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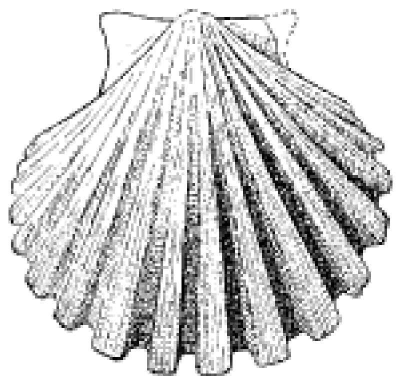
Stanford Earth Young Investigators: Biodiversity
Lab 3 – Mollusca



Molluscs are among the most abundant and diverse of all invertebrate groups. More than 50,000 extant species have been described, as well as some 35,000 fossil species. At first glance, the constituent classes within the Mollusca appear quite distinct from one another -- bivalves, gastropods, cephalopods, chitons, and several smaller groups. In terms of basic anatomy, however, molluscs are united by a number of features, including a muscular **foot** for locomotion, an epidermal **mantle** that covers the viscera and, in most molluscs, a calcareous shell, a **mantle cavity** that contains distinctive feather- or comb-like gills called **ctenidia**, and a tooth-like rasping organ called the **radula**. Most molluscs also have distinctive larva called **trochophore**, which allies them to several other phyla including the annelid worms.

Molluscan Classes

Monoplacophora: Small molluscs with a limpet-like shell; multiple pairs of ctenidia, nephridia, and pedal retractor muscles along the anterior-posterior axis. Monoplacophorans originated during the Cambrian Period but until the middle of the last century were thought to be long extinct. Now a limited diversity of living monoplacophorans is known from deep ocean environments.

Polyplacophora: The chitons have a dorso-ventrally flattened body covered by **eight imbricated calcareous plates.** Like monoplacophorans, chitons have multiple pairs of ctenidia. Known from Upper Cambrian rocks, chitons are represented by about 800 extant species.

Aplacophora: Generally small, worm-like molluscs with calcareous spicules but no conchiferan shell. About 300 extant species, many in deeper marine sediments; negligible fossil record.

Gastropoda: Snails, sea slugs, and terrestrial slugs all belong to this most diverse (35,000 species) and widespread of molluscan classes. Gastropods are characterized by a well-developed head, an **asymmetrically spiraled shell** (absent in sea slugs and slugs), and **torsion** -- the twisting of the viscera, mantle, and mantle cavity by 180 degrees during development. Stem conchiferan molluscs with planispiral shells occur in Lower Cambrian rocks, but unambiguous gastropods first appear later in the Cambrian Period.

Scaphopoda: The tusk shells are molluscs that live buried in sand. The elongate body is covered by a long conical shell open at both ends. Ca. 350 extant species and a fossil record that goes back to the Ordovician Period.

Bivalvia: Molluscs with a **bivalved calcareous shell** articulated along a dorsal hinge, head much reduced, and mantle cavity enlarged to contain large ctenidia. See below.

Cephalopoda: The chambered nautilus, octopus, squid, and cuttlefish are distinctive molluscs in which muscular tentacles arise from the head region. About 600 extant species are known, but more than 7,500 fossil nautiloids and, especially, ammonites (an extinct group allied to living squids despite their coiled, chambered shells) have been described. Latest Cambrian-Recent.

Rostroconchia: An extinct class of molluscs with a **pseudobivalved calcareous shell** that gaped at both ends. Anterior gape generally formed an elongated tube called the **rostrum**. Lower Cambrian - Permian.

