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What is a Mollusk?



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Defining the mollusk

Mollusca, from the Latin root for “soft,” might seem an odd descriptor for these animals if you’re mostly familiar with mollusks in a culinary, shell-collecting, or decorative context. In many of our most familiar mollusks, the hard shell is widely considered either the most interesting and valuable part or the chief barrier between you and your meal.

If you’re inclined to agree with the former, you view mollusks in much the same way as many snail and bivalve taxonomists do. If you hold the “barrier” view, you are in sympathy with a wide range of marine wildlife, in addition to billions of human diners. Either way, you have a valid point, but it neglects several important groups of mollusks. In addition to the bivalves and snails that immediately spring to the shell-focused mind, consider the octopus and squid, whose highly reduced “shells” are completely internal. And let’s not forget the slugs. There are several branches within the Gastropoda with reduced, barely noticeable shells, much like the cephalopods, and others whose shells have been entirely lost. Then there are the aplacophorans, which throughout their evolution never possessed a shell. If we are to define the mollusks using traits widely shared among the major groups, we must rely heavily on features of their soft tissue.

Habitat, physiological characters, and behavior

Mollusks are very efficient in the use of their body parts. They never settle for one function when an organ could serve two or six purposes at once. A good example of this is the mantle, a membranous projection of a mollusk body wall. The mantle encloses and protects the animal's internal organs, leaving room for an open internal space called the mantle cavity. The cavity is positioned differently in different mollusk groups and is filled with air or water—whatever is in the outside environment of the animal. It can serve as a space to exchange carbon dioxide for oxygen from that air or water (respiration, in either case), a chamber through which to pump water and filter out food particles, a sampling area for sensory organs to test the air or water, a threshold through which to dump waste products, or a safe place to keep eggs while they mature. Some groups use it for all five (Tudge, 2000).

The mantle also secretes the shell, in those mollusks that have one. In many gastropods and cephalopods, the mantle is brightly colored and important for communication. In giant clams, the outer mantle tissue is colonized by symbiotic algae that provide their host with food energy in exchange for shelter. Since in bivalves the mantle is the tissue closest to the outside world, it's the best place to put sensory organs, like eyes or sensory tentacles, or both. In many bivalves and snails, and in cephalopods, part of the mantle is modified into a siphon, which can be used to pump water through the mantle cavity for respiration, feeding and/or jet propulsion.

Freshwater and marine mollusks have gills (called ctenidia) for respiration, located in the mantle cavity. In most bivalves, these are enlarged and serve to trap food particles as well (Morton 1983).

The nephridia, or kidneys, are responsible for final processing of urine, receiving it from the coelom, filtering out any usable nutrients and dumping in additional waste products before ejecting it into the mantle cavity. In many mollusks, the gonads also feed into the coelom, and the egg and sperm cells they send there also need to get to the mantle cavity. The nephridia perform this function, too (Ruppert et al. 2004).

Most mollusk groups do share one other structure that is neither soft nor (apparently) multipurpose: the radula, a filelike feeding apparatus; all groups but the bivalves and some aplacophorans have one. Though the structure is shared among many species, its shape and features vary widely according to the diet of the owner, and it can be an important characteristic in classification.

Masters of mucus

If you're acquainted with terrestrial mollusks, you're already aware of the importance of mucus to these animals. In mollusks that move by gliding along on their muscular foot, lubricating mucus is an important part of this process. Locomotory mucus can take up to 23% of the energy budget of some intertidal snails (Davies et al. 1989). In the evolution of the shelled mollusks, an early stage of the shell probably involved a protective mucus coating, which eventually became a rigid cuticle before finally becoming hardened with calcium carbonate into the familiar modern mollusk shells (Marin et al. 2000). The most widespread function of mucus in the mollusks is for digestion. Strands of mucus originating at the mouth trap and transport food particles through the digestive tract to the anus. In the standard body plan all of this is internal, but some marine species go fishