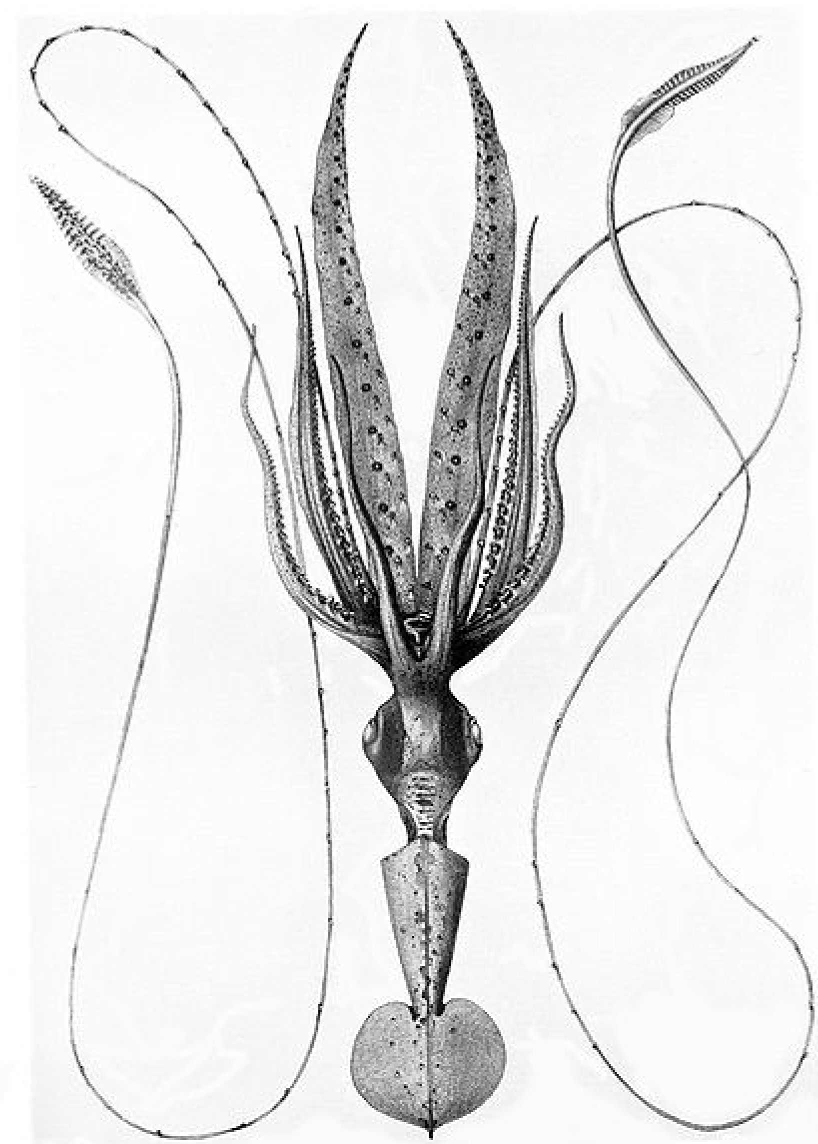
The gene *engrailed* is expressed first in the arms, funnel and optic vesicles, and is only later present in the tentacles and eyelids. It is expressed in embryonic stages 17–19 in all arm buds, and subsequently in the future-tentacles in stages 24–5, suggesting that it may serve a role in the differential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





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

Right: 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. Their position within the Mollusca is currently wide open to interpretation.

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

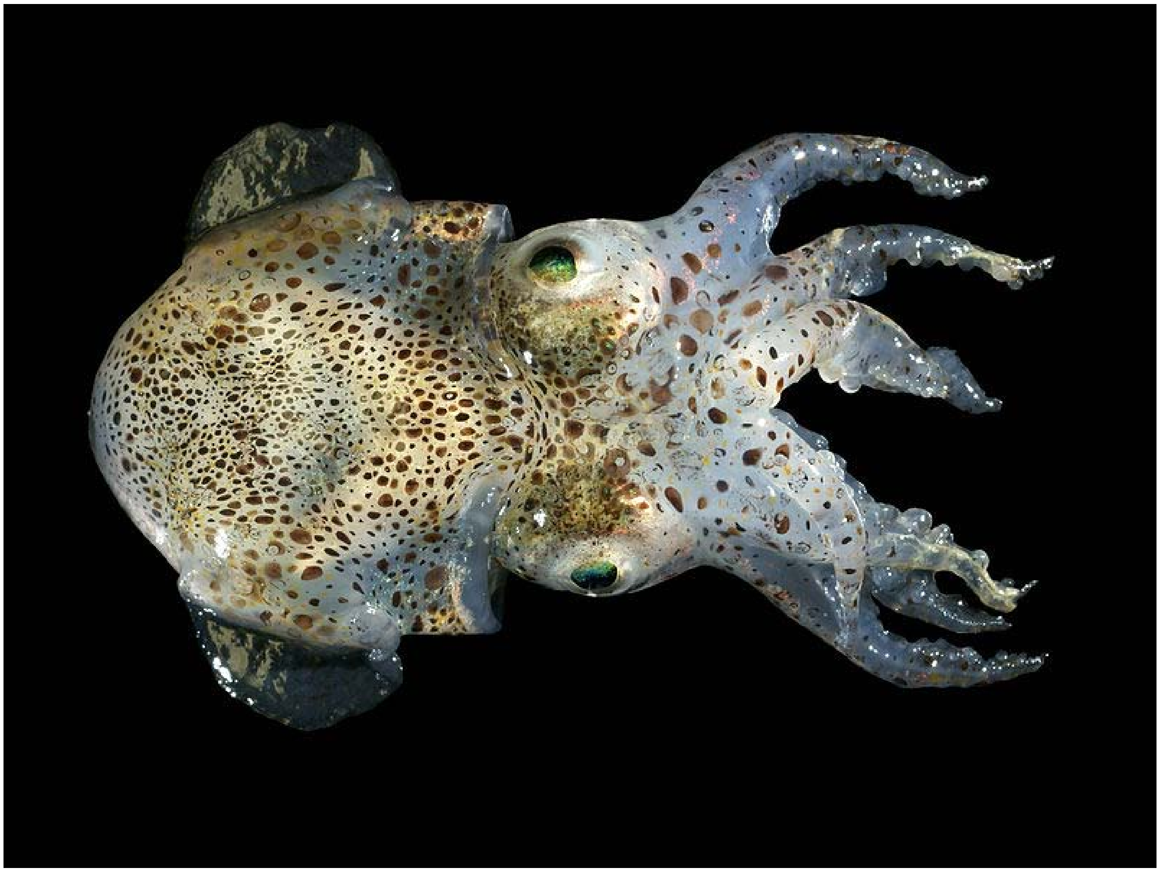
The internal phylogeny of the cephalopods is difficult to constrain; many molecular techniques have been adopted, but the results produced are conflicting. *Nautilus* tends to be considered an outgroup, with *Vampyroteuthis* forming an outgroup to other squid; however in one analysis the nautiloids, 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*)

European Squid (*Loligo vulgaris*)

Common Octopus (*Octopus 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

Holotype of *Ostenoteuthis siroi* from family Ostenoteuthidae.

A fossilised belemnite

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 † Basslerocerida (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, cephalopodsdecay 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 2

Octopus

Octopus	
	
The Common Octopus, *Octopus vulgaris*.	
Scientific classification [e]	
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

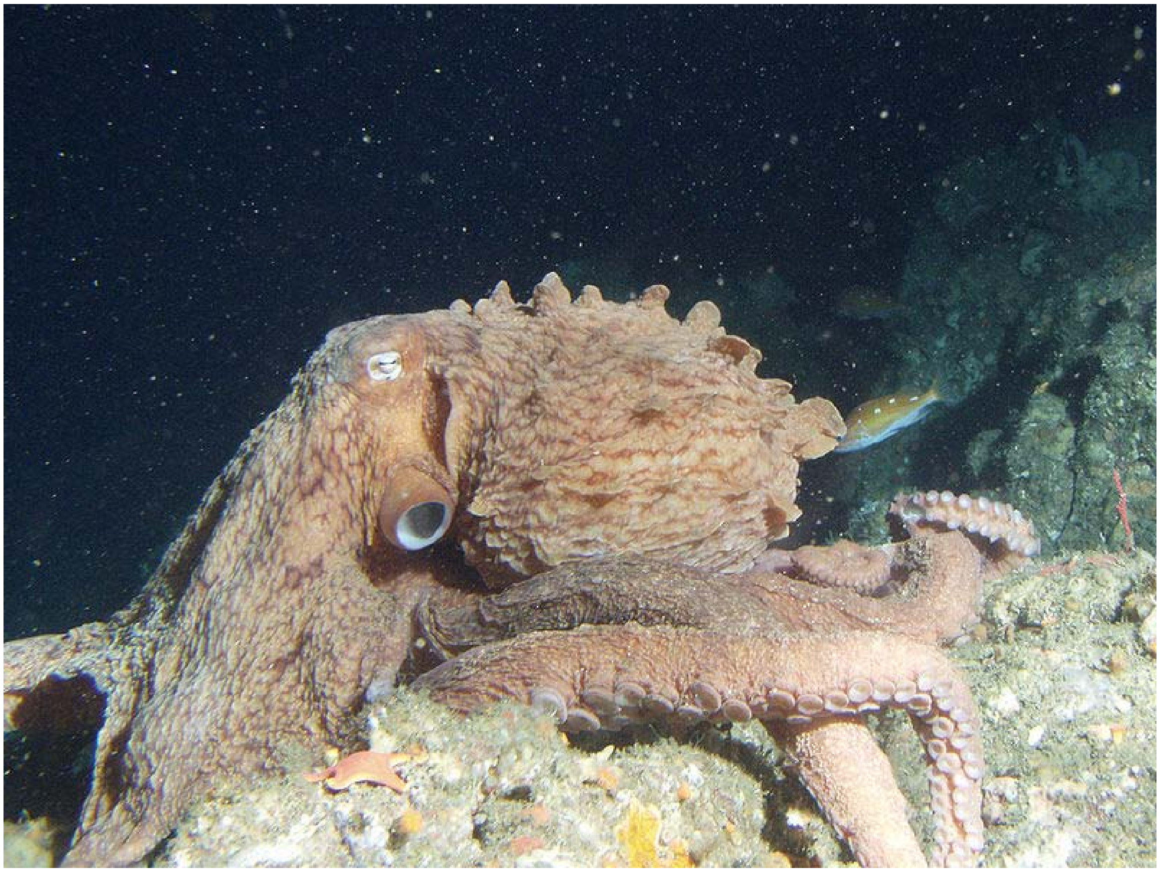
An octopus in its natural habitat

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.

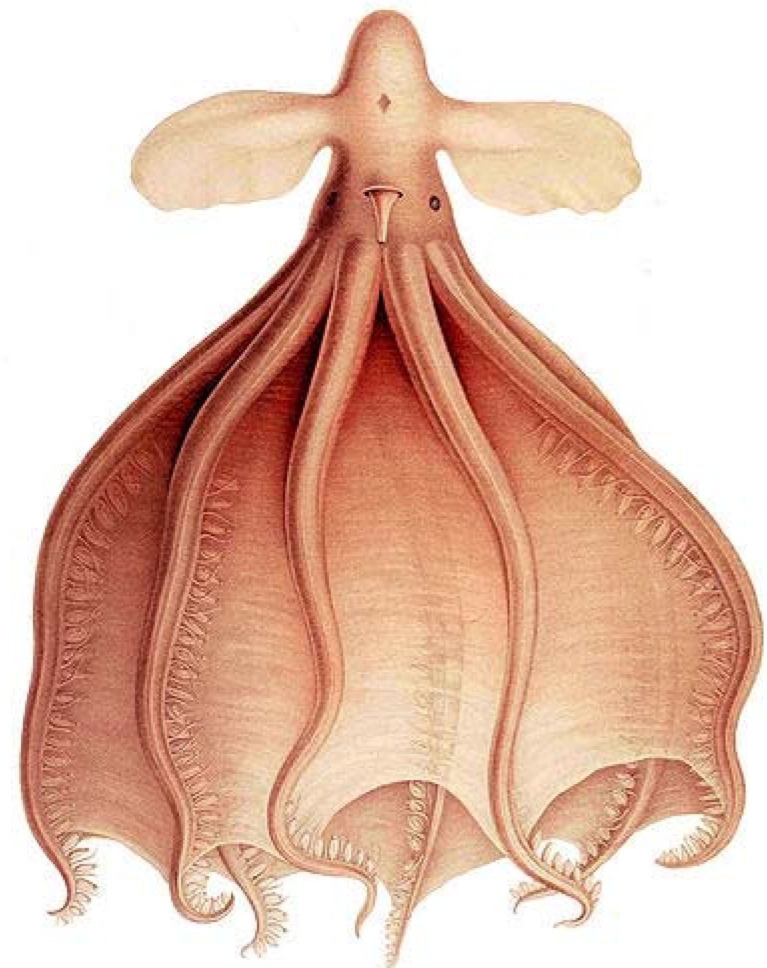
In literature

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

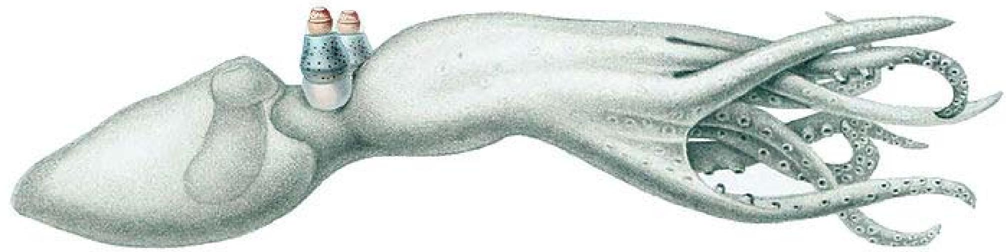
As a metaphor

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.

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

Chapter 3

Squid

Squid Temporal range: (at least) Late Cretaceous–Recent	
	
Bigfin Reef Squid, *Sepioteuthis lessoniana*	
Scientific classification [e]	
Kingdom:	Animalia
Phylum:	Mollusca
Class:	Cephalopoda
Superorder:	Decapodiformes
Order:	**Teuthida** A. Naef, 1916
Suborders	
†Plesioteuthididae (*incertae sedis*) Myopsina Oegopsina	

Squid are marine cephalopods of the order **Teuthida**, which comprises around 300 species. Like all other cephalopods, squid have a distinct head, bilateral symmetry, a mantle, and arms. Squid, like cuttlefish, have eight arms arranged in pairs and two, usually longer, tentacles. Squid are strong swimmers and certain species can 'fly' for short distances out of the water.

Modification from ancestral forms

Squid have differentiated from their ancestral molluscs such that the body plan has been condensed antero-posteriorly and extended dorso-ventrally. What before may have been the foot of the ancestor is modified into a complex set of tentacles and highly developed sense organs, including advanced eyes similar to those of vertebrates.

The ancestral shell has been lost, with only an internal gladius, or pen, remaining. The pen is a feather-shaped internal structure that supports the squid's mantle and serves as a site for muscle attachment. It is made of a chitin-like substance.

Anatomy

European Squid (*Loligo vulgaris*)

The main body mass is enclosed in the mantle, which has a swimming fin along each side. These fins, unlike in other marine organisms, are not the main source of locomotion in most species.

The skin is covered in chromatophores, which enable the squid to change color to suit its surroundings, making it effectively invisible. The underside is also almost always lighter than the topside, to provide camouflage from both prey and predator.

Under the body are openings to the mantle cavity, which contains the gills (ctenidia) and openings to the excretory and reproductive systems. At the front of the mantle cavity lies the siphon, which the squid uses for locomotion via precise jet propulsion. In this form of locomotion, water is sucked into the mantle cavity and expelled out of the siphon in a fast, strong jet. The direction of the siphon can be changed, to suit the direction of travel.

Inside the mantle cavity, beyond the siphon, lies the visceral mass, which is covered by a thin, membranous epidermis. Under this are all the major internal organs.

Nervous system

The giant axon, which may be up to 1 mm (0.04 inches) in diameter in some larger species, innervates the mantle and controls part of the jet propulsion system.

As cephalopods, squid exhibit relatively high intelligence among invertebrates. For example, groups of Humboldt squid hunt cooperatively, using active communication.

Reproductive system

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

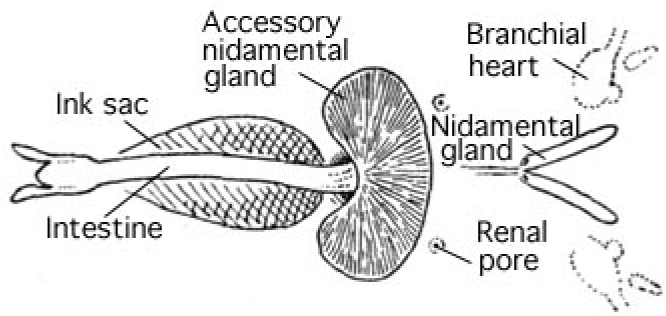
In females the ink sac is hidden from view by a pair of white nidamental glands, which lie anterior to the gills. There are also red-spotted accessory nidamental glands. Both organs are associated with food manufacture and shells for the eggs. Females also have a large translucent ovary, situated towards the posterior of the visceral mass.

Males do not possess these organs, but instead have a large testis in place of the ovary, and a spermatophoric gland and sac. In mature males, this sac may contain spermatophores, which are placed inside the female's mantle during mating.

Shallow water species of the continental shelf and epipelagic/mesopelagic zones are characterised by the presence of hectocotyli, specially modified arms used to fertilise the female's eggs. Most deep sea squid lack hectocotyli and have longer penises; Ancistrocheiridae and Cranchiinae are exceptions. Giant squid of the genus *Architeuthis* are unusual in that they possess both a large penis and modified arm tips, although it is uncertain whether the latter are used for spermatophore transfer. Penis elongation has been observed in the deep water species *Onykia ingens*; when erect, the penis may be as long as the mantle, head and arms combined. As such, 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.

Digestive system

Like all cephalopods, squid have complex digestive systems. The muscular stomach is found roughly in the midpoint of the visceral mass. From there, the bolus moves into the caecum for digestion. The caecum, a long, white organ, is found next to the ovary or testis. In mature squid, more priority is given to reproduction such that the stomach and caecum often shrivel up during the later life stages. Finally, food goes to the liver (or digestive gland), found at the siphon end, for absorption. Solid waste is passed out of the rectum. Beside the rectum is the ink sac, which allows a squid to rapidly discharge black ink into the mantle cavity.