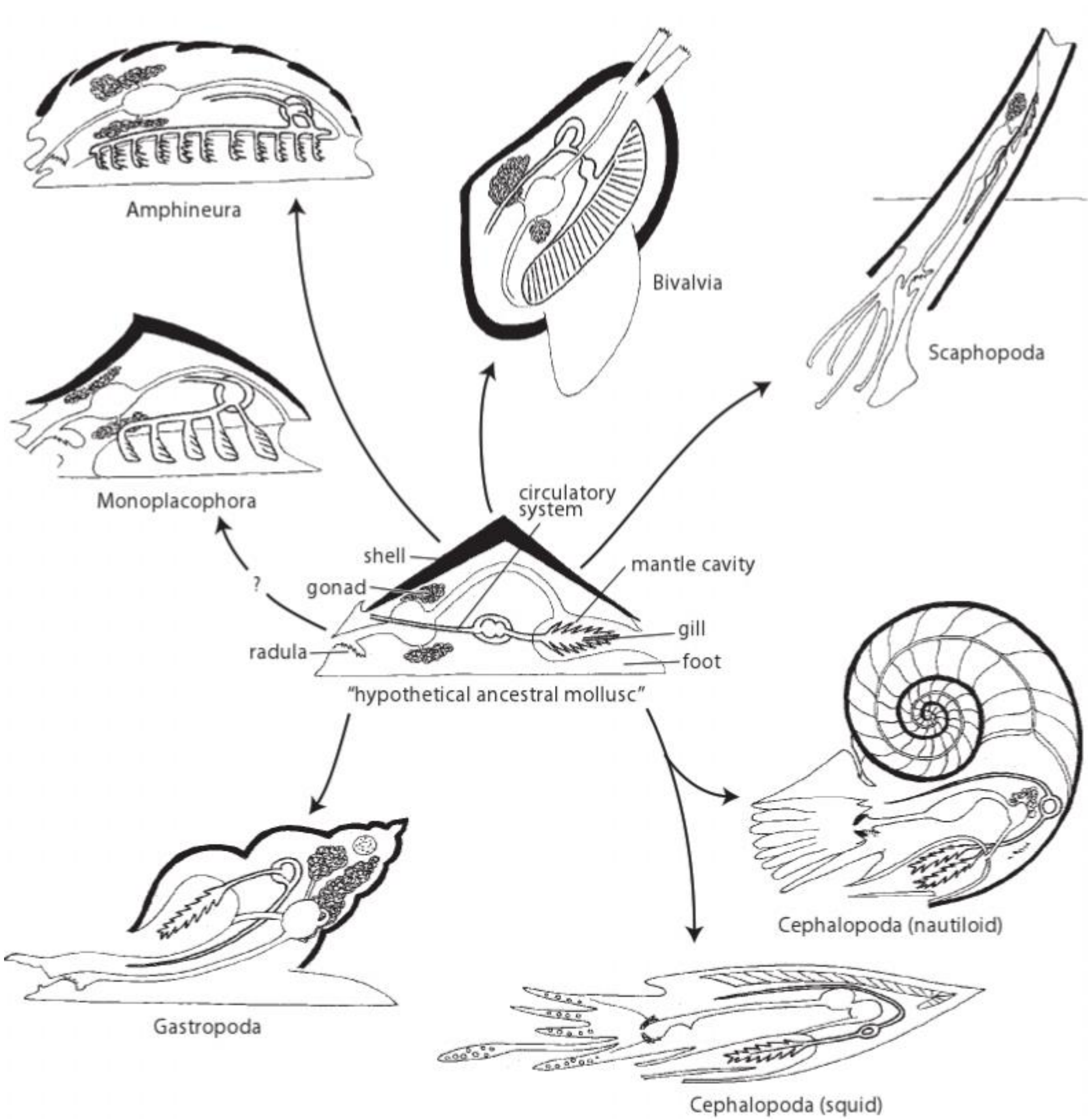


Fig. 1. Clarkson's (1993) radiation of the molluscs from the "hypothetical ancestral mollusc." (Prothero 2013)

Bivalves

Bivalves have a laterally compressed body (and foot) enclosed within two dorsally hinged shells. There is little head development, but the ctenidia are large – they are commonly used to gather food as well as exchange gases. Bivalves originated early in the Cambrian period and are today represented by some 15,000 species in marine and freshwater environments. Bivalves can be epifaunal or infaunal; some can swim (not well!) and others bore into wood or limestone. Most are filter feeders, but deposit-feeding groups are known, as are taxa that harbor symbiotic bacteria or algae. In many cases, shell morphology provides a reliable clue to life habits, making bivalves excellent subjects for research in functional morphology.

The shell of the common quahog provides a good introduction to bivalve shell morphology. Ovoid scars at the anterior and posterior ends of the shell are **muscle scars** that record the positions of adductor muscles. Adductors work to close the bivalve shell; energy stored in the proteinaceous **ligament** causes the shell to open when the adductors relax. The shell is precipitated within a fluid environment defined by the mantle; the **pallial line** that runs parallel to the ventral shell margin reflects mantle attachment to the shell. Near the posterior end of the pallial line, this feature may be indented; this **pallial sinus** records the place where mantle tissues fused to form **siphons**. Inhalant and exhalant siphons direct water movement through shells buried in sediment. Deep-burrowing bivalves commonly have deep pallial sinuses; the pallial sinus is not seen in epifaunal bivalves that lack siphons. Valves articulate via **teeth and sockets.** Growth lines and other ornamentation may be seen on external shell surfaces.

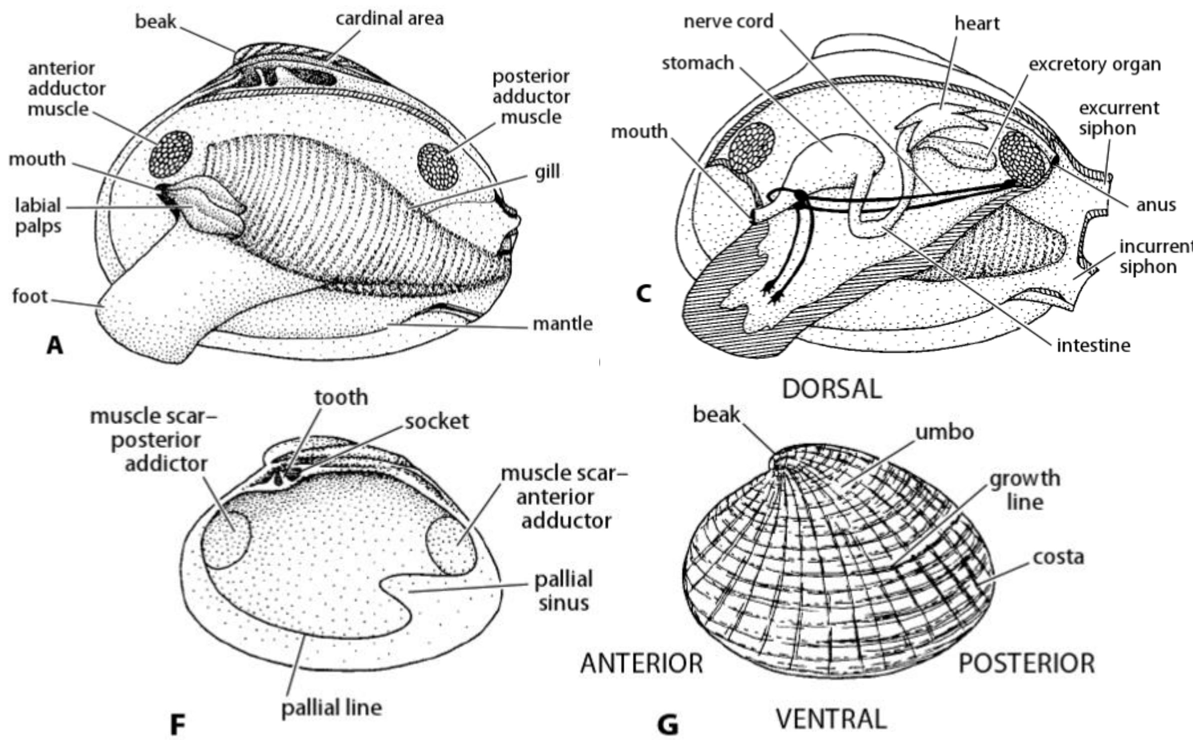


Fig. 2. Soft (A, C) and hard (F, G) anatomical features of bivalves. (Prothero 2013)

Major groups of bivalves include:

Protobranchia (**Palaeotaxodonta** and **Cryptodonta** of Boardman et al.): Generally small, infaunal bivalves that have a single pair of bipectinate (feather-like) gills. Many are deposit feeders, although the solemyids harbor chemosynthetic bacteria. Ordovician (?Cambrian) - Recent. *Nucula, Yoldia, Solemya*