Ventral view of the viscera of the female *Chtenopteryx sicula*

Cardiovascular system

Squid have three hearts. Two branchial hearts feed the gills, each surrounding the larger systemic heart that pumps blood around the body. Squid blood contains the copper-rich protein hemocyanin for transporting oxygen. The faintly greenish hearts are surrounded by the renal sacs - the main excretory system. The kidneys are difficult to identify and stretch from the hearts (located at the posterior side of the ink sac) to the liver. The systemic heart is made of three chambers, a lower ventricle and two upper auricles.

Head

The head end bears 8 arms and 2 tentacles, each a form of muscular hydrostat containing many suckers along the edge. These tentacles do not grow back if severed. In the mature male, one basal half of the left ventral tentacle is hectocotylised — and ends in a copulatory pad rather than suckers. It is used for intercourse.

The mouth is equipped with a sharp horny beak mainly made of chitin and cross-linked proteins, and is used to kill and tear prey into manageable pieces. The beak is very robust, but does not contain minerals, unlike the teeth and jaws of many other organisms, including marine species. Captured whales often have indigestible squid beaks in their stomachs. The mouth contains the radula (the rough tongue common to all molluscs except bivalvia and aplacophora).

The eyes, on either side of the head, each contain a hard lens. The image is focused by changing the position of the lens, as in a camera or telescope, rather than changing the shape of the lens, as in the human eye.

Squids appear to have limited hearing.

Size

Giant squid in Melbourne Aquarium

The majority are no more than 60 centimetres (24 in) long, although the giant squid may reach 13 metres (43 ft).

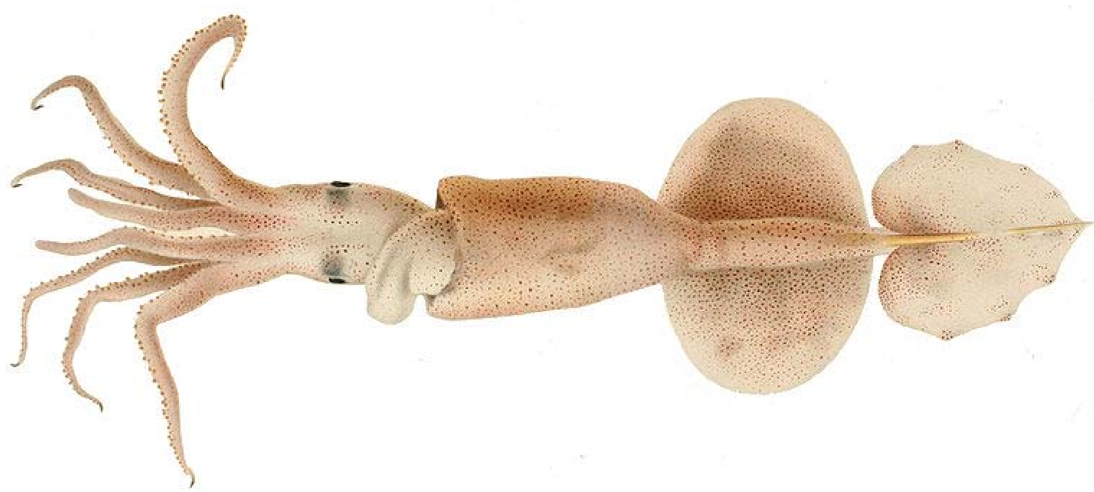
In 1978, sharp, curved claws on the suction cups of squid tentacles cut up the rubber coating on the hull of the USS *Stein*. The size suggested the largest squid known at the time.

In 2003, a large specimen of an abundant but poorly understood species, *Mesonychoteuthis hamiltoni* (the Colossal Squid), was discovered. This species may grow to 14 metres (46 ft) in length, making it the largest invertebrate. Squid have the largest eyes in the animal kingdom. Giant squid are featured in literature and folklore with a frightening connotation. The Kraken is a legendary tentacled monster possibly based on sightings of real giant squid.

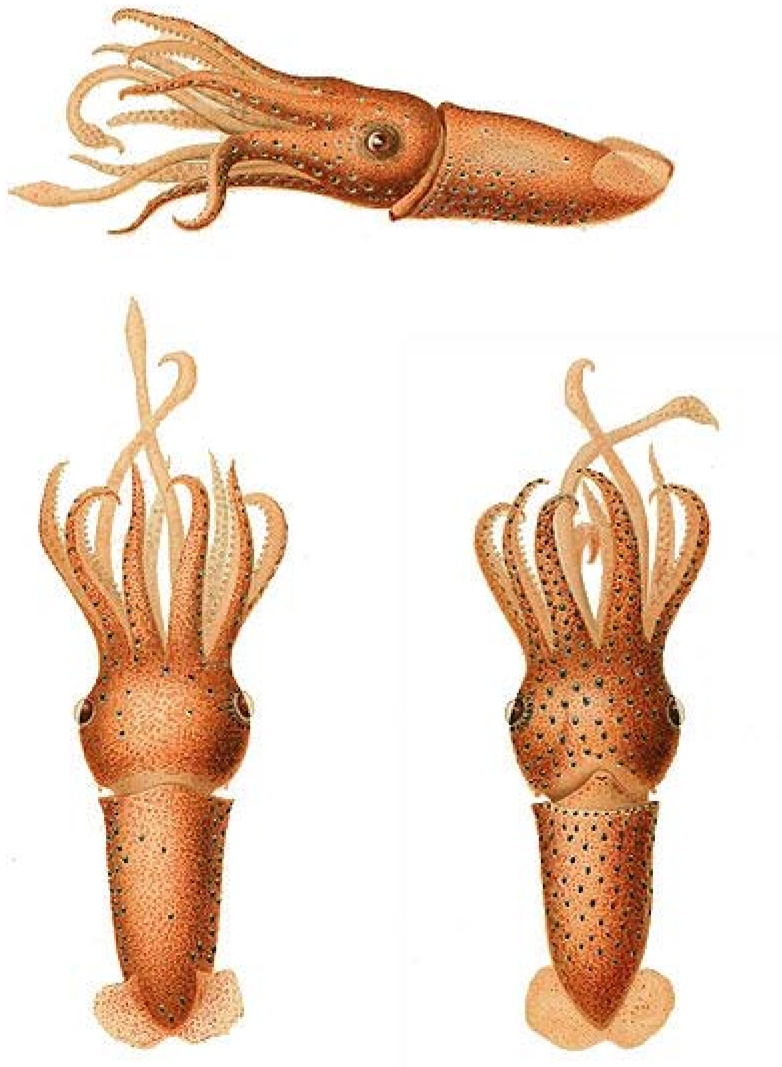
In February 2007, a New Zealand fishing vessel caught a Colossal Squid weighing 495 kilograms (1,090 lb) and measuring around 10 metres (33 ft) off the coast of Antarctica. This specimen represents the largest cephalopod to ever be scientifically documented.

Classification

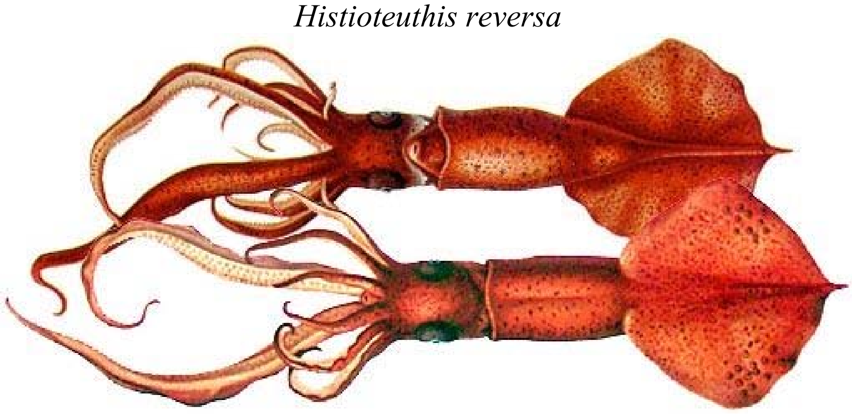
Bathyteuthis abyssicola



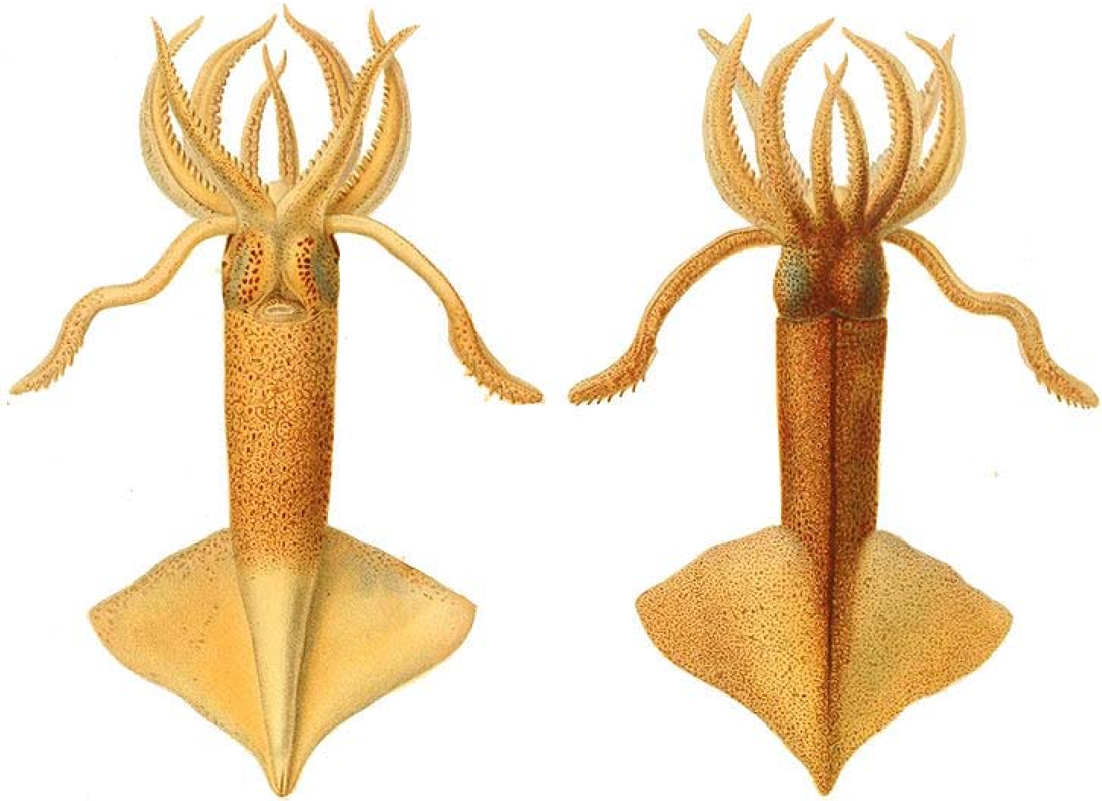
Grimalditeuthis bonplandi



Histioteuthis reversa



Mastigoteuthis flammea



Onychoteuthis banksii

Pterygioteuthis giardi

Squid are members of the class Cephalopoda, subclass Coleoidea, order **Teuthida**, of which there are two major suborders, Myopsina and Oegopsina (including giant squids like *Architeuthis dux*). Teuthida is the largest cephalopod order with around 300 species classified into 29 families.

The order Teuthida is a member of the superorder Decapodiformes (from the Greek for "ten legs"). Two other orders of decapodiform cephalopods are also called squid, although they are taxonomically distinct from Teuthida and differ recognizably in their gross anatomical features. They are the bobtail squid of order Sepiolida and the ram's horn squid of the monotypic order Spirulida. The vampire squid, however, is more closely related to the octopuses than to any squid.

CLASS CEPHALOPODA

- Subclass Nautiloidea: nautilus
- Subclass Coleoidea: squid, octopus, cuttlefish
    - Superorder Octopodiformes
    - Superorder Decapodiformes
        - ?Order †Boletzkyida
        - Order Spirulida: Ram's Horn Squid
        - Order Sepiida: cuttlefish
        - Order Sepiolida: bobtail squid

Order Teuthida: squid

- Family †Plesioteuthididae (*incertae sedis*)
- Suborder Myopsina
    - Family Australiteuthidae
    - Family Loliginidae: inshore, calamari, and grass squid
- Suborder Oegopsina
    - Family Ancistrocheiridae: Sharpear Enope Squid
    - Family Architeuthidae: giant squid
    - Family Bathyteuthidae
    - Family Batoteuthidae: Bush-club Squid
    - Family Brachioteuthidae
    - Family Chiroteuthidae
    - Family Chtenopterygidae: comb-finned squid

- Family Cranchiidae: glass squid
- Family Cycloteuthidae
- Family Enoploteuthidae
- Family Gonatidae: armhook squid
- Family Histioteuthidae: jewel squid
- Family Joubiniteuthidae: Joubin's Squid
- Family Lepidoteuthidae: Grimaldi Scaled Squid
- Family Lycoteuthidae
- Family Magnapinnidae: bigfin squid
- Family Mastigoteuthidae: whip-lash squid
- Family Neoteuthidae
- Family Octopoteuthidae
- Family Ommastrephidae: flying squid
- Family Pholidoteuthidae
- Family Promachoteuthidae
- Family Psychroteuthidae: Glacial Squid
- Family Pyroteuthidae: fire squid
- Family Thysanoteuthidae: rhomboid squid
- Family Walvisteuthidae

- Parateuthis tunicata *(*incertae sedis*)*

Commercial fishing

According to the FAO, the cephalopod catch for 2002 was 3,173,272 tonnes (6.995867×10^9 lb). Of this, 2,189,206 tonnes, or 75.8 percent, was squid. The following table lists the squid species fishery catches which exceeded 10,000 tonnes (22,000,000 lb) in 2002.

World squid catch in 2002

Species	Family	Common name	Catch tonnes	Percent
Loligo gahi	Loliginidae	Patagonian squid	24,976	1.1
Loligo pealei	Loliginidae	Longfin squid	16,684	0.8
Common squids nei	Loliginidae		225,958	10.3
Ommastrephes bartramii	Ommastrephidae	Neon flying squid	22,483	1.0
Illex argentinus	Ommastrephidae	Argentine shortfin squid	511,087	23.3
Dosidicus gigas	Ommastrephidae	Jumbo flying squid	406,356	18.6
Todarodes pacificus	Ommastrephidae	Japanese flying squid	504,438	23.0
Nototoda russloani	Ommastrephidae	Wellington Flying Squid	62,234	2.8
Squids nei	Various		414,990	18.6
Total squid			2,189,206	100.0

Chapter 4

Cuttlefish

Cuttlefish	
	
Sepia latimanus, East Timor	
Scientific classification [e]	
Kingdom:	Animalia
Phylum:	Mollusca
Class:	Cephalopoda
Superorder:	Decapodiformes
Order:	**Sepiida** Zittel, 1895
Suborders and Families	

- †Vasseuriina
  - †Vasseuriidae
  - †Belosepiellidae
- Sepiina
  - †Belosaepiidae
  - Sepiadariidae
  - Sepiidae

Cuttlefish are marine animals of the order **Sepiida**. They belong to the class Cephalopoda (which also includes squid, octopuses, and nautiluses). Despite their name, cuttlefish are not fish but molluscs. Recent studies indicate that cuttlefish are among the most intelligent invertebrates. Cuttlefish also have one of the largest brain-to-body size ratios of all invertebrates.

The origin of the word cuttlefish can be found in the old English term *cudele*, which derived in the 15th century from the Norwegian *koddi* (cushion, testicle) and the Middle German *kudel* (pouch), a good description of the cephalopod's shape. The Greco-Roman world valued the cephalopod as a source of the unique brown pigment that the creature releases from its siphon when it is alarmed. The word for it in Greek and Latin, *sepia* (later *seppia* in Italian), is used to refer to a brown pigment in English.

Cuttlefish have an internal shell (the cuttlebone), large W-shaped pupils, and eight arms and two tentacles furnished with denticulated suckers, with which they secure their prey. They generally range in size from 15 cm (5.9 in) to 25 cm (9.8 in), with the largest species, *Sepia apama*, reaching 50 cm (20 in) in mantle length and over 10.5 kg (23 lb) in weight.

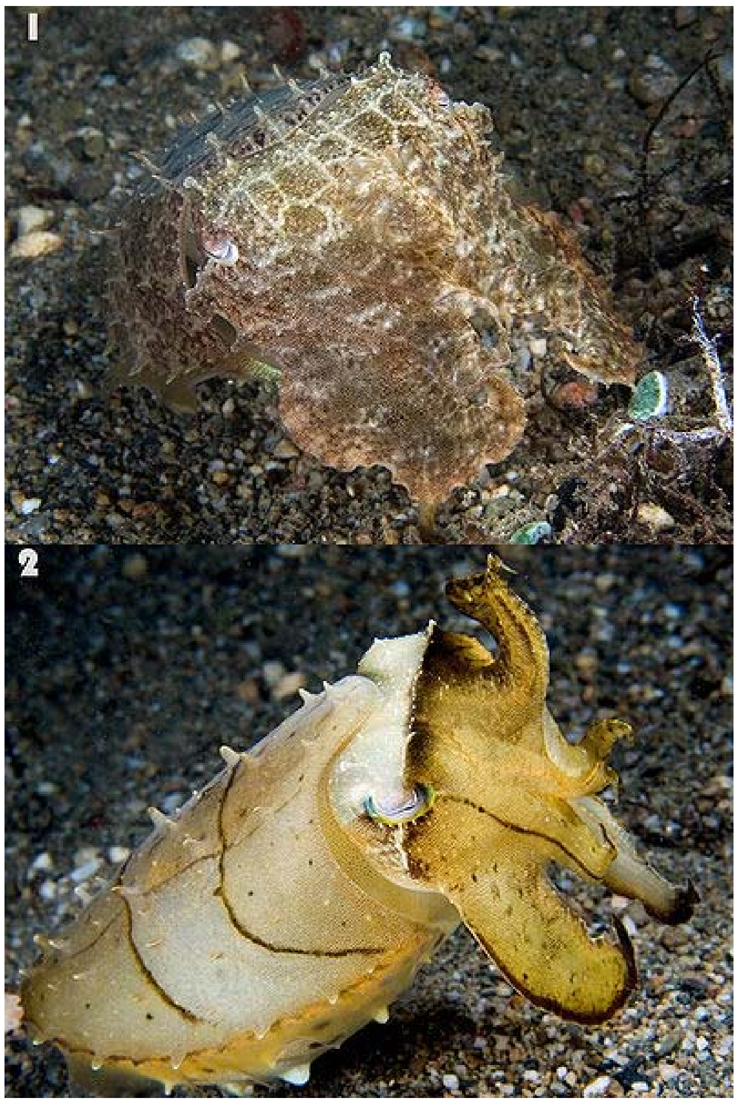
Cuttlefish eat small molluscs, crabs, shrimp, fish, octopuses, worms, and other cuttlefish. Their predators include dolphins, sharks, fish, seals and other cuttlefish. Their life expectancy is about one to two years.