Pteriomorphia (Includes **Isofilibranchia** of Boardman et al.): Epibenthic bivalves with unfused mantle margins. Most attached to substrate by **byssus** or cemented. Early Ordovician - Recent. Mussels, oysters, pearl oysters, scallops

Palaeoheterodonta: Equivalve bivalves with distinctive hinge teeth, inner nacreous layer to shell, usually without siphons. Fresh water “mussels” (Unionids), *Trigonia*

Heterodonta (Heteroconchia of Boardman et al.): Equivalve bivalves with distinctive hinge teeth, no nacreous layer, and usually with siphons. Ordovician - Recent. Cockles, quahogs, razor clams, soft-shell clams (*Mya*), wood borers (*Teredo*), *Tridacna* (the giant clam), *Lucina*.

Anomalodesmata: Equivalves with no hinge teeth. Middle Ordovician - Recent.

Geological History

Tiny conchiferan molluscs are principal constituents of the so-called small shelly faunas found in Lower Cambrian rocks. Many resemble simple gastropods and monoplacophorans, but most are today interpreted as stem conchiferans; true monoplacophorans, gastropods, and cephalopods emerged only in the Late Cambrian. The extinct rostroconchs evolved early in the Cambrian, as did tiny (stem?) bivalves. A few bivalves also occur in younger Cambrian rocks, but they are not common. In contrast, bivalves that are large, abundant, and readily allied to extant major taxa radiated during the Ordovician. Most were epifaunal or semi-infaunal, except for protobranch deposit feeders and symbiont farmers in organic-rich muds. Bivalves invaded freshwaters by the Carboniferous, but in general, the group remained ecologically subordinate until the end of the Permian.

Bivalves weathered the P-Tr extinction relatively well and diversified through the Triassic to become major elements of marine faunas. Oysters and their relatives are particularly abundant in upper Triassic through Cretaceous strata. Two distinctive bivalve groups radiated during the later Mesozoic -- the concentrically wrinkled **inoceramids** in basinal environments near the oxycline and the massive **rudists** in inner shelf and platform environments. Neither survived the end of the Cretaceous. Indeed, both may have gone extinct before the end of the period.

A major structural innovation in bivalve evolution was the fusion of mantle tissues to form siphons. During the later Mesozoic, as shell-crushing predators grew increasingly abundant, siphonate bivalves radiated in the infauna. Infaunal bivalves are major constituents of Cenozoic faunas and dominate in most subtidal environments today.

Gastropoda

The gastropods are mollusks characterized by an asymmetric spiral shell and torsion. About 30,000 extant and 15,000 extinct species have been described. Marine and freshwater species are widespread, and one group, the pulmonates, converted the mantle cavity into a lung, enabling these snails to live on land.

Most gastropods move by means of a muscular **foot**. An anterior head, with tentacles, contains a mouth for intake of food. A **radula** within the oral cavity facilitates feeding. Where present, the calcareous **shell** is secreted by mantle tissues; the posterior of the snail may contain a small proteinaceous or calcareous disc called the **operculum**, used to plug the shell's aperture when the snail has retreated within it.

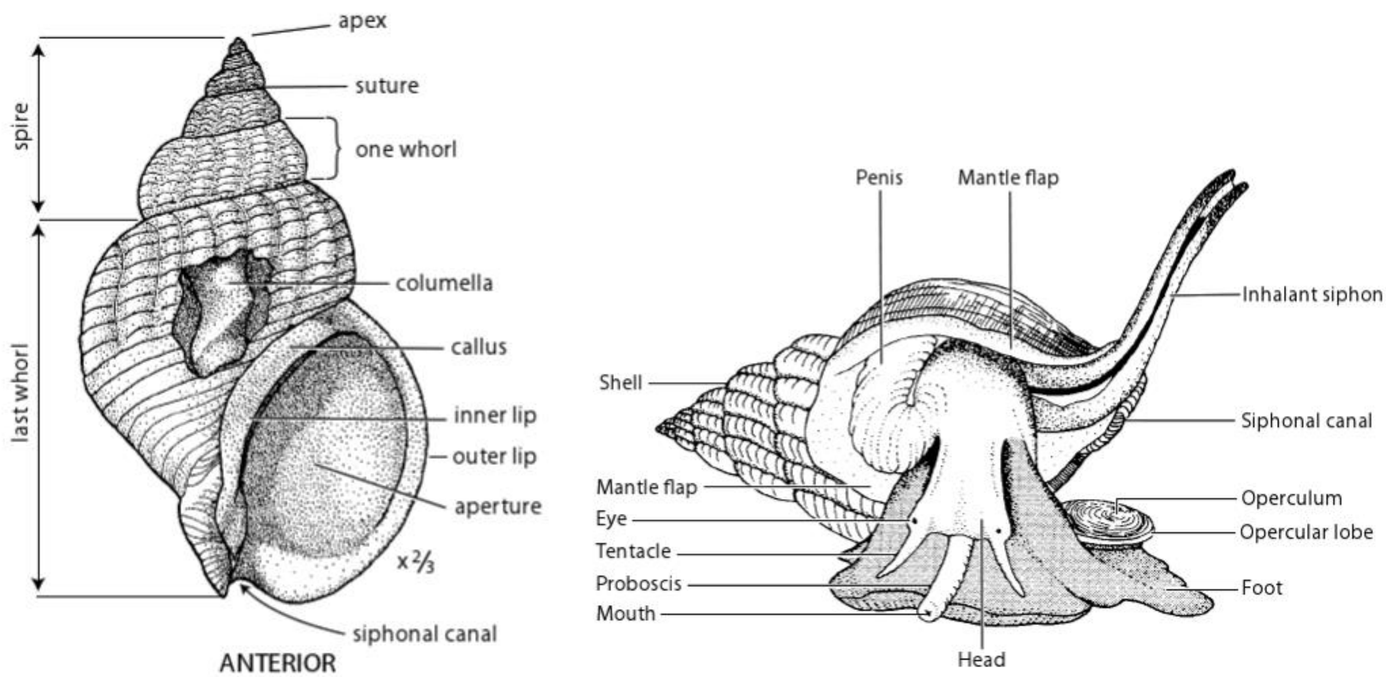


Fig. 3. Hard and soft anatomical features of a gastropod. (Prothero 2013)

Taxonomy:

Prosobranchia: All gastropods with gills and obvious torsion.

Archaeogastropoda: Bipectinate gills, commonly with holes or slits to facilitate waste removal. Found predominantly on rock surfaces and seaweeds; herbivorous. Abalone, keyhole limpets, limpets, slit snails, turban and top snails. Cambrian to Recent.

Mesogastropoda: Monopectinate gills modified so that snails can inhabit soft sediment environments. Marine, fresh water, and one land clade; some herbivores, but many predators. Periwinkles, high-spired turritelids, vermetids, slipper snails, conchs, cowries, moon shells (naticids). Middle Ordovician to Recent.

Neogastropoda: Modified gills, as in mesogastropods, differing in details of radula and sensory organs. Mantle margin modified to form anterior siphon that draws water into mantle cavity. Marine. Mostly carnivorous. Whelks, muricids, olive snails, cone snails. Cretaceous to Recent.

(Note: Many systematists now view the archaeogastropods as a paraphyletic group and the meso- and neogastropods as intermingled within a monophyletic subset of the archaeogastropods.)

Opisthobranchia: Torted only 90 degrees during ontogeny. Shell may be reduced or absent. Distinct folded gill structure. Shell and mantle cavity usually much reduced or absent. Mostly marine. Sea slugs, the pelagic pteropods. Mississippian to Recent.

Pulmonata: Detorted snails with no gills; mantle cavity modified to form a lung. Most (16,000 species!) land snails, including slugs. Pennsylvanian to Recent.