A cuttlefish in its natural habitat

Physiology

Cuttlebone

Cuttlefish possess an internal structure called the cuttlebone, which is porous and is made of aragonite. This provides the cuttlefish with buoyancy. Buoyancy can be regulated by changing the gas-to-liquid ratio in the chambered cuttlebone via the ventral siphuncle. Each species has a distinct shape, size, and pattern of ridges or texture on the cuttlebone. The cuttlebone is unique to cuttlefish, one of the features that distinguishes them from their squid relatives. Jewelers and silversmiths traditionally use cuttlebones as moulds for casting small objects but they are probably better known as the tough material given to parakeets and other caged birds as a source of dietary calcium.



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

Skin

An infant cuttlefish protects itself with camouflage

Cuttlefish are sometimes referred to as the chameleon of the sea because of their remarkable ability to rapidly alter their skin color at will. Cuttlefish change color and light polarity to communicate to other cuttlefish and to camouflage themselves from predators.

This color-changing function is produced by groups of red, yellow, brown, and black pigmented chromatophores above a layer of reflective iridophores and leucophores, with up to 200 of these specialized pigment cells per square millimeter, which corresponds to about 359 DPI. The pigmented chromatophores have a sac of pigment and a large membrane that is folded when retracted. There are 6-20 small muscle cells on the sides which can contract to squash the elastic sac into a disc against the skin. Yellow chromatophores (xanthophores) are closest to the surface of the skin, red and orange are below (erythrophores), and brown or black are just above the iridophore layer (melanophores). The iridophores reflect blue and green light. Iridophores are plates of chitin or protein, which can reflect the environment around a cuttlefish. They are responsible for the metallic blues, greens, golds, and silvers often seen on cuttlefish. All of these cells can be used in combinations. For example, orange is produced by red and yellow chromatophores, while purple can be created by a red chromatophore and an iridophore. The cuttlefish can also use an iridophore and a yellow chromatophore to produce a brighter green. As well as being able to influence the color of light as it reflects off their skin, cuttlefish can also affect the light's polarization, which can be used to signal to other marine animals, many of which can also sense polarization.

Eyes

Close up of a cuttlefish eye

Cuttlefish eyes are among the most developed in the animal kingdom. The organogenesis of cephalopod eyes differs fundamentally from that of vertebrates like humans. Superficial similarities between cephalopod and vertebrate eyes are thought to be examples of convergent evolution. The cuttlefish pupil is a smoothly-curving W shape. Although they cannot see color, they can perceive the polarization of light, which enhances their perception of contrast. They have two spots of concentrated sensor cells on their retina (known as foveae), one to look more forward, and one to look more backward. The lenses, instead of being reshaped as they are in humans, are pulled around by reshaping the entire eye to change focus. Unlike the vertebrate eye, there is no blind spot as the optic nerve is positioned behind the retina.

Scientists have speculated that cuttlefish's eyes are fully developed before birth and start observing their surroundings while still in the egg. One team of French researchers has additionally suggested that cuttlefish prefer to hunt the prey they saw before hatching.

Circulation

The blood of a cuttlefish is an unusual shade of green-blue because it uses the copper-containing protein hemocyanin to carry oxygen instead of the red iron-containing protein hemoglobin that is found in vertebrates' blood. The blood is pumped by three separate hearts: two branchial hearts pump blood to the cuttlefish's pair of gills (one heart for each), and the third pumps blood around the rest of the body. Cuttlefish blood must flow more rapidly than most other animals because hemocyanin carries substantially less oxygen than hemoglobin.

Ink

Cuttlefish have ink, like squid and octopuses, which they use to help evade predators.

Toxicity

Like octopuses and some squid, all cuttlefish have bacterially-produced neurotoxins in their saliva.

Pfeffer's Flamboyant Cuttlefish from Sipadan, Malaysia

The muscles of Pfeffer's Flamboyant Cuttlefish contain a highly toxic compound that is yet to be identified. Mark Norman with Museum Victoria in Victoria, Australia, has shown the toxin to be as lethal as that of a fellow cephalopod, the blue-ringed octopus.

Ecology

Diet

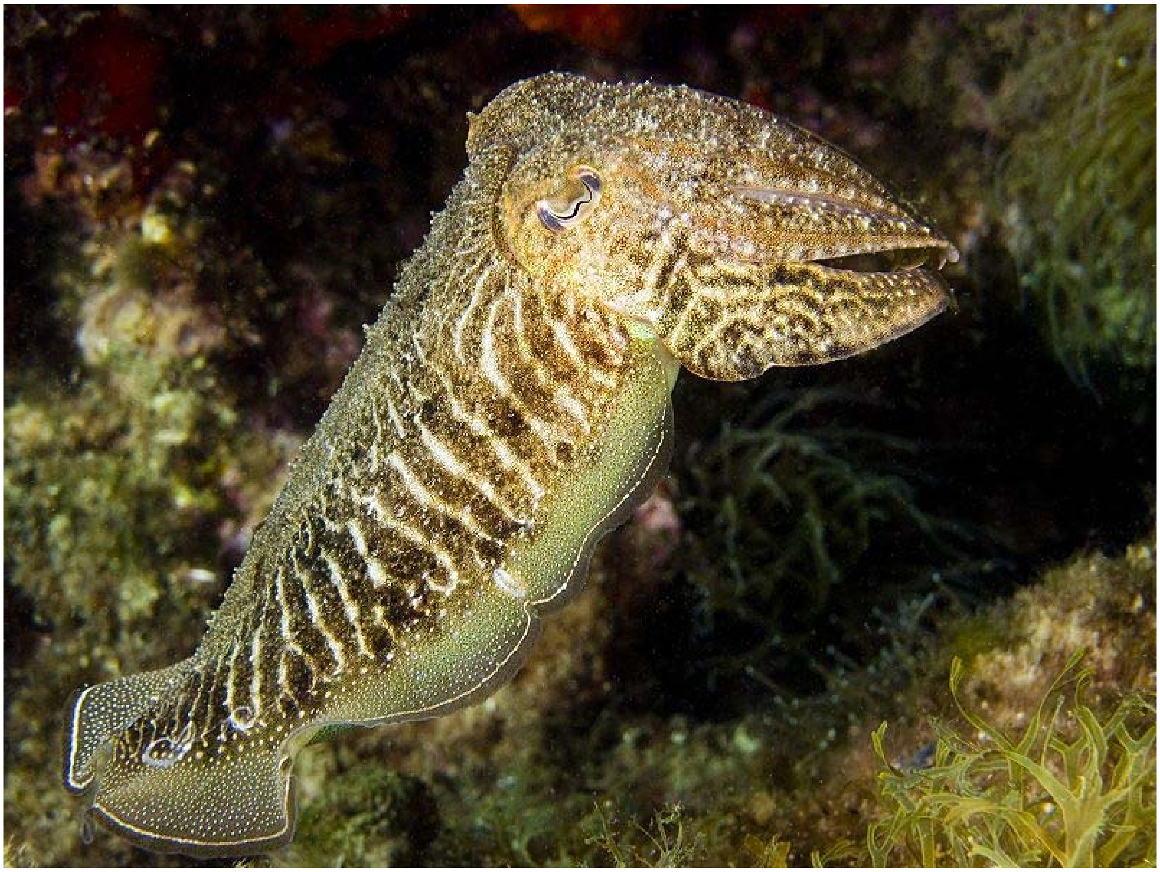
The preferred diet of the cuttlefish is crabs and fish.

The cuttlefish uses its camouflage to hunt and sneak up on its prey. When it gets close enough, it opens its eight arms and shoots out two long feeding tentacles. On the end of each is a pad covered in suckers that grabs and pulls prey toward its beak.

Range and habitat

Family Sepiidae, which contains all cuttlefish, inhabit tropical/temperate ocean waters. They are mostly shallow-water animals although they are known to go to depths of about 600 metres (2,000 ft). They have an unusual biogeographic pattern: totally absent from the Americas, but present along the coasts of east and south Asia, western Europe, the Mediterranean, as well as all coasts of Africa and Australia. By the time the family evolved, ostensibly in the Old World, the north Atlantic possibly had become too cold and deep for these warm water species to cross.

Taxonomy



Sepia officinalis from Turkish waters

There are over 120 species of cuttlefish currently recognised, grouped into 5 genera. Sepiadariidae contains seven species and 2 genera; all the rest are in Sepiidae.

- CLASS CEPHALOPODA
  - Subclass Nautiloidea: nautilus
  - Subclass Coleoidea: squid, octopus, cuttlefish
    - Superorder Octopodiformes
    - Superorder Decapodiformes
      - ?Order †Boletzkyida
      - Order Spirulida: Ram's Horn Squid
      - Order **Sepiida**: cuttlefish
        - Suborder †Vasseuriina
          - Family †Vasseuriidae
          - Family †Belosepiellidae
        - Suborder Sepiina
          - Family †Belosaepiidae

        - Family Sepiadariidae
        - Family Sepiidae
    - Order Sepiolida: bobtail squid
    - Order Teuthida: squid

Chapter 5

Nautiloid

Nautiloids **Temporal range: 495–0 Ma** **Late Cambrian – Recent**	
 *Orthoceras*	
Scientific classification [e]	
Kingdom:	Animalia
Phylum:	Mollusca
Class:	Cephalopoda
Subclass:	**Nautiloidea** Agassiz, 1847
Orders	

Palcephalopoda

- †Plectronocerida
- †Ellesmerocerida
- †Actinocerida
- †Pseudorthocerida
- †Ascocerida
- †Endocerida
- †Tarphycerida
- †Oncocerida
- †Discosorida

- Nautilida

Neocephalopoda (in part)

- †Orthocerida
- †Lituitida
- †Bactritida

Nautiloids are a large and diverse group of marine cephalopods (Mollusca) belonging to the subclass **Nautiloidea** that began in the Late Cambrian and are represented today by the living *Nautilus*. Nautiloids flourished during the early Paleozoic era, where they constituted the main predatory animals, and developed an extraordinary diversity of shell shapes and forms. Some 2,500 species of fossil nautiloids are known, but only a handful of species survive to the present day.

Taxonomic relationships

Nautiloids are among the group of animals known as cephalopods, an advanced class of mollusks which also includes ammonoids, belemnites and modern coleoids such as octopus and squid. Other mollusks include gastropods, scaphopods and pelecypods.

Traditionally, the most common classification of the cephalopods has been a three-fold division (by Bather, 1888), into the nautiloids, ammonoids, and coleoids.

Cladistically speaking, nautiloids are a paraphyletic assemblage united by shared primitive (plesiomorphic) features not found in derived cephalopods. In other words, they are a grade group that is thought to have given rise to both ammonoids and coleoids, and are defined by the exclusion of both those descendent groups. Both ammonoids and coleoids have traditionally been assumed to have descended from bactritids, which in turn arose from straight-shelled orthocerid nautiloids.

The ammonoids (a group which includes the ammonites and the goniatites) are extinct cousins of the nautiloids that evolved early in the Devonian period, some 400 million years ago.

Some workers apply the name Nautiloidea to a more exclusive group, called Nautiloidea *sensu stricto*. This taxon consists only of those orders that are clearly related to the modern nautilus. The membership assigned varies somewhat from author to author, but usually includes Tarphycerida, Oncocerida, and Nautilida.

Characteristics

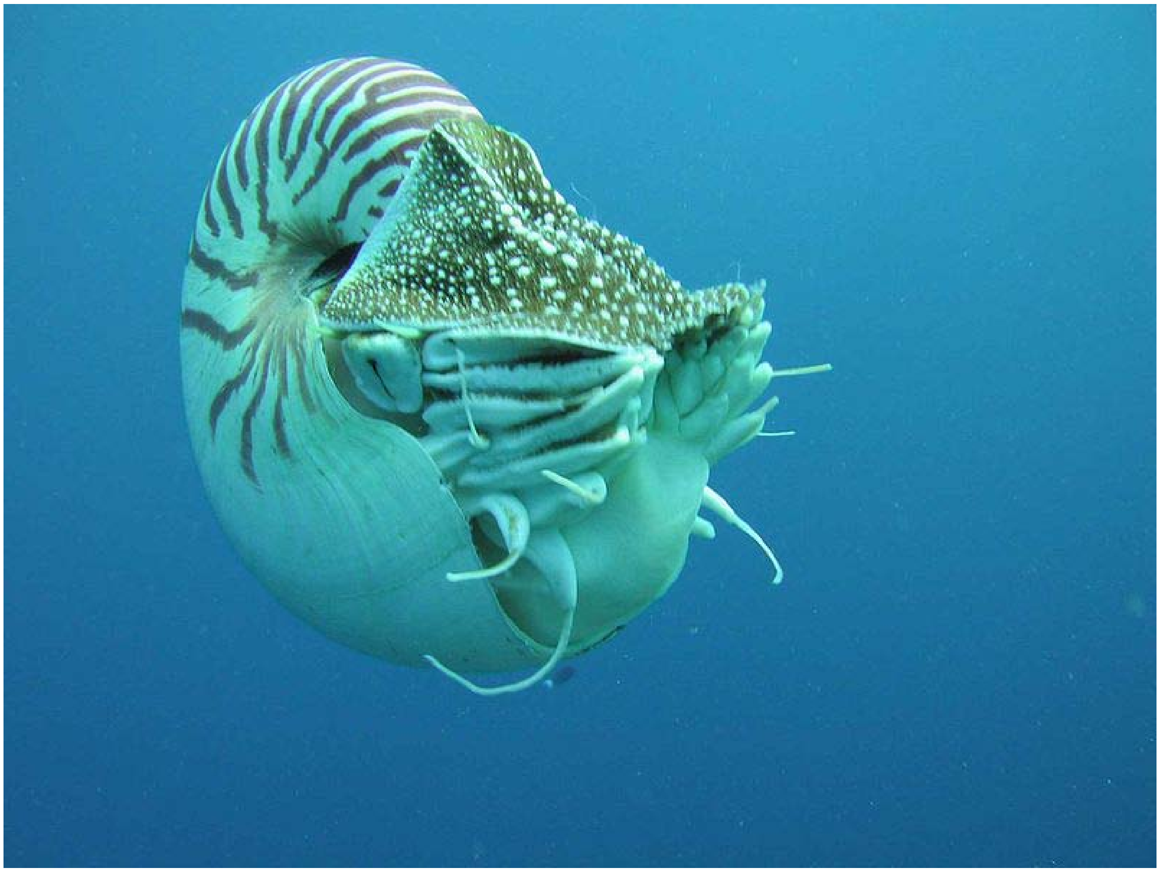
The subclass nautiloidea, in the broad original sense, is distinguished by two main characters, simple concave septa, concave in the forward direction, that produce generally simple sutures, and a siphuncle in which the septal necks point to the rear, i.e. is retrosiphonate, throughout the ontogeny of the animal.

The septa between the chambers (camerae) of the phragmocone (the chambered part of the shell) are formed during growth spurts of the animal. At that time the rear of the mantle secretes a new septum adding another chamber while the more forward part adds on to the shell. The body of the animal, its viscera, continues to occupy the last chamber of the shell – the living chamber.

The septa are perforated by the siphuncle, which runs through each of the internal chambers of the shell. Surrounding the fleshy tube of the siphuncle are structures made of Aragonite (a polymorph of Calcium Carbonate – which during fossilisation is converted to Calcite): septal necks and connecting rings. Some of the earlier nautiloids deposited calcium carbonate in the empty chambers (called *cameral deposits*) or within the siphuncle (*endosiphuncular deposits*), a process which may have been connected with controlling buoyancy. The nature of the siphuncle and its position within the shell are important in classifying nautiloids.

Sutures (or suture lines) are visible as a series of narrow wavy lines on the surface of the shell, and they appear where each septum contacts the wall of the outer shell. The sutures of the nautiloids are simple in shape, being either straight or slightly curved. This is different from the "zigzag" sutures of the goniatites and the highly complex sutures of the ammonites.

Modern nautiloids



Nautilus belauensis

Much of what is known about the extinct nautiloids is based on what we know about modern nautiluses, such as the Chambered Nautilus, which is found in the southwest Pacific Ocean from Samoa to the Philippines, and in the Indian Ocean off the coast of Australia. It is not usually found in waters less than 100 meters deep and may be found as far down as 500 to 700 meters (2,300 ft).

Nautiluses are free swimming animals that possess a head with two simple lens-free eyes and arms (or tentacles). They have a smooth shell over a large body chamber, which is divided into subchambers filled with an inert gas (similar to the composition of atmospheric air, but with more nitrogen and less oxygen) making the animal neutrally buoyant in the water. As many as 90 tentacles are arranged in two circles around the mouth. The animal is predatory, and has jaws which are horny and beak-like, allowing it to feed on crustaceans.

Empty nautilus shells may drift a considerable distance and have been reported from Japan, India and Africa. Undoubtedy the same applies to the shells of fossil nautiloids, the gas inside the shell keeping it buoyant for some time after the animal's death, allowing the empty shell to be carried some distance from where the animal lived before finally sinking to the seafloor.

Nautiluses propel themselves by jet propulsion, expelling water from an elongated funnel called the hyponome, which can be pointed in different directions to control their movement. Unlike the belemnites and other cephalopods, modern nautiluses do not have an ink sac, and there is no evidence to suggest that the extinct forms possessed one either. Furthermore, unlike the extinct ammonoids, the modern nautilus lacks any sort of plate for closing its shell. With one exception, no such plate has been found in any of the extinct nautiloids either.

The coloration of the shell of the modern nautilus is quite prominent, and, although somewhat rarely, the shell coloration has been known to be preserved in fossil nautiloids. They often show color patterns only on the dorsal side, suggesting that the living animals swam horizontally.

Fossil record

Fossil nautiloid *Trilacinoceras* from the Ordovician of China.

Fossil orthoconic nautiloid from the Ordovician of Kentucky; an internal mold showing siphuncle and half-filled camerae, both encrusted.