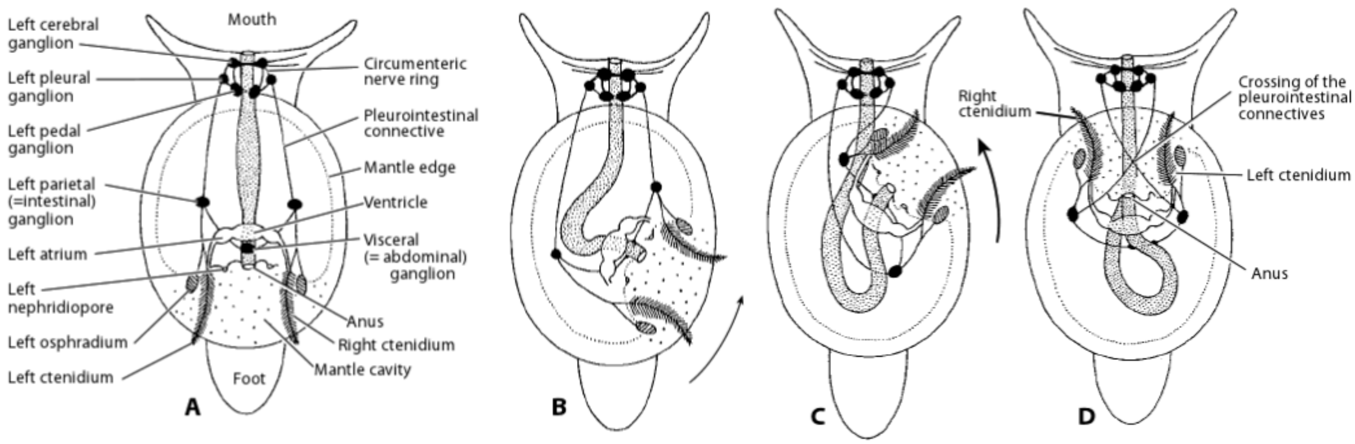


Fig. 4. Dorsal views of an adult gastropod. (A) Hypothetical untorted gastropod. (B and C) Stages of torsion as they might appear in an adult snail. (D) After torsion. (Prothero 2013)

Geologic History:

Conchiferan molluscs with spiral shells appeared early in the Cambrian. Some have been called gastropods, but most are now interpreted as stem conchiferans or monoplacophorans. Indeed, most planispirally coiled, non-sepatate shells are now assigned to the Monoplacophora, including such common Paleozoic fossils as bellerophontids. Unambiguous gastropods were present by the Late Cambrian and radiated along with other groups during the Ordovician.

Although mesogastropods evolved early, nearly all Paleozoic gastropod fossils are those of archaeogastropods. Pulmonates invaded the land as early as the Pennsylvanian period. Meso- and neogastropods began a tremendous diversification ca. 100 million years ago; they dominate most Cenozoic gastropod assemblages. These latter gastropods are mostly carnivores, and their radiation has influenced the evolution of prey animals, including bivalves.

Cephalopoda

The cephalopods are pelagic, predaceous molluscs with the anterior portion of the foot modified into **tentacles** that surround the mouth (cephalopod, literally “head foot”) and the mantle margin modified into a **funnel** that facilitates movement by jet propulsion. Cephalopods include the largest and most behaviorally sophisticated of all invertebrates. They are currently represented by about 600 species, but more than 7500 fossil cephalopod species have been described – mostly ammonites.

Shells straight, planispiral,(rarely) asymmetrically spiral, reduced, or absent. Where the shell is complete, it is divided into gas-filled **chambers**. The shell is divided internally by transverse **septa**. The juncture between septum and side wall is called the **suture**; it can be simple or remarkably complex. A tube called the **siphuncle** runs the length of the shell interior, perforating the septa and permitting gas exchange with empty chambers.