Nautiloids are often found as fossils in early Palaeozoic rocks (less so in more recent strata). The shells of fossil nautiloids may be either straight (i.e., orthoconic as in *Orthoceras* and *Rayonnoceras*), curved (as in *Cyrtoceras*) coiled (as in *Cenoceras*), or rarely a helical coil (as in *Lorieroceras*). Some species' shells—especially in the late Paleozoic and early Mesozoic—are ornamented with spines and ribs, but most have a smooth shell.

The shells are formed of aragonite, although the cameral deposits may consist of primary calcite.

The rocks of the Ordovician period in the Baltic coast and parts of the United States contain a variety of nautiloid fossils, and specimens such as *Discitoceras* and *Rayonnoceras* may be found in the limestones of the Carboniferous period in Ireland. The marine rocks of the Jurassic period in Britain often yield specimens of *Cenoceras*, and nautiloids such as *Eutrephoceras* are also found in the Pierre Shale formation of the Cretaceous period in the north-central United States.

Specimens of the Ordovician nautiloid *Endoceras* have been recorded measuring up to 3.5 meters (13 ft) in length, and *Cameroceras* is (somewhat doubtfully) estimated to have reached 11 meters (36 ft). These large nautiloids must have been formidable predators of other marine animals at the time they lived.

In some localities, such as Scandinavia and Morocco, the fossils of orthoconic nautiloids accumulated in such large numbers that they form *Orthoceras limestones*. Although the term *Orthoceras* now only refers to a Baltic coast Ordovician genus, in prior times it was employed as a general name given to all straight-shelled nautiloids that lived from the Ordovician to the Triassic periods (but were most common in the early Paleozoic era.

Evolutionary history

Nautiloids are first known from the late Cambrian Fengshan Formation of northeastern China, where they seem to have been quite diverse (at the time this was a warm shallow sea rich in marine life). However, although four orders have been proposed from the 131 species named, there is no certainty that all of these are valid, and indeed it is likely that these taxa are seriously oversplit.

Most of these early forms died out, but a single family, the Ellesmeroceratidae, survived to the early Ordovician, where it ultimately gave rise to all subsequent cephalopods. In the Early and Middle Ordovician the nautiloids underwent an evolutionary radiation. Some eight new orders appeared at this time, covering a great diversity of shell types and structure, and ecological lifestyles.

Nautiloids remained at the height of their range of adaptations and variety of forms throughout the Ordovician, Silurian, and Devonian periods, with various straight, curved and coiled shell forms coexisting at the same time. Several of the early orders became extinct over that interval, but others rose to prominence.

Nautiloids began to decline in the Devonian, perhaps due to competition with their descendants and relatives the Ammonoids and Coleoids, with only the Nautilida holding their own (and indeed increasing in diversity). Their shells became increasingly tightly coiled, while both numbers and variety of non-nautilid species continued to decrease throughout the Carboniferous and Permian.

The massive extinctions at the end of the Permian were less damaging to nautiloids than to other taxa and a few groups survived into the early Mesozoic, including pseudorthocerids, bactritids, nautilids and possibly orthocerids. The last straight-shelled forms were long thought to have disappeared at the end of the Triassic, but a possible orthocerid has been found in Cretaceous rocks. Apart from that exception, only a single nautiloid suborder, the Nautilina, continued throughout the Mesozoic, where they co-existed quite happily with their more specialised ammonoid cousins. Most of these forms differed only slightly from the modern nautilus. They had a brief resurgence in the early Tertiary (perhaps filling the niches vacated by the ammonoids in the end Cretaceous extinction), and maintained a worldwide distribution up until the middle of the Cenozoic Era. With the global cooling of the Miocene and Pliocene, their geographic distribution shrank and these hardy and long-lived animals declined in diversity again. Today there are only six living species, all belonging to two genera, *Nautilus* (the pearly nautilus), and *Allonautilus*.

Classification

Classifications vary and a subject to change as new information is found and in accordance with the perspective of various workers. The taxonomy of the Taxo Box is one such scheme,Teichert's 1988 classification is another, that of Teichert et al. 1964 in the Treatise Part K , still another.

Wade (1988) divided the subclass Nautiloidea into 6 superorders, combing orders that are phylogenetically related. They are the:

- Plectronoceratoidea = Plectronocerida, Protactinocerida, Yanhecerida,and Ellesmerocerida.
- Endoceratoidea = Endocerida
- Orthoceratoidea: = Orthocerida, Ascocerida, and Pseudorthocerida (the Orthoceratoidea of Kroger 1007)
- Nautilitoidea = Tarphycerida, Oncocerida, and Nautilida.
- Actinoceratoidea = Actinocerida
- Discosoritoidea = Discosorida

Three of them are established as equivalent places to put the Endocerida, Actinocerida, and Discosorida. Three unite related orders that share a common ancestor and form a branch of the nautiloid taxonomic tree; the Plectronoceratoidea which are mostly small Cambrian forms that include the ancestors of subsequent stocks; the Orthoceratoidea which unites different primarily orthoconic orders of which one is the source for the Bacritida and Ammonoidea; and the Nautilitoidea which includes the first coilded cephalopods, the Tarphycerida, as well as the Nautilida which includes the recent Nautilus

Another order, the Bactritida, which are derived from the Orthocerida are sometimes included with the Nautiloidea, sometimes with the ammonoidea, and sometimes are placed in a subclass of their own, the Bactritoidea.

Recently some workers in the field have come to recognize the Dissidocerida as a distinct order, along with the Pseudorthocerida, both previously included in the Orthoceridaas subtaxa.

A more recent interpretation (Engeser 1997-1998) suggests that nautiloids, and indeed cephalopods in general, fall into two main groups, the Palcephalopoda (including all the nautiloids except Orthocerida and Ascocerida) and the Neocephalopoda (the rest of the cephalopods).

Chapter 6

Nautilus

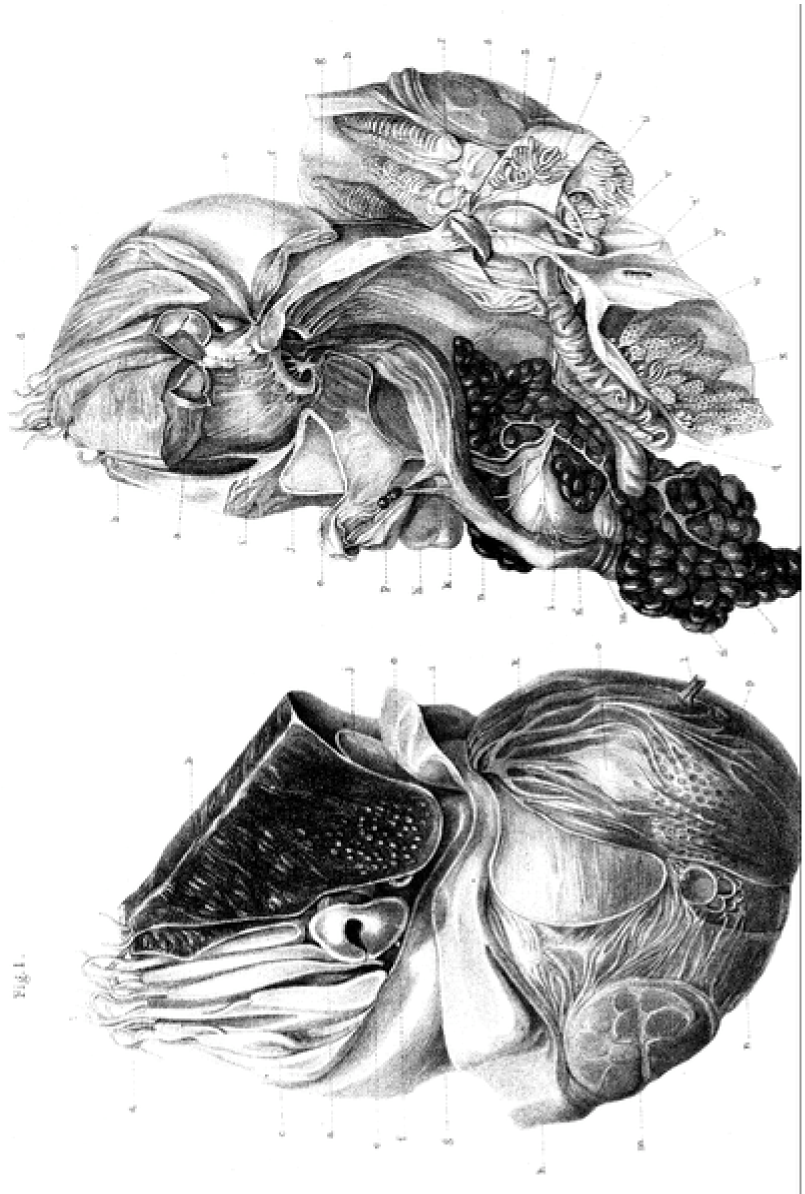
Nautilus Temporal range: Triassic–Present	
	
Nautilus belauensis	
Scientific classification	
Kingdom:	Animalia
Phylum:	Mollusca
Class:	Cephalopoda
Subclass:	Nautiloidea
Order:	Nautilida
Superfamily:	Nautilaceae
Family:	**Nautilidae** Blainville, 1825
Genera	
†*Carinonautilus* †*Cenoceras* †*Eutrephoceras* †*Pseudocenoceras* †*Strionautilus* *Allonautilus* *Nautilus*	

Nautilus is the common name of marine creatures of cephalopod family **Nautilidae**, the sole extant family of the superfamily Nautilaceae and of its smaller but near equal suborder, Nautilina. It comprises six living species in two genera, the type of which is the genus *Nautilus*. Though it more specifically refers to species *Nautilus pompilius*, the name chambered nautilus is also used for any species of the Nautilidae.

Nautilidae, both extant and extinct, are characterized by involute or slightly evolute shells that are generally smooth, with compressed or depressed whorl sections, straight to sinuous sutures, and a tubular, generally central siphuncle. Having survived relatively unchanged for millions of years, nautiluses represent the only living members of the subclass Nautiloidea, and are often considered "living fossils."

The name "Nautilus" originally referred to the *Argonauta*, otherwise known as paper nautiluses, because the ancients believed these animals used their two expanded arms as sails (cf. Aristotle *Historia Animalium* 622b). However, this octopus is not closely related to the Nautiloidea.

Anatomy



The anatomy of *Nautilus*. The top figure is dissected; the bottom just has the shell removed.

The nautilus is similar in general form to other cephalopods, with a prominent head and tentacles. Nautiluses typically have more tentacles than other cephalopods, up to ninety. These tentacles are arranged into two circles and, unlike the tentacles of other cephalopods, they have no suckers, are undifferentiated and retractable. The radula is wide and distinctively has nine teeth. There are two pairs of gills. These are the only remnants of the ancestral metamerism to be visible in extant cephalopods.

Nautilus pompilius is the largest species in the genus. One form from western Australia may reach 26.8 centimetres (10.6 in) in diameter. However, most other nautilus species never exceed 20 centimetres (7.9 in). *Nautilus macromphalus* is the smallest species, usually measuring only 16 centimetres (6.3 in).

Shell

Nautilus hemishell showing the camerae in a logarithmic spiral

A nautilus shell viewed from above (left), and from underneath (right)

Nautiluses are the sole living cephalopods whose bony body structure is externalized as a shell. The animal can withdraw completely into its shell and close the opening with a leathery hood formed from two specially folded tentacles. The shell is coiled, aragonitic, nacreous and pressure resistant, imploding at a depth of about 800 metres (2,600 ft). The nautilus shell is composed of 2 layers: a matte white outer layer, and a striking white iridescent inner layer. The innermost portion of the shell is a pearlescent blue-gray. The **osmena pearl**, contrarily to its name, is not a pearl, but a jewelry product derived from this part of the shell.

Internally, the shell divides into camerae (chambers), the chambered section being called the phragmocone. The divisions are defined by septa, each of which is pierced in the middle by a duct, the siphuncle. As the nautilus matures it creates new, larger camerae, and moves its growing body into the larger space, sealing the vacated chamber with a new septum. The camerae increase in number from around four at the moment of hatching to thirty or more in adults.

The shell coloration also keeps the animal cryptic in the water. When seen from above, the shell is darker in color and marked with irregular stripes, which helps it blend into the dark water below. The underside is almost completely white, making the animal indistinguishable from brighter waters near the surface. This mode of camouflage is named countershading.

The nautilus shell presents one of the finest natural examples of a logarithmic spiral, although it is not a golden spiral. The use of nautilus shells in art and literature is covered at nautilus shell.

Tentacles

Nautilus tentacles differ from those of other cephalopods. Lacking pads, the tentacles stick to prey by virtue of their ridged surface. Nautiloids have a powerful grip. Attempts to take an object already seized by a nautilus may tear tentacles away from the creature, which remain firmly attached to the surface of the object. Two pairs of tentacles are separate from the other 90-ish, the pre-ocular and post-ocular, situated before and behind the eye. These are more evidently grooved, with more pronounced ridges. They are extensively ciliated and serve an olfactory purpose.

Physiology

Buoyancy and movement

Nautilus locomotion
File format: Ogg
File size: 1.29 MB
Duration: 5.0s

Nautilus with extended tentacles and hyponome visible

In order to swim, the nautilus draws water into and out of the living chamber with its hyponome, which uses jet propulsion. While water is inside the chamber, the siphuncle extracts salt from it and diffuses it into the blood. The animal adjusts its buoyancy by osmotically pumping gas and fluid into or out of the camerae along the siphuncles. This limits them; they cannot operate under the extreme hydrostatic pressures found at depths greater than approximately 800 metres (2,600 ft).

In the wild, nautiluses usually inhabit depths of about 300 metres (980 ft), rising to around 100 metres (330 ft) at night to feed, mate and to lay eggs.

Senses

Head of *Nautilus pompilius* showing the eye

Unlike many other cephalopods, they do not have good vision; their eye structure is highly developed but lacks a solid lens. They have a simple "pinhole" eye open to the environment.

Instead of vision, the animal is thought to use olfaction as the primary sense for foraging, locating or identifying potential mates.

Reproduction and lifespan

Nautiluses reproduce by laying eggs. Gravid females attach the fertilized eggs to rocks in shallow waters, whereupon the eggs take eight to twelve months to develop until the 30 millimetres (1.2 in) juveniles hatch. Females spawn once per year and regenerate their gonads, making nautiluses the only cephalopods to present iteroparity or polycyclic spawning.

Nautiluses are sexually dimorphic, in that males have four tentacles modified into an organ, called the "spadix," which transfers sperm into the female's mantle during mating.

The lifespan of nautiluses may exceed 20 years, which is exceptionally lengthy for a cephalopod.

Ecology

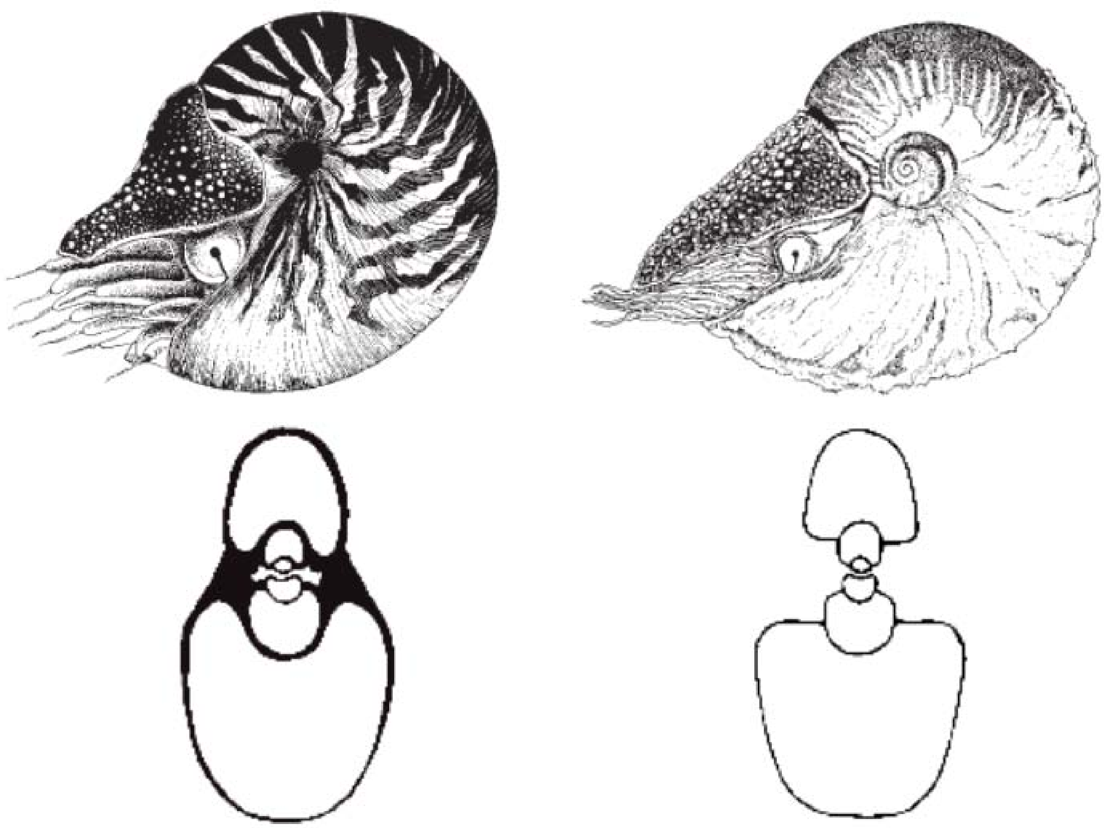
Diet

Nautiluses are predators that feed mainly on shrimp, small fish and crustaceans, which are captured by the tentacles. Due to the limited energy they expend in swimming, nautiloids only need to eat once a month.

Range and habitat

Nautiluses are only found in the Indo-Pacific, from 30° N to 30° S latitude and 90° to 185° W longitude. They inhabit the deep slopes of coral reefs.

Evolution



Shell characters of the genera *Allonautilus* and *Nautilus*

Fossil records indicate that nautiluses have not evolved much during the last 500 million years. Many were initially straight-shelled, as in the extinct genus *Lituites*. They developed in the Cambrian period and became a significant sea predator in the Ordovician period. Certain species reached over 2.5 metres (8 ft 2 in) in size. The other cephalopod subclass, Coleoidea, diverged from the Nautilidae long ago and the nautilus has remained relatively unchanged since. Nautiloids were much more extensive and varied 200 million years ago. Extinct relatives of the nautilus include ammonites, such as the baculites and goniatites.

The Nautilidae has its origin in the Trigonocerataceae (Centroceratina), specifically in the Syringonautilidae of the Late Triassic and continues to this day with *Nautilus*, the type genus, and its close relative, *Allonautilus*.

Fossil genera

The Nautilidae begin with *Cenoceras* in the Late Triassic, a highly varied genus that makes up the Jurassic *Cenoceras* complex. *Cenoceras* is evolute to involute, and globular to lentincular; with a suture that generally has a shallow ventral and lateral lobe and a siphuncle that is variable in position but never extremely ventral or dorsal. *Cenoceras* is not found above the Middle Jurassic and is followed by the Upper Jurassic-Miocene *Eutrephoceras*.

Eutrephoceras is generally subgobular, broadly rounded laterally and ventrally, with a small to occluded umbilicus, broadly rounded hyponomic sinus, only slightly sinuous sutures, and a small siphuncle that is variable in position.

Next to appear is the Lower Cretaceous *Strionautilus* from India and the European ex-USSR, named by Shimankiy in 1951. *Strionautilus* is compressed, involute, with fine longitudinal striations. Whorl sections are subrectangular, sutures sinuous, the siphuncle subcentral.

Also from the Cretaceous is *Pseudocenoceras*, named by Spath in 1927. *Pseudocenoceras* is compressed, smooth, with subrectangular whorl sections, flattened venter, and a deep umbilicus. The suture crosses the venter essentially straight and has a broad, shallow, lateral lobe. The siphuncle is small and subcentral. *Pseudocenoceras* is found in the Crimea and in Libya.

Carinonautilus is a genus from the Upper Cretaceous of India, named by Spengler in 1919. *Carinonautilus* is a very involute form with high whorl section and flanks that converge on a narrow venter that bears a prominent rounded keel. The umbilicus is small and shallow, the suture only slightly sinuous. The siphuncle is unknown.

Taxonomy

Nautilus shells: *N. macromphalus* (left), *A. scrobiculatus* (centre), *N. pompilius* (right)

The family Nautilidae contains six extant species and several extinct species.

- Genus ***Allonautilus***
    - *A. perforatus*
    - *A. scrobiculatus*
- Genus ***Nautilus***
    - *N. belauensis*
    - †*N. cookanum*
    - *N. macromphalus*
    - *N. pompilius* (type)
        - *N. p. pompilius*
        - *N. p. suluensis*
    - †*N. praepompilius*
    - *N. stenomphalus*

Dubious or uncertain taxa

The following taxa associated with the family Nautilidae are of uncertain taxonomic status:

Binomial name and author citation	Current systematic status	Type locality	Type repository
N. alumnus Iredale, 1944	Species dubium [*fide* Saunders (1987:49)]	Queensland, Australia	Not designated [*fide* Saunders (1987:49)]
N. ambiguus Sowerby, 1848	Species dubium [*fide* Saunders (1987:48)]	Not designated	Unresolved
N. beccarii Linne, 1758	Non-cephalopod; Foraminifera [*fide* Frizzell and Keen (1949:106)]		
N. calcar Linne, 1758	?Non-cephalopod; Foraminifera Lenticulina	Adriatic Sea	Unresolved; Linnean Society of London?
N. crispus Linne, 1758	Undetermined	Mediterranean Sea	Unresolved; Linnean Society of London?
N. crista Linne, 1758	Non-cephalopod; *Turbo* [*fide* Dodge (1953:14)]		
N. fascia Linne, 1758	Undetermined	Adriatic Sea	Unresolved; Linnean Society of London?
N. granum Linne, 1758	Undetermined	Mediterranean Sea	Unresolved; Linnean Society of London?
N. lacustris Lightfoot, 1786	Non-cephalopod; *Helix* [*fide* Dillwyn (1817:339)]		
N. legumen Linne, 1758	Undetermined	Adriatic Sea	Unresolved; Linnean Society of London?
N. micrombilicatus Joubin, 1888	*Nomen nudum*		
N. obliquus Linne, 1758	Undetermined	Adriatic Sea	Unresolved; Linnean Society of London?
N. pompilius marginalis Willey, 1896	Species dubium [*fide* Saunders (1987:50)]	New Guinea	Unresolved
N. pompilius moretoni Willey, 1896	Species dubium [*fide* Saunders (1987:49)]	New Guinea	Unresolved
N. pompilius perforatus Willey, 1896	Species dubium [*fide* Saunders (1987:49)]	New Guinea	Unresolved
N. radicula Linne, 1758	?Non-cephalopod; Foraminifera Nodosaria	Adriatic Sea	Unresolved; Linnean Society of London?
N. raphanistrum Linne, 1758	Undetermined	Mediterranean Sea	Unresolved; Linnean Society of London?
N. raphanus Linne, 1758	Undetermined	Adriatic Sea	Unresolved; Linnean Society of London?
N. semi-lituus Linne, 1758	Undetermined	Liburni, Adriatic Sea	Unresolved; Linnean Society of London?
N. sipunculus Linne, 1758	Undetermined	"freto Siculo"	Unresolved; Linnean Society of London?
N. texturatus Gould, 1857	*Nomen nudum*		

Octopodia nautilus Schneider, 1784	Rejected specific name [*fide* Opinion 233, ICZN (1954:278)]

Chapter 7

Ammonite

Ammonites **Temporal range: 400–65.5 Ma** **Devonian - Cretaceous**	
 Artist's reconstruction of *Asteroceras*	
Scientific classification [e]	
Kingdom:	Animalia
Phylum:	Mollusca
Class:	Cephalopoda
Subclass:	**†Ammonoidea** Zittel, 1884
Orders and Suborders	

Order Anarcestida

- Anarcestina
- Pharciceratina
- Prolobinina

Order Ammonitida

- Ammonitina
- Ancyloceratina

- Phylloceratina
- Lytoceratina

Order Ceratitida

- Ceratitina
- Otoceratina
- Noritacina
- Clydonitina

Order Clymeniida

- Clymeniina
- Gonioclymeniina
- Cyrtoclymeniina

Order Goniatitida

- Goniatitina
- Tornoceratina

Order Prolecanitida

- Prolecanitina
- Medlicottiana

Ammonites are an extinct group of marine invertebrate animals in the subclass **Ammonoidea** of the class Cephalopoda. These molluscs are more closely related to living coleoids (i.e. octopuses, squid, and cuttlefish) than they are to shelled nautiloids such as the living *Nautilus* species.

Ammonites are excellent index fossils, and it is often possible to link the rock layer in which they are found to specific geological time periods. Their fossil shells usually take the form of planispirals, although there were some helically-spiraled and non-spiraled forms (known as *heteromorphs*).

The name *ammonite*, from which the scientific term is derived, was inspired by the spiral shape of their fossilized shells, which somewhat resemble tightly-coiled rams' horns. Pliny the Elder (d. 79 AD. near Pompeii) called fossils of these animals *ammonis cornua* ("horns of Ammon") because the Egyptian god Ammon (Amun) was typically depicted wearing ram's horns. Often the name of an ammonite genus ends in -*ceras*, which is Greek (κέρας) for "horn".

Classification

Originating from within the bactritoid nautiloids, the ammonoid cephalopods first appeared in the Devonian (circa 400 million years ago) and became extinct at the close of the Cretaceous (65.5 Ma) along with the dinosaurs. The classification of ammonoids is based in part on the ornamentation and structure of the septa comprising their shells' gas chambers; by these and other characteristics we can divide subclass Ammonoidea into three orders and eight known suborders. While nearly all nautiloids show gently curving sutures, the ammonoid suture line (the intersection of the septum with the outer shell) was folded, forming saddles (or peaks) and lobes (or valleys).

Suture patterns

Three major types of suture patterns in Ammonoidea have been noted:

- *Goniatitic* - numerous undivided lobes and saddles; typically 8 lobes around the conch. This pattern is characteristic of the Paleozoic ammonoids.
- *Ceratitic* - lobes have subdivided tips, giving them a saw-toothed appearance, and rounded undivided saddles. This suture pattern is characteristic of Triassic ammonoids and appears again in the Cretaceous "pseudoceratites".
- *Ammonitic* - lobes and saddles are much subdivided (fluted); subdivisions are usually rounded instead of saw-toothed. Ammonoids of this type are the most important species from a biostratigraphical point of view. This suture type is characteristic of Jurassic and Cretaceous ammonoids but extends back all the way to the Permian.

Orders and suborders

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

Iridescent ancient ammonite fossil on display at the American Museum of Natural History, New York City, around 2.5 feet in diameter.

The Ammonoidea can be divided into eight orders, listed here starting with the most primitive and going to the more derived.

- Anarcestida, Devonian
- Clymeniida, Upper Devonian
- Goniatitida, Middle Devonian - Upper Permian
- Prolecanitida, Upper Devonian - Upper Triassic
- Ceratitida, Permian - Triassic
- Phylloceratida, Triassic - Cretaceous
- Lytoceratida, Jurassic - Cretaceous
- Ammonitida, Lower Jurassic - Upper Cretaceous

Note that in some classifications these are referred to as suborders, included in only three orders: Goniatitida, Ceratitida, and Ammonitida.

Taxonomy of the Treatise

The Treatise on Invertebrate Paleontology (1964) includes the Ammonitina, Lytoceratina, and Phylloceratina as separate suborders within the subclass Ammonoidea, without the use of orders, and divides them into superfamilies. In other, subsequent taxonomies the Ammonitina, Lytoceratina, and Phylloceratina are placed within the order, Ammonitida.

The Ancyloceratina which is sometimes treated as a separate suborder is treated as a superfamily, the Ancylocerataceae in the Lytoceratina in the Treatise.

According to the Treatise, the Ammonitina are derived from the Phyllocerarina and Lytoceratina beginning in the Early Jurassic with the Psilocerataceae and ending with nine superfamilies, although not all extant at the same time. These are the Acanthocerataceae, Desmocerataceae, Eoderocerataceae, Haploceratacea, Hildocerataceae, Hoplitaceae, Perispinctaceae, Psilocerataceae, and Stephanocerataceae.

The Eoderocerataceae, Hildocerataceae, Psilocerataceae, and Stephanocerataceae are strictly Jurassic groups. The Acanthocerataceae, Desmocerataceae, and Hoplitaceae are known only from the Cretaceous. But the Haplocerataceae and Peripinctaceae extend from the Jurassic well into the Cretaceous.

Life

Jeletzkytes, a Cretaceous ammonite from the USA

Asteroceras, a Jurassic ammonite from England

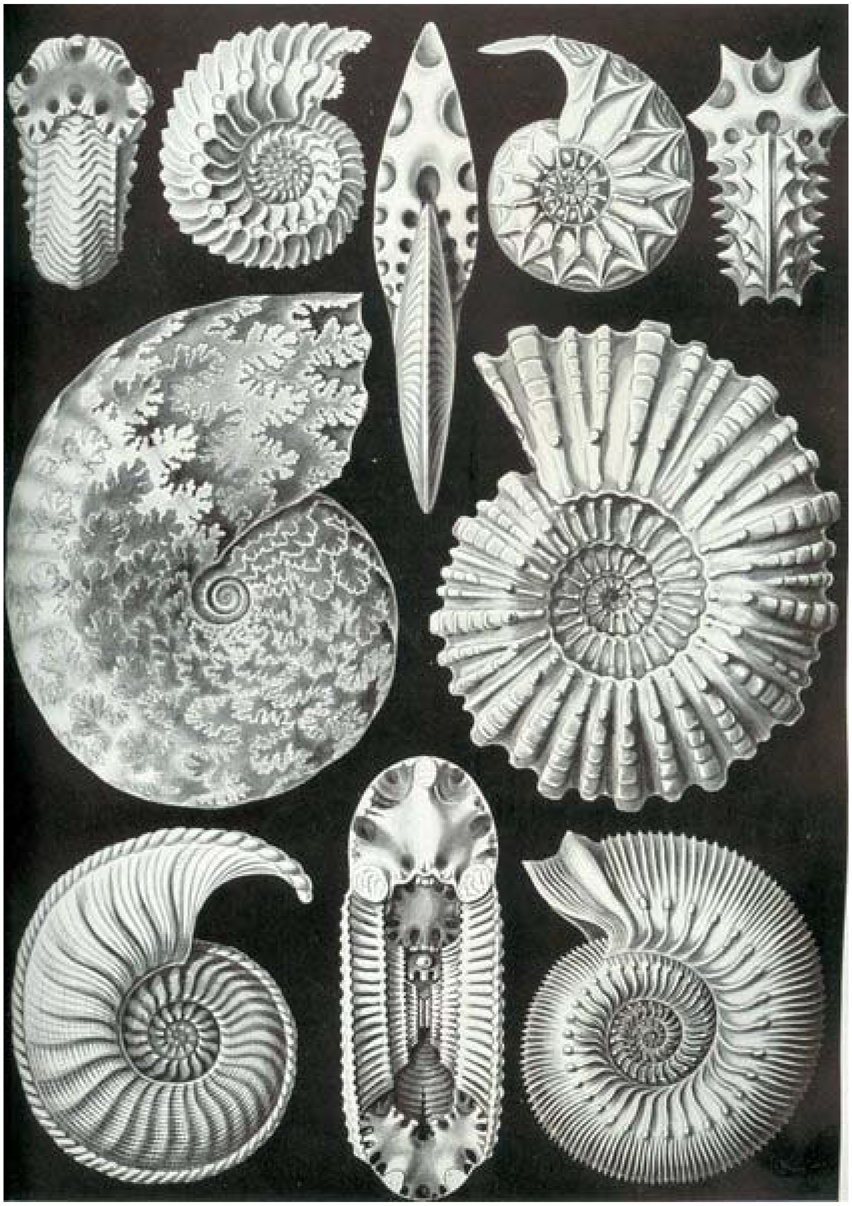
Because ammonites and their close relatives are extinct, little is known about their way of life. Their soft body parts are very rarely preserved in any detail. Nonetheless, much has been worked out by examining ammonoid shells and by using models of these shells in water tanks.

Many ammonoids probably lived in the open water of ancient seas, rather than at the sea bottom. This is suggested by the fact that their fossils are often found in rocks that were laid down under conditions where no bottom-dwelling life is found. Many of them (such as *Oxynoticeras*) are thought to have been good swimmers with flattened, discus-shaped, streamlined shells, although some ammonoids were less effective swimmers and were likely to have been slow-swimming bottom-dwellers. Synchrotron analysis of an aptychophoran ammonite revealed remains of isopod and mollusc larva in its buccal cavity, indicating that at least this kind of ammonite fed on plankton. Fossilized ammonoids have been found showing tooth marks from such attacks. They may have avoided predation by squirting ink, much like modern cephalopods; ink is occasionally preserved in fossil specimens.

The soft body of the creature occupied the largest segments of the shell at the end of the coil. The smaller earlier segments were walled off and the animal could maintain its buoyancy by filling them with gas. Thus the smaller sections of the coil would have floated above the larger sections.

Shell anatomy and diversity

Basic shell anatomy

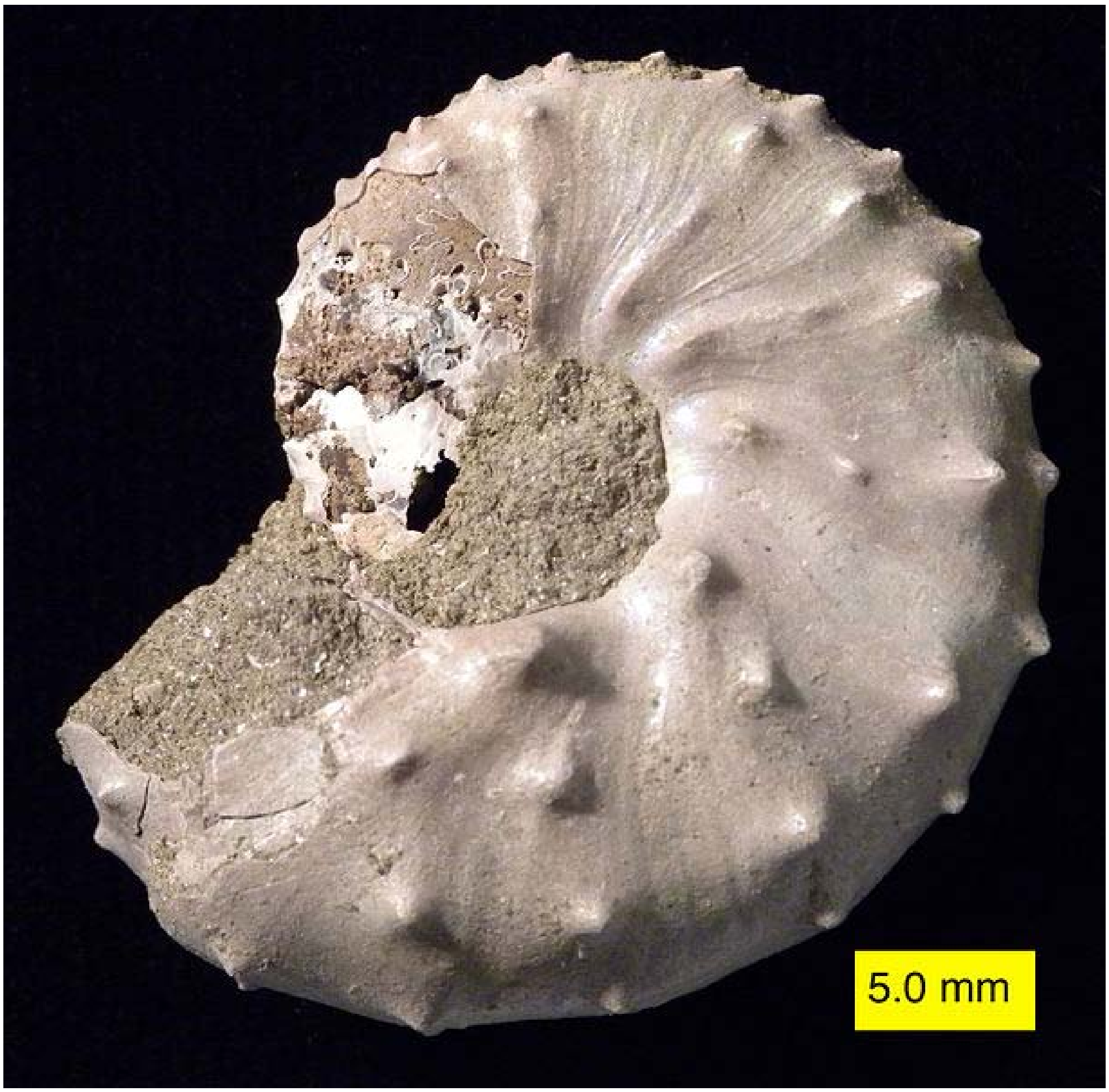


A variety of ammonite forms, from Ernst Haeckel's 1904 *Kunstformen der Natur* (Artforms of Nature).