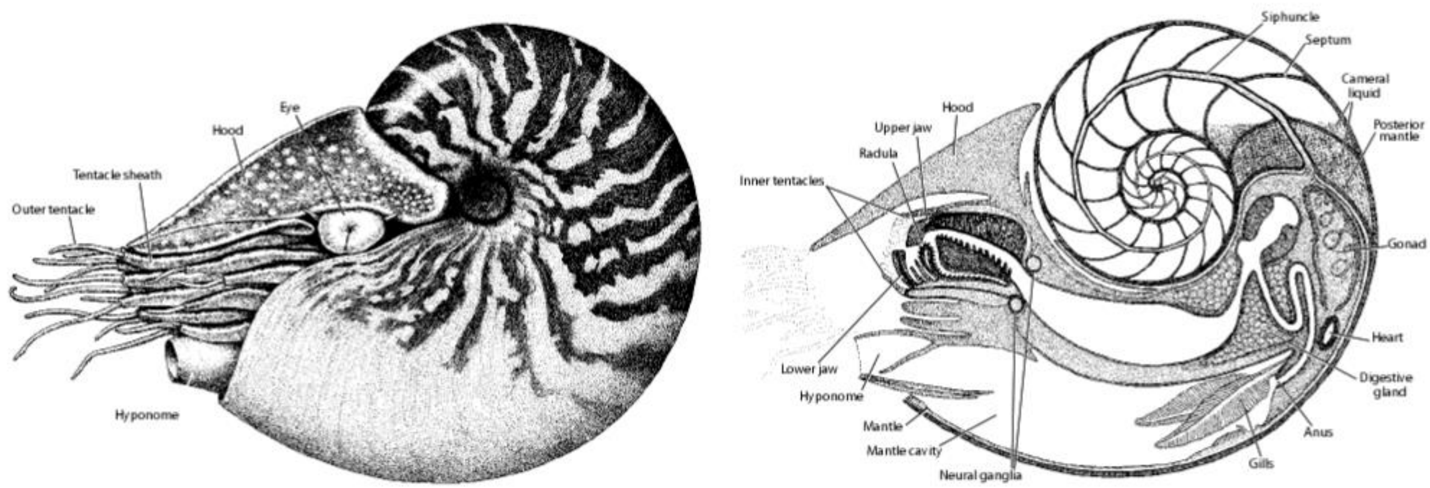


Fig. 5. The external and internal features of the living *Nautilus*. (Prothero 2013)

Taxonomy:

Nautiloidea: Coiled or straight external shells with simple sutures. Numerous tentacles, two pair of gills. Late Cambrian to Recent. The only living nautiloid is the chambered nautilus (*Nautilus*).

Ammonoidea: Extinct cephalopods with coiled shells characterized by complex septa and sutures. Ceratites, goniatites, and ammonites. Devonian to Cretaceous.

Coleoidea: Thought to be a sister group of the ammonoids. Shells internal, reduced, or absent. One pair of gills; eight to ten tentacles with suckers. Includes the extinct **belemnites**, cuttle fish, squid, octopus. Devonian to Recent.

Geologic History:

Nautiloid cephalopods appeared late in the Cambrian and emerged as important members of marine ecosystems by the Ordovician. Ordovician faunas are dominated by straight-shelled nautiloids. Various groups are recognized on the basis of shell features associated with buoyancy control, including secondary calcification of empty chambers and shedding of distal portions of the shell. By the Devonian Period, coiled nautiloids had begun to diversify, as had coiled ammonoid cephalopods. Most Paleozoic ammonoids have relatively simple suture patterns, termed **goniatitic** and **ceratitic**, but **ammonites** appeared late in the Paleozoic Era. Following major extinction at the Permo-Triassic boundary, the **ammonites** diversified to become dominant components of Mesozoic marine ecosystems (as well as key biostratigraphic indicators in Mesozoic rocks). At the K-T boundary, their luck ran out, and ammonites became extinct. Nautiloids show lower “volatility”; they have not been major players since the end of the Triassic, but persist today as the single genus *Nautilus*, with half a dozen species.

Coleoids evolved as early as the Devonian. The best known coleoid fossils are those of **belemnites**, cigar-shaped internal shells that are common in Cretaceous rocks.