The chambered part of the ammonite shell is called a *phragmocone*. The phragmocone contains a series of progressively larger chambers, called *camerae* (sing. *camera*) that are divided by thin walls called *septa* (sing. *septum*). Only the last and largest chamber, the body chamber, was occupied by the living animal at any given moment. As it grew, it added newer and larger chambers to the open end of the coil. A thin living tube called a *siphuncle* passed through the septa, extending from the ammonite's body into the empty shell chambers. Through a hyperosmotic active transport process, the ammonite emptied water out of these shell chambers. This enabled it to control the buoyancy of the shell and thereby rise or descend in the water column.

A primary difference between ammonites and nautiloids is that the siphuncle of ammonites (excepting Clymeniina) runs along the ventral periphery of the septa and camerae (i.e., the inner surface of the outer axis of the shell), while the siphuncle of nautiloids runs more or less through the center of the septa and camerae.

Sexual dimorphism



Discoscaphites iris, Owl Creek Formation (Upper Cretaceous), Ripley, Mississippi.

One feature found in shells of the modern Nautilus is the variation in the shape and size of the shell according to the sex of the animal, the shell of the male being slightly smaller and wider than that of the female. This sexual dimorphism is thought to be an explanation for the variation in size of certain ammonite shells of the same species, the larger shell (called a **macroconch**) being female, and the smaller shell (called a **microconch**) being male. This is thought to be because the female required a larger body size for egg production. A good example of this sexual variation is found in *Bifericeras* from the early part of the Jurassic period of Europe.

It is only in relatively recent years that the sexual variation in the shells of ammonites has been recognized. The **macroconch** and **microconch** of one species were often previously mistaken for two closely related but different species occurring in the same rocks. However, these "pairs" were so consistently found together that it became apparent that they were in fact sexual forms of the same species.

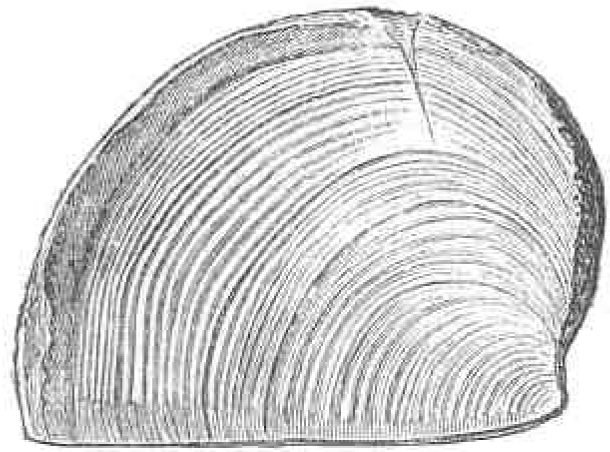
Variations in shape

The majority of ammonite species feature a shell that is a planispiral flat coil, but other species feature a shell that is nearly straight (as in baculites). Still other species' shells are coiled helically, superficially like that of a large gastropod (as in *Turrilites* and *Bostrychoceras*). Some species' shells are even initially uncoiled, then partially coiled, and finally straight at maturity (as in *Australiceras*). These partially uncoiled and totally uncoiled forms began to diversify mainly during the early part of the Cretaceous and are known as **heteromorphs**.

Perhaps the most extreme and bizarre looking example of a heteromorph is *Nipponites*, which appears to be a tangle of irregular whorls lacking any obvious symmetrical coiling. However, upon closer inspection the shell proves to be a three-dimensional network of connected "U" shapes. *Nipponites* occurs in rocks of the upper part of the Cretaceous in Japan and the USA.

Ammonites vary greatly in the ornamentation (surface relief) of their shells. Some may be smooth and relatively featureless, except for growth lines, and resemble that of the modern *Nautilus*. In others various patterns of spiral ridges and ribs or even spines are shown. This type of ornamentation of the shell is especially evident in the later ammonites of the Cretaceous.

Aptychus



A drawing of an aptychus named "Trigonellites latus" from the Kimmeridge Clay Formation in England

Some ammonites have been found in association with a single horny plate or a pair of calcitic plates. In the past it was assumed that these plates served to close the opening of the shell in much the same way as an operculum, however more recently it has been postulated that they were instead a jaw apparatus.

The plates are collectively termed the *aptychus* or *aptychi* in the case of a pair of plates, and *anaptychus* in the case of a single plate. The paired aptychi were symmetrical to one another and equal in size and appearance.

Anaptychi are relatively rare as fossils. They are found representing ammonites from the Devonian period through those of the Cretaceous period.

Calcified aptychi only occur in ammonites from the Mesozoic era. They are almost always found detached from the shell, and are only very rarely preserved in place. Still, sufficient numbers have been found closing the apertures of fossil ammonite shells as to leave no doubt as to their identity as part of the anatomy of an ammonite.

Large numbers of detached aptychi occur in certain beds of rock (such as those from the Mesozoic in the Alps). These rocks are usually accumulated at great depths. The modern *Nautilus* lacks any calcitic plate for closing its shell, and only one extinct nautiloid genus is known to have borne anything similar. *Nautilus* does, however, have a leathery head shield (the hood) which it uses to cover the opening when it retreats inside.

There are many forms of aptychus, varying in shape and the sculpture of the inner and outer surfaces, but because they are so rarely found in position within the shell of the ammonite it is often unclear to which species of ammonite one kind of aptychus belongs. A number of aptychi have been given their own genus and even species names independent of their unknown owners' genus and species, pending future discovery of verified occurrences within ammonite shells.

Non-mineralized anatomy

Annomoids bore a radula and beak, a marginal siphuncle, and probably ten arms. They operated by direct development with sexual reproduction, were carnivorous and had a crop for food storage. It is unlikely that any ammonoids dwelt in fresh or brackish water.

Soft parts

Although ammonites do occur in exceptional lagerstatten such as the Solnhofen limestone, their soft part record is surprisingly bleak - beyond a tentative ink sac and possible digestive organs, no soft parts are known at all. It can be tentatively assumed that they had numerous tentacles, each quite weak, and engulfed prey almost whole.

Size

2-metre (6.5-foot) *Parapuzosia seppenradensis* cast in Germany

Few of the ammonites occurring in the lower and middle part of the Jurassic period reach a size exceeding 23 centimetres (9 inches) in diameter. Much larger forms are found in the later rocks of the upper part of the Jurassic and the lower part of the Cretaceous, such as *Titanites* from the Portland Stone of Jurassic of southern England, which is often 53 centimetres (2 feet) in diameter, and *Parapuzosia seppenradensis* of the Cretaceous period of Germany, which is one of the largest known ammonites, sometimes reaching 2 metres (6.5 feet) in diameter. The largest documented North American ammonite is *Parapuzosia bradyi* from the Cretaceous with specimens measuring 137 centimetres (4.5 feet) in diameter, although a new 2.3-metre (7.5-foot) British Columbian specimen, if authentic, would appear to trump even the European champion.

Distribution

A specimen of *Hoploscaphites* from the Pierre Shale of South Dakota. Much of the original shell, including the nacre, has survived.

Starting from the mid-Devonian, ammonoids were extremely abundant, especially as ammonites during the Mesozoic era. Many genera evolved and ran their course quickly, becoming extinct in a few million years. Due to their rapid evolution and widespread distribution, ammonoids are used by geologists and paleontologists for biostratigraphy. They are excellent index fossils, and it is often possible to link the rock layer in which they are found to specific geological time periods.

Due to their free-swimming and/or free-floating habits, ammonites often happened to live directly above seafloor waters so poor in oxygen as to prevent the establishment of animal life on the seafloor. When upon death the ammonites fell to this seafloor and were gradually buried in accumulating sediment, bacterial decomposition of these corpses often tipped the delicate balance of local redox conditions sufficiently to lower the local solubility of minerals dissolved in the seawater, notably phosphates and carbonates. The resulting spontaneous concentric precipitation of minerals around a fossil is called a concretion and is responsible for the outstanding preservation of many ammonite fossils.

When ammonites are found in clays their original mother-of-pearl coating is often preserved. This type of preservation is found in ammonites such as *Hoplites* from the Cretaceous Gault clay of Folkestone in Kent, England.

The Cretaceous Pierre Shale formation of the United States and Canada is well known for the abundant ammonite fauna it yields, including *Baculites*, *Placenticeras*, *Scaphites*, *Hoploscaphites*, and *Jeletzkytes*, as well as many uncoiled forms. Many of these also have much or all of the original shell, as well as the complete body chamber, still intact. Many Pierre Shale ammonites, and indeed many ammonites throughout earth history, are found inside concretions.

An iridescent ammonite from Madagascar.

Other fossils, such as many found in Madagascar and Alberta (Canada), display iridescence. These iridescent ammonites are often of gem quality (*ammolite*) when polished. In no case would this iridescence have been visible during the animal's life; additional shell layers covered it.

The majority of ammonoid specimens, especially those of the Paleozoic era, are preserved only as internal molds; that it to say, the outer shell (composed of aragonite) has been lost during the fossilization process. It is only in these internal-mold specimens that the suture lines can be observed; in life the sutures would have been hidden by the outer shell.

The ammonoids as a group continued through several major extinction events, although it appears that often only a few species survived. Each time, however, this handful of species diversified into a multitude of forms. Ammonite fossils became less abundant during the latter part of the Mesozoic, with none surviving into the Cenozoic era. The last surviving lineages disappeared, along with the dinosaurs, 65 million years ago in the Cretaceous-Tertiary extinction event. The reason why no ammonites survived the extinction event at the end of the Cretaceous, whereas some nautiloid cousins survived, might be due to differences in ontogeny. If their extinction was due to a bolide strike, plankton around the globe could have been severely diminished, thereby dooming ammonite reproduction during its planktonic stage.

Extinction

The extinction of the ammonites along with other marine animals and of course, non-avian dinosaurs, has been attributed to a bolide impact, marking the end of the Cretaceous Period. Regardless of what effect an impact may have had, many of these groups, including ammonoids, were already in serious decline. Previously ammonoid cephalopods barely survived several earlier major extinction events, often with only a few species surviving from which a multitude of forms diversified.

Eight or so species from only two families made it almost to the end of the Cretaceous, the order having gone through a more or less steady decline since the middle of the period. Six other families made it well into the upper Maastrichtian (uppermost stage of the Cretaceous) but were extinct well before the end. All told, 11 families entered the Maastrichtian, a decline from the 19 families known from the Cenomanian in the middle of the Cretaceous.

One reason given for their demise is that Cretaceous ammonites, being closely related to coleoids, had a similar reproductive strategy in which a huge number of eggs is laid in a single batch at the end of the life span. These, along with juvenile ammonites, are thought to have been part of the plankton at the surface of the ocean where they were killed off by the effects of an impact. Nautiloids, exemplified by modern nautiluses, are thought on the other hand to have had a reproductive strategy in which eggs were laid in smaller batches many times during the life span and on the sea floor well away from any direct effects of such a bolide strike, and thus survived.

Mythology

In medieval Europe, fossilised ammonites were thought to be petrified coiled snakes, and were called "snakestones" or, more commonly in medieval England, "serpentstones". They were considered to be evidence for the actions of saints such as Saint Hilda and Saint Patrick, and were held to have healing or oracular powers. Traders would occasionally carve the head of a snake onto the empty, wide end of the ammonite fossil, and then sell them to the public. In other cases the snake's head would be simply painted on. Ammonites from the Gandaki river in Nepal are known as saligrams, and are believed by Hindus to be a concrete manifestation of God or Vishnu.

Terminological note

The words *ammonite* and *ammonoid* are both used quite loosely in common parlance to refer to any member of subclass Ammonoidea. However, in stricter usage the term *ammonite* is reserved for members of suborder Ammonitina (or sometimes even order Ammonitida).

Chapter 8

Belemnoidea

Belemnites **Temporal range: Devonian–Cretaceous**	
 Belemnite guards from the Jurassic of Wyoming, USA.	
Scientific classification [e]	
Kingdom:	Animalia
Phylum:	Mollusca
Class:	Cephalopoda
Subclass:	Coleoidea
cohort:	†**Belemnoidea**
Orders	
Aulacocerida Phragmoteuthida Belemnitida Diplobelida Belemnoteuthina	

Belemnites (or belemnoids) are an extinct group of marine cephalopod, very similar in many ways to the modern squid and closely related to the modern cuttlefish. Like them, the belemnites possessed an ink sac, but, unlike the squid, they possessed ten arms of roughly equal length, and no tentacles. The name "belemnoid" comes from the Greek word *belemnon* meaning "a dart or arrow" and the Greek word *eidos* meaning "form".

Occurrence

Belemnites were numerous during the Jurassic and Cretaceous periods, and their fossils are abundant in Mesozoic marine rocks, often accompanying their cousins the ammonites. The belemnites become extinct at the end of the Cretaceous period along with the ammonites. The belemnites' origin lies within the bactritoid nautiloids, which date from the Devonian period; well-formed belemnite guards can be found in rocks dating from the Mississippian (or Early Carboniferous) onward through the Cretaceous. Other fossil cephalopods include baculites, nautiloids and goniatites.

Anatomy

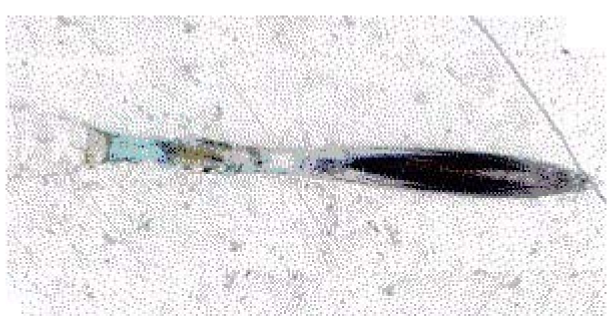
Belemnites possessed a central phragmocone made of aragonite and with negative buoyancy. To the rear of the creature was a heavy calcite guard whose main role appears to have been to counterbalance the front of the organism; it positions the centre of mass below the centre of buoyancy, increasing the stability of the swimming organism. The guard would account for between a third and a fifth of the length of the complete organism, arms included.

Like some modern squid, belemnite arms carried a series of small hooks for grabbing prey. Belemnites were efficient carnivores that caught small fish and other marine animals with their arms and ate them with their beak-like jaws. In turn, belemnites appear to have formed part of the diet of marine reptiles such as Ichthyosaurs, whose fossilized stomachs frequently contain phosphatic hooks from the arms of cephalopods.

Ecology

Belemnites were effectively neutrally buoyant, and swam in near-shore to mid-shelf oceans. Their fins could be used to their advantage in all water speeds; in a gentle current they could be flapped for propulsion; in a stronger current they could be held erect to generate lift; and when swimming rapidly by jet propulsion they could be tucked in to the body for streamlining.

Preservation

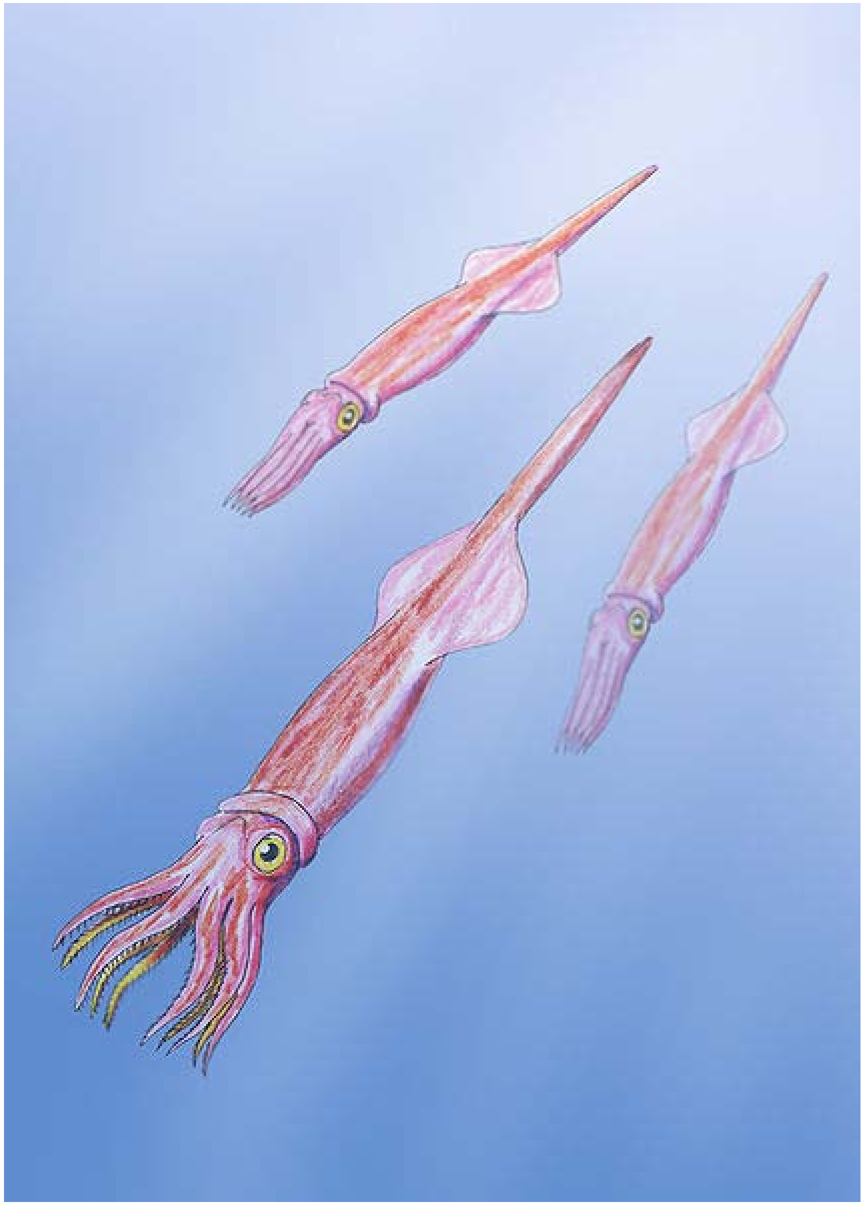


A belemnite fossil from the Franconian Jura.

Normally with fossil belemnites only the back part of the shell (called the *guard* or *rostrum*) is found. The guard is elongated and bullet-shaped, that is to say, cylindrical and pointed or rounded at one end. The hollow region at the front of the guard is termed the *alveolus*, and this houses a chambered conical-shaped part of the shell (called the *phragmocone*). The phragmocone is usually only found with the better preserved specimens. Projecting forwards from one side of the phragmocone is the thin *pro-ostracum*.

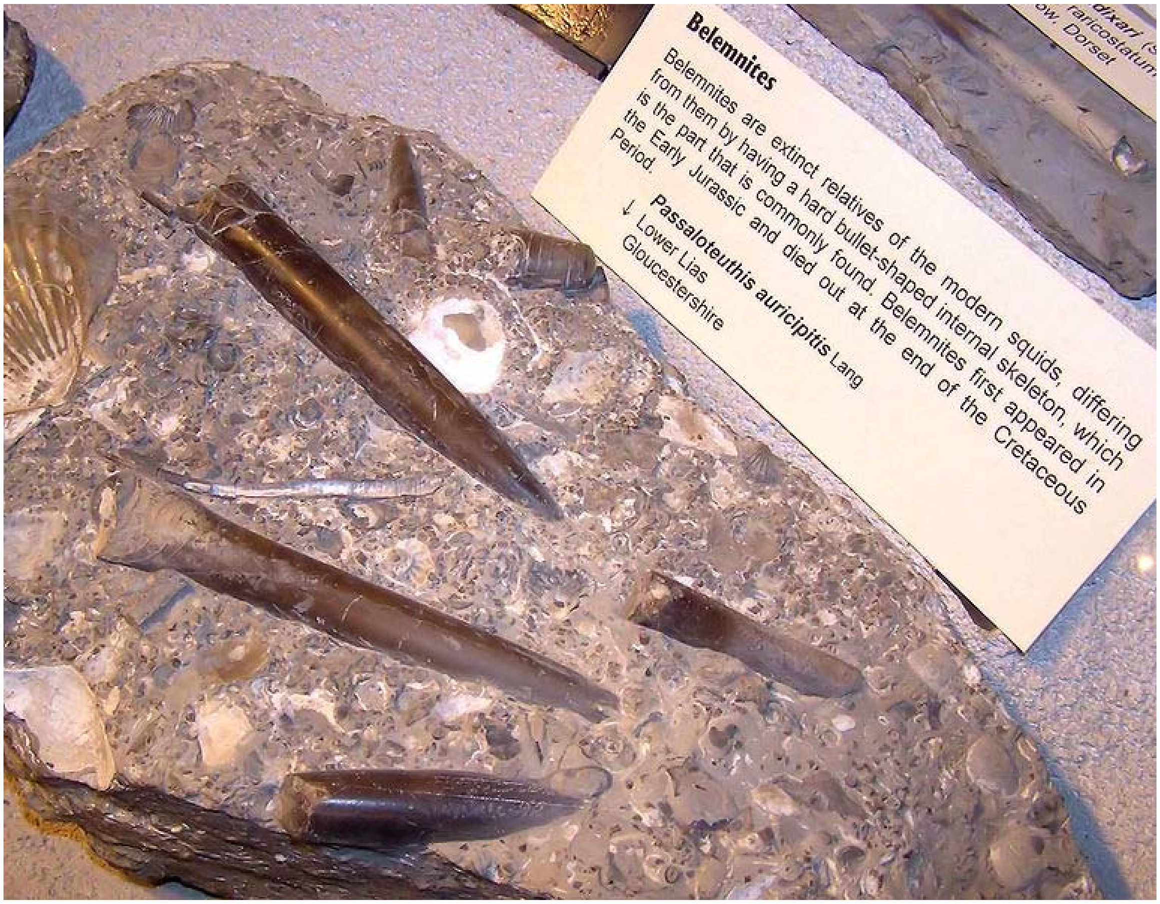
While belemnite phragmocones are homologous with the shells of other cephalopods and are similarly composed of aragonite, belemnite guards are evolutionarily novel and are composed of calcite, thus tending to preserve well. Broken guards show a structure of radiating calcite fibers and may also display concentric growth rings.

The guard, phragmocone and pro-ostracum were all internal to the living creature, forming a skeleton which was enclosed entirely by soft muscular tissue. The original living creature would have been larger than the fossilized shell, with a long streamlined body and prominent eyes. The guard would have been in place toward the rear of the creature, with the phragmocone behind the head and the pointed end of the guard facing backward.



Belemnites

The guard of the belemnite *Megateuthis gigantea*, which is found in Europe and Asia, can measure up to 46 cm in length (18 inches), giving the living animal an estimated length of 3 metres (10 feet).



Belemnite fossils at Bristol City Museum, Bristol, England. Found in the Lower Lias strata, Gloucestershire, England.

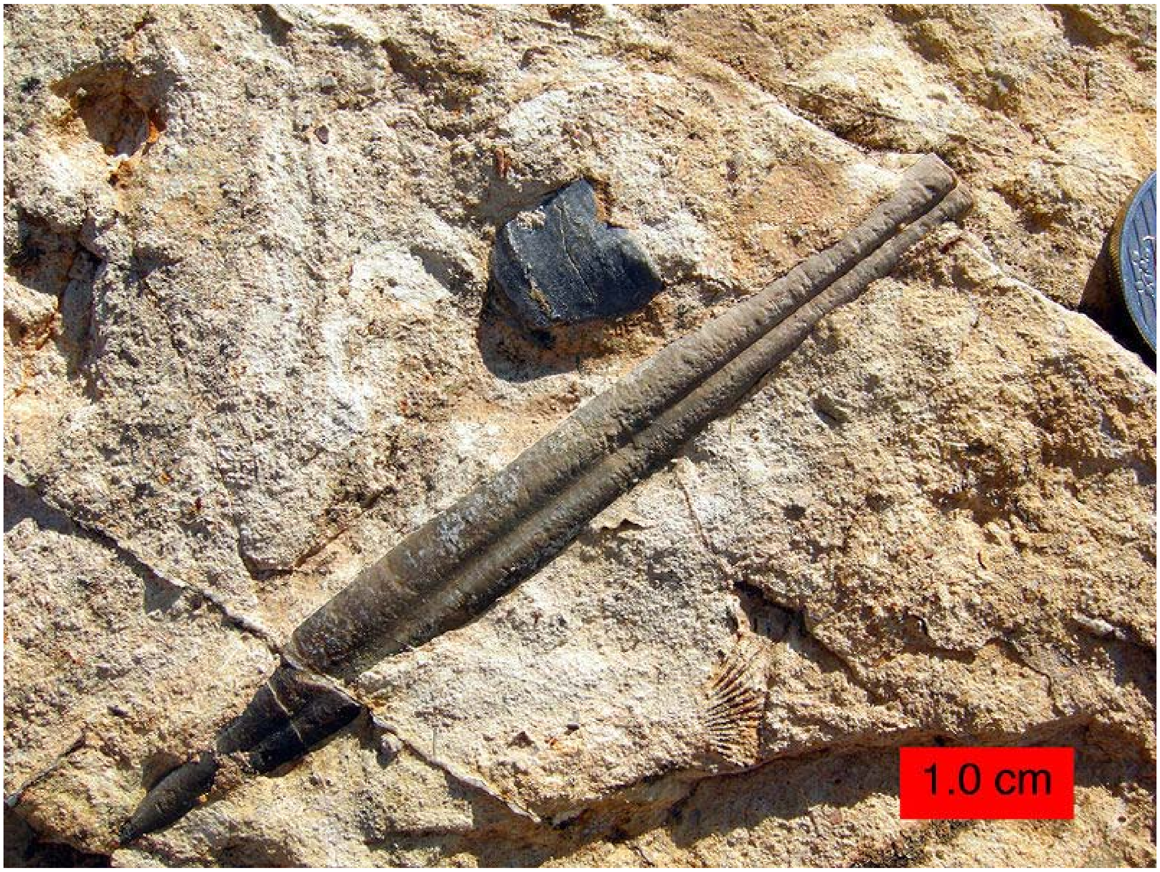
Very exceptional belemnite specimens have been found showing the preserved soft parts of the animal. Elsewhere in the fossil record, bullet-shaped belemnite guards are locally found in such profusion that such deposits are referred to semi-formally as "belemnite battlefields" (cf. "orthocone orgies"). It remains unclear whether these deposits represent post-mating mass death events, as are common among modern cephalopods and other semelparous creatures.

Uses

The bulk geochemical signature contained within belemnite guards of the Peedee Formation (Cretaceous, southeast USA) has long been used as a global standard ("PDB") against which all other geochemical samples are measured, for both carbon isotopes and oxygen isotopes.

Some belemnites (such as *Belemnites*) serve as index fossils, particularly in the Cretaceous Chalk Formation of Europe, enabling geologists to date the age the rocks in which they are found.

Classification



Belemnite in the very top bedding plane of the Zohar Formation (Jurassic) near Neve Atif, the Golan. Note the central fold along the axis characteristic of some genera.

Fossilised belemnite

- **Cohort Belemnoidea**
    - Basal and unresolved
        - Genus *Jeletzkya*
        - Genus *Belemnotheutis*
    - Order Aulacocerida
        - Family Aulacoceratidae
        - Family Dictyoconitidae
        - Family Hematitidae
        - Family Palaeobelemnopseidae
        - Family Xiphoteuthidae
    - Order Belemnitida
        - Suborder Belemnitina
            - Family Cylindroteuthidae
            - Family Hastitidae
            - Family Oxyteuthidae
            - Family Passaloteuthidae
            - Family Salpingoteuthidae
        - Suborder Belemnopseina
            - Family Belemnitellidae
            - Family Belemnopseidae
            - Family Dicoelitidae
            - Family Dimitobelidae
            - Family Duvaliidae
        - Suborder Belemnotheutina
            - Family Belemnotheutidae
            - Family Chitinobelidae
            - Family Sueviteuthidae
    - Order Diplobelida
        - Family Chondroteuthidae
        - Family Diplobelidae
    - Order Phragmoteuthida
        - Family Phragmoteuthidae
        - Family Rhiphaeoteuthidae

Chapter 9

Argonaut (Animal)

Argonauts Temporal range: Miocene – Recent	
	
Female *Argonauta argo* with eggs	
Scientific classification	
Kingdom:	Animalia
Phylum:	Mollusca
Class:	Cephalopoda
Order:	Octopoda
Superfamily:	Argonautoida
Family:	Argonautidae
Genus:	***Argonauta*** Linnaeus, 1758
Species	
†*Argonauta absyrtus* *Argonauta argo* (type) *Argonauta bottgeri* *Argonauta cornuta** *Argonauta hians* †*Argonauta itoigawai* †*Argonauta joanneus* *Argonauta nodosa*	

Argonauta nouryi
*Argonauta pacifica**
†*Argonauta tokunagai*
*Species status questionable.

Synonyms

- *Argonautarius*
  Dumeril, 1806
- *Todarus nom. nud.*
  Rafinesque, 1815
- *Todarus*
  Rafinesque, 1840
- *Trichocephalus*
  Chiaje, 1827 *in* 1823-1831

The **argonauts** (genus ***Argonauta***, the only extant genus in the Argonautidae family) are a group of pelagic octopuses. They are also called **paper nautiluses**, referring to the paper-thin eggcase that females secrete. This structure lacks the gas-filled chambers present in chambered nautilus shells and is not a true cephalopod shell, but rather an evolutionary innovation unique to the genus *Argonauta*. It is used as a brood chamber and for trapped surface air to maintain buoyancy.

Argonauts are found in tropical and subtropical waters worldwide; they live in the open ocean, i.e. they are pelagic. Like most octopuses, they have a rounded body, eight arms and no fins. However, unlike most octopuses, argonauts live close to the sea surface rather than on the seabed. *Argonauta* species are characterised by very large eyes and small distal webs. The mantle-funnel locking apparatus is a major diagnostic feature of this taxon. It consists of knob-like cartilages in the mantle and corresponding depressions in the funnel. Unlike the closely allied genera *Ocythoe* and *Tremoctopus*, *Argonauta* species lack water pores.

Of its names, "argonaut" means "sailor on the Argo"; "nautilus" is derived from the Greek ναυτίλος, meaning "sailor", because it was formerly supposed that *Argonauta* used their shell-secreting arms as sails when they were at the surface.

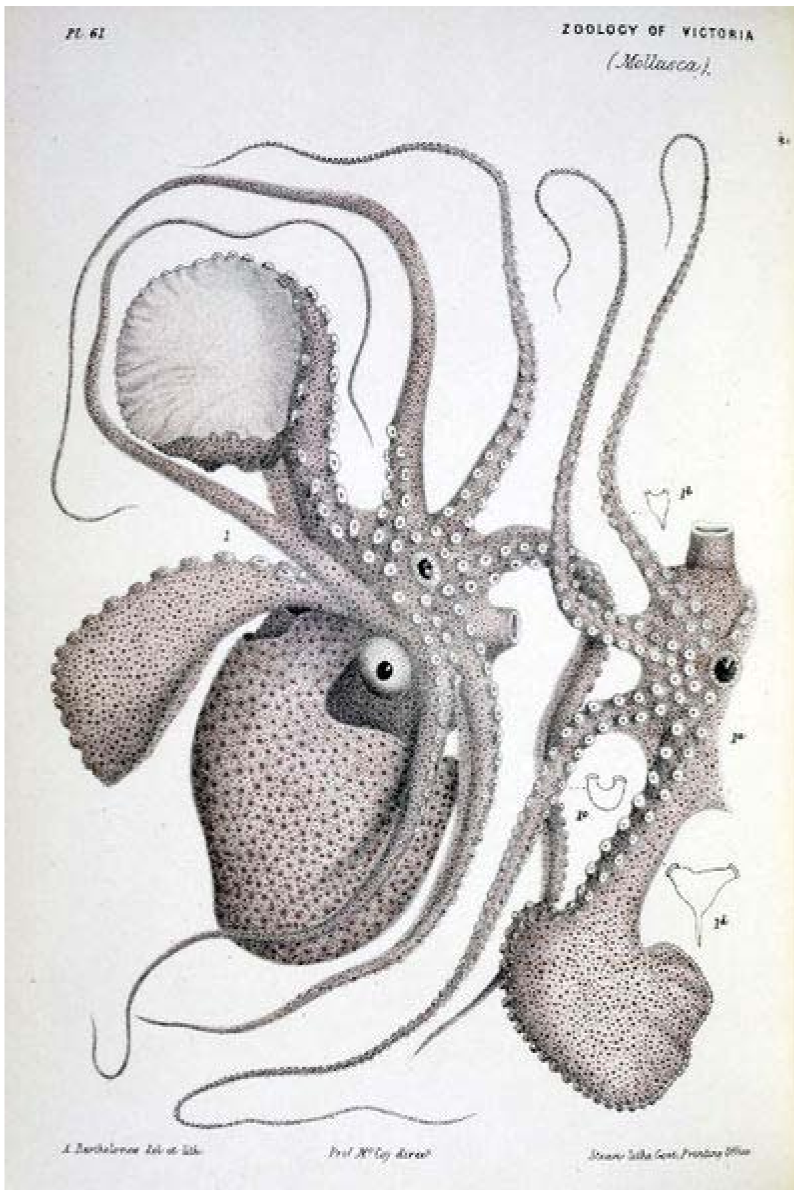
The chambered nautilus was later named after the argonaut, but belongs to a different order, the Nautilida.

Physical description

Sexual dimorphism and reproduction

Argonauts exhibit extreme sexual dimorphism in size and lifespan. Females grow up to 10 cm and make shells up to 30 cm, while males rarely surpass 2 cm. The males only mate once in their short lifetime, whereas the females are iteroparous, capable of having offspring many times over the course of their lives. In addition, the females have been known since ancient times, while the males were only described in the late 19th century.

The males lack the dorsal tentacles used by the females to create their eggcases. The males use a modified arm, the hectocotylus, to transfer sperm to the female. For fertilization, the arm is inserted into the female's pallial cavity, then is detached from the male. The hectocotylus when found in females was originally described as a parasitic worm.



Mature female *A. nodosa*

Juvenile female *A. hians*

Immature male *A. hians*

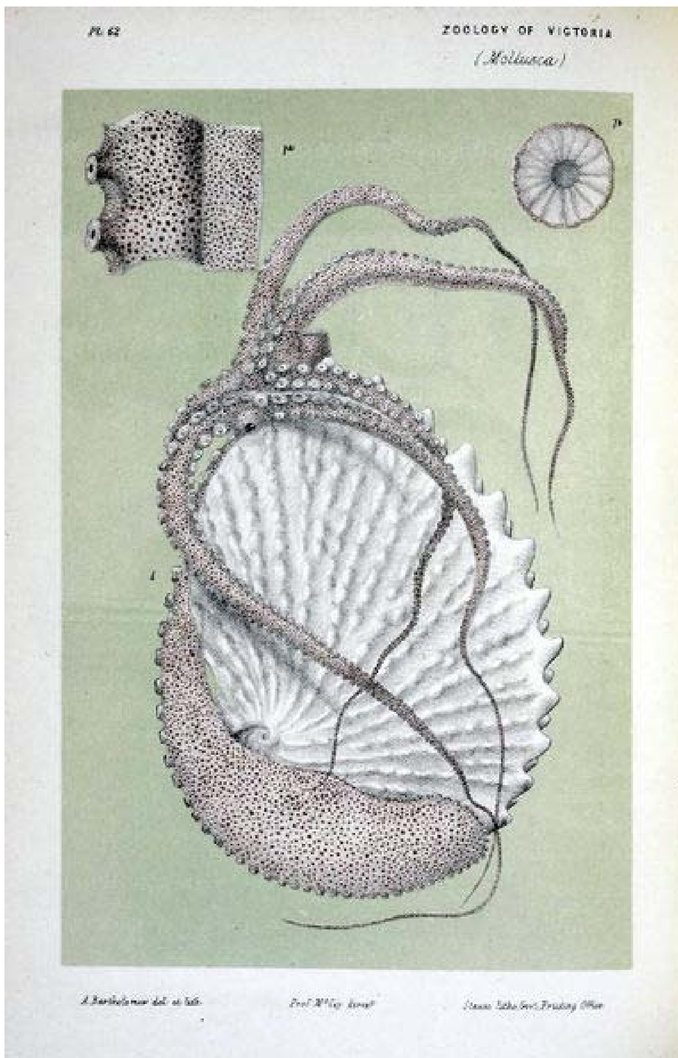
Eggcase

Female argonauts produce a laterally-compressed calcareous eggcase in which they reside. This "shell" has a double keel fringed by two rows of alternating tubercles. The sides are ribbed with the centre either flat or having winged protrusions. The eggcase curiously resembles the shells of extinct ammonites. It is secreted by the tips of the female's two greatly expanded dorsal tentacles (third left arms) before egg laying. After she deposits her eggs in the floating eggcase, the female takes shelter in it, often retaining the male's detached hectocotylus. She is usually found with her head and tentacles protruding from the opening, but she retreats deeper inside if disturbed. These ornate curved white eggcases are occasionally found floating on the sea, sometimes with the female argonaut clinging to it. It is not made of aragonite as most other shells are, but of calcite, with a three-layered structure and a higher proportion of magnesium carbonate (7%) than other cephalopod shells.