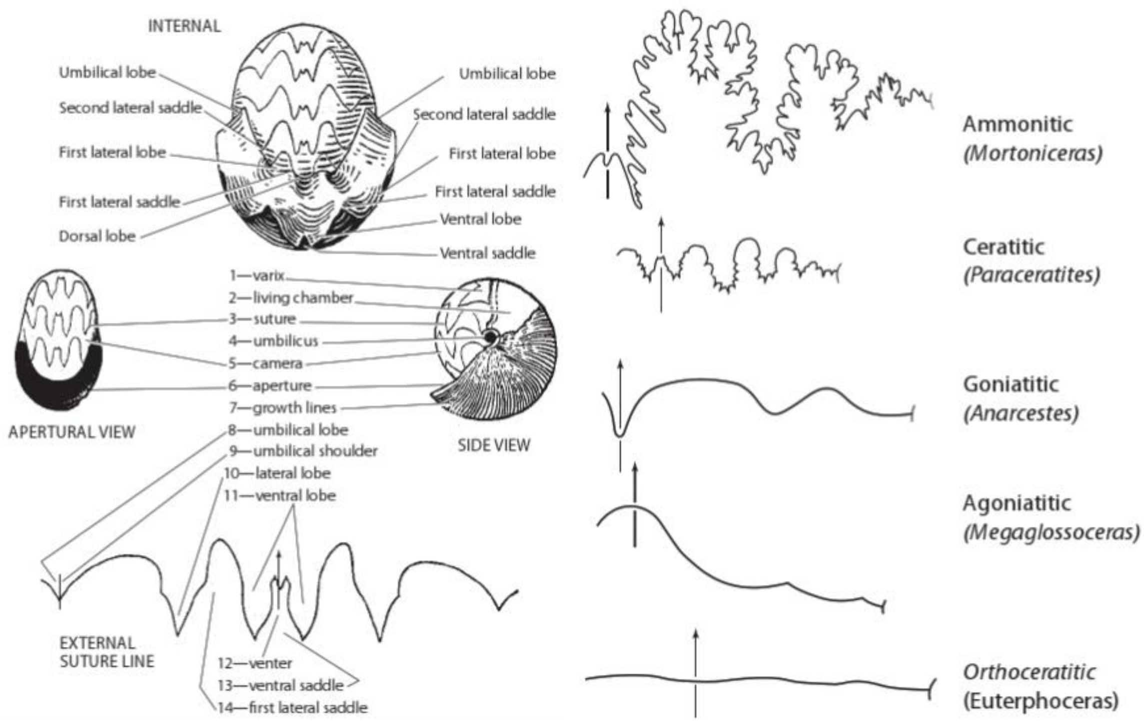


Fig. 6. The terminology of the ammonoid suture and the five commonly recognized cephalopod suture types. (Prothero 2013)

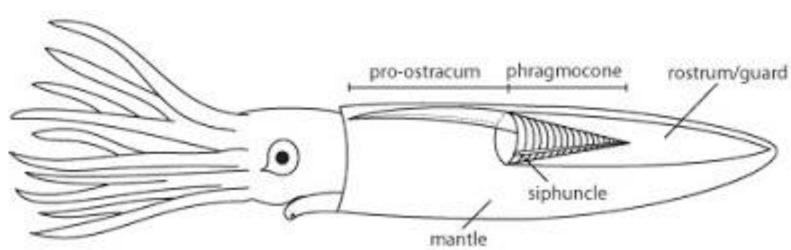


Fig. 7. The anatomical features of belemnites. (Prothero 2013)

Questions

1. You will work in two groups of five for this exercise. Each group has a bunch of modern and fossil mollusk specimens. Your first task is to work as a group to identify each specimen to the class level: Bivalvia, Cephalopoda, or Gastropoda.

2. Now that you've sorted your specimens into classes, now use the paper on your table to draw a phylogeny of all the specimens. When constructing a phylogeny you want to identify characters that are shared between closely related groups. The purpose of this exercise is not for you to come up with the "correct" phylogeny (scientists are still actually working on that today), but rather to get you to observe the morphology and identify features that you think demonstrate shared evolutionary history.

3. What different life habits have molluscs evolved to fill? Circle all that apply and give an example of a class (for example, gastropoda) for each:

Pelagic Epifaunal Infaunal Neofaunal

Sessile (stationary) Motile along sea bottom Planktonic (floating) Nektonic (swimming)

Marine Freshwater Aerial Terrestrial

Primary producer Filter feeder Sediment feeder Herbivore Carnivore