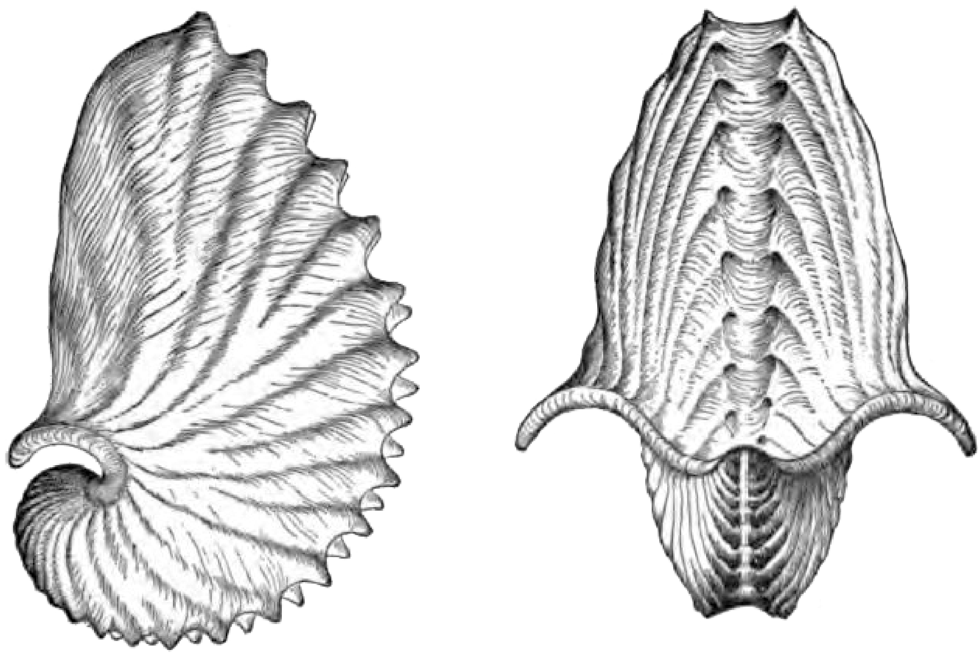
The eggcase contains a bubble of air that the animal captures at the surface of the water and uses for buoyancy, in a manner similar to other shelled cephalopods, although it does not have a chambered phragmocone as do other shelled cephalopods. Once thought to contribute to occasional mass strandings on beaches, the air bubble is under sophisticated control, evident from the behaviour of animals from which air has been removed under experimental diving conditions.

Most other octopuses lay eggs in caves; Neale Monks and C. Phil Palmer speculate that, before ammonites died out during the Cretaceous–Tertiary extinction event, the argonauts may have evolved to use discarded ammonite shells for their egg laying, eventually becoming able to mend the shells and perhaps make their own shells. However, this is uncertain and it is unknown whether this is the result of convergent evolution.

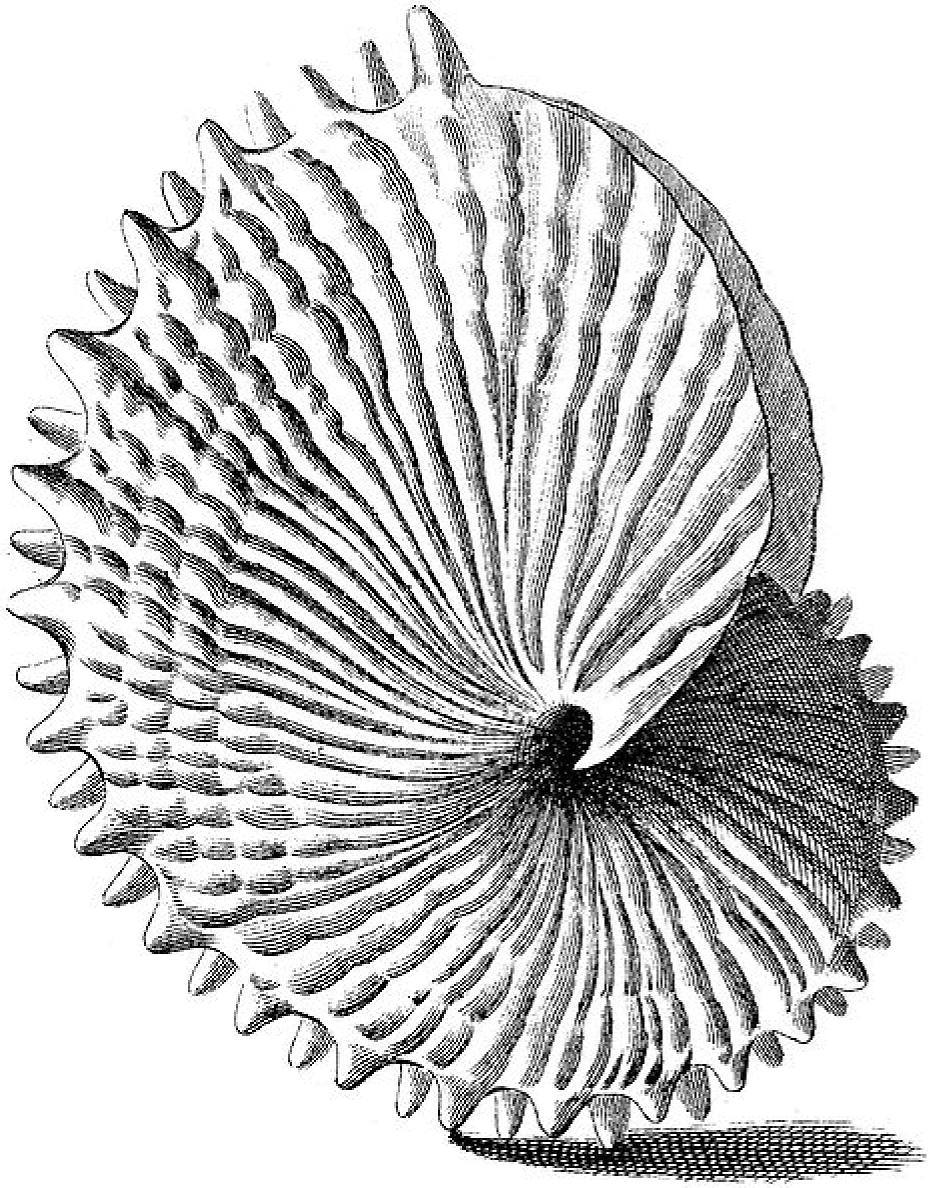
Argonauta argo is the largest species in the genus and also produces the largest eggcase, which may reach a length of 300 mm. The smallest species is *Argonauta bottgeri*, with a maximum recorded size of 67 mm.



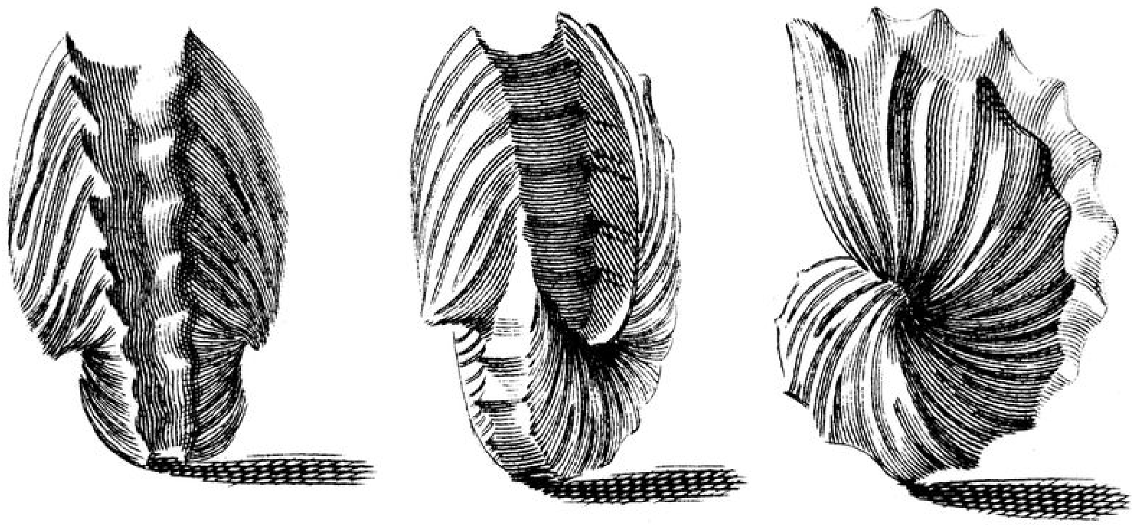
Female *A. nodosa* with its eggcase



The eggcase of *A. argo*



The eggcase of *A. nodosa*



The eggcase of *A. hians*

Beak

The beaks of *Argonauta* species are distinctive, being characterised by a very small rostrum and a fold that runs to the lower edge or near the free corner. The rostrum is 'pinched in' at the sides, making it much narrower than in other octopuses, with the exception of the closely allied monotypic genera *Ocythoe* and *Vitreledonella*. The jaw angle is curved and indistinct. Beaks have a sharp shoulder, which may or may not have posterior and anterior parts at different slopes. The hood lacks a notch and is very broad, flat, and low. The hood to crest ratio (*f/g*) is approximately 2-2.4. The lateral wall of the beak has no notch near the wide crest. Argonaut beaks are most similar to those of *Ocythoe tuberculata* and *Vitreledonella richardi*, but differ in 'leaning back' to a greater degree than the former and having a more curved jaw angle than the latter.

Feeding and defense

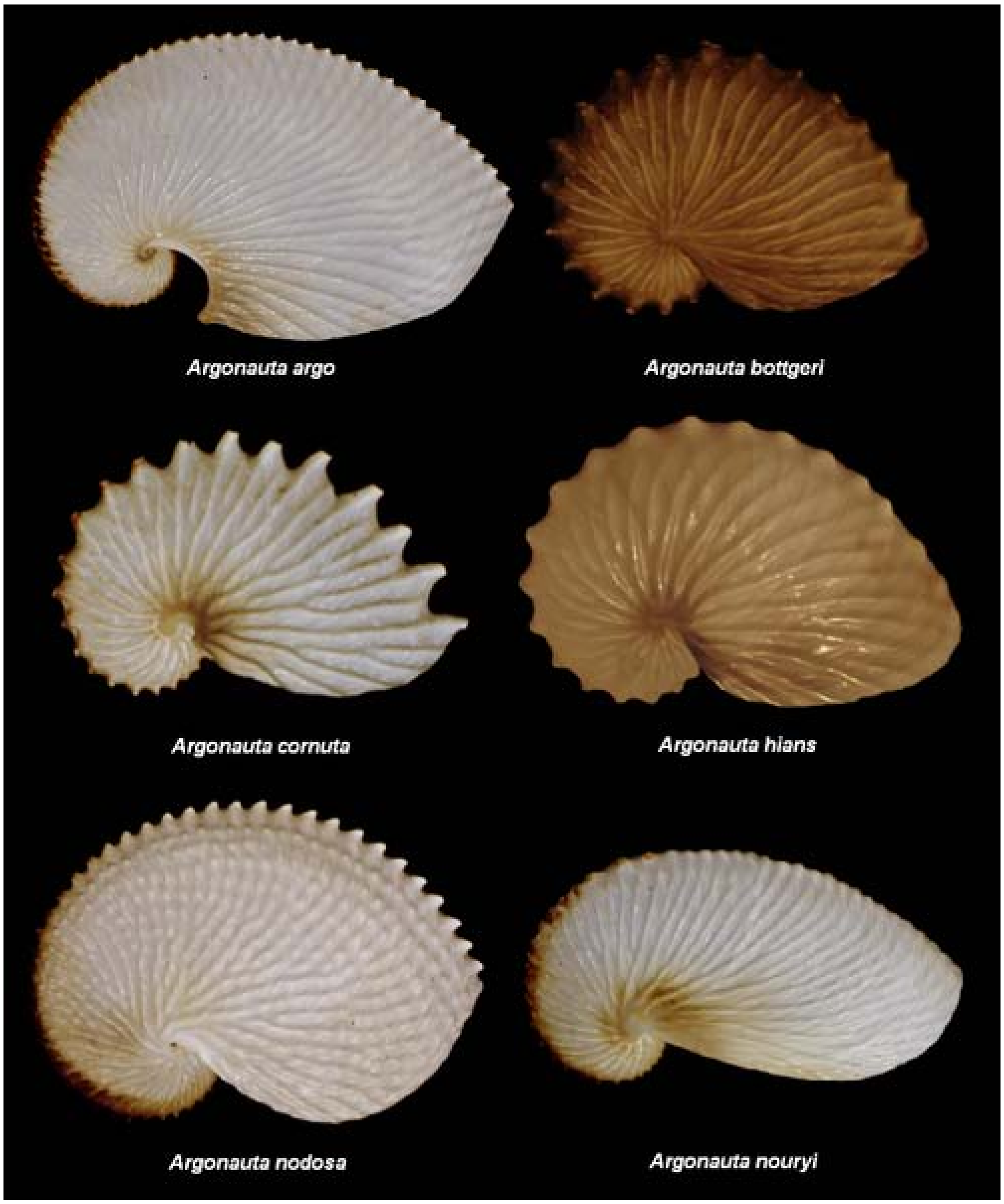
Feeding mostly occurs during the day. Argonauts use tentacles to grab prey and drag it toward the mouth. It then bites the prey to inject it with poison from the salivary gland. They feed on small crustaceans, molluscs, jellyfish and salps. If the prey is shelled, the argonaut uses its radula to drill into the organism, then inject the poison.

Argonauts are capable of altering their color. They can blend in with their surroundings to avoid predators. They also produce ink, which is ejected when the animal is being attacked. This ink paralyzes the olfaction of the attacker, providing time for the argonaut to escape. The female is also able to pull back the web covering of her shell, making a silvery flash, which may deter a predator from attacking.

Argonauts are preyed upon by tunas, billfishes, and dolphins. Shells and remains of argonauts have been recorded from the stomachs of *Alepisaurus ferox* and *Coryphaena hippurus*.

Male argonauts have been observed residing inside salps, although little is known about this relationship.

Classification



Shells of various *Argonauta* species

The genus *Argonauta* contains up to seven extant species. Several extinct species are also known.

†*Argonauta absyrtus*
Argonauta argo (type)
Argonauta bottgeri
*Argonauta cornuta**
Argonauta hians
†*Argonauta itoigawai*
†*Argonauta joanneus*
Argonauta nodosa
Argonauta nouryi
*Argonauta pacifica**
†*Argonauta tokunagai*

The extinct species *Obinautilus awaensis* was originally assigned to *Argonauta*, but has since been transferred to the genus *Obinautilus*.

Dubious or uncertain taxa

The following taxa associated with the family Argonautidae are of uncertain taxonomic status:

Binomial name and author citation	Current systematic status	Type locality	Type repository
Argonauta arctica Fabricius, 1780	Undetermined	Unresolved; ?Tullukaurfak, Greenland	Unresolved
Argonauta bibula Röding, 1798	Undetermined	Unresolved	Unresolved
Argonauta compressa Blainville, 1826	Undetermined	Mer de Indes	Unresolved; [other Blainville types at MNHN] [not reported by Lu *et al.* (1995)]
Argonauta conradi Parkinson, 1856	Species of uncertain status [*fide* Robson (1932:200)]	"New Nantucket, Pacific Ocean"	Unresolved
Argonauta cornu Gmelin, 1791	Undetermined	Unresolved	Unresolved; LS?
Argonauta cymbium Linné, 1758	Non-cephalopod; foraminiferous shell [*fide* Von Martens (1867:103)		
Argonauta fragilis Parkinson, 1856	Species of uncertain status [*fide* Robson (1932:200)]	Not designated	Unresolved
Argonauta geniculata Gould, 1852	Species of uncertain status [*fide* Robson (1932:200)]	Near Sugarloaf Mountain, Rio de Janeiro, Brazil	Type not extant [*fide* Johnson (1964:32)]
Argonauta maxima Dall,	*Nomen nudum*		

1871			
Argonauta navicula Lightfoot, 1786	Species dubium [*fide* Rehder (1967:11)]	Not designated	Unresolved
Argonauta rotunda Perry, 1811	Non-cephalopod; *Carcinaria* sp. [*fide* Robson (1932:201)]		
Argonauta rufa Owen, 1836	*Incertae sedis* [*fide* Robson (1932:181)]	"Indian seas" ["South Pacific ocean" *fide* Owen (1842:114)]	Unresolved; Museum of the Royal College of Surgeons? Holotype
Argonauta sulcata Lamarck, 1801	*Nomen nudum*		
Argonauta tuberculata f. *aurita* Von Martens, 1867	Undetermined	Unresolved	ZMB
Argonauta tuberculata f. *mutica* Von Martens, 1867	Undetermined	Coast of Brazil	ZMB Holotype
Argonauta tuberculata f. *obtusangula* Von Martens, 1867	Undetermined	Not designated	ZMB Syntypes
Argonauta vitreus Gmelin, 1791	Undetermined	Not designated	Unresolved; LS?
Octopus (Ocythoe) raricyathus Blainville, 1826	Undetermined [*Argonauta*?]	Not designated	MNHN Holotype; specimen not extant [*fide* Lu *et al.* (1995:323)]
Ocythoe punctata Say, 1819	*Argonauta* sp. [*fide* Robson (1929d:215)]	Atlantic Ocean near the North American coast (from stomach of dolphin)	Unresolved; ANSP? Holotype [not traced by Spamer and Bogan (1992)]
Tremoctopus hirondellei Joubin, 1895	*Argonauta* or *Ocythoe* [*fide* Thomas (1977:386)]	44°28′56″N 46°48′15″W / 44.48222°N 46.80417°W (Atlantic Ocean)	MOM Holotype [station 151] [*fide* Belloc (1950:3)]

In design

The argonaut was inspiration for a number of classical and modern art and decorative forms including use on pottery and architectural elements. Some early examples are found in Minoan art from Crete. A variation known as the *double argonaut* design was also found in Minoan jewelry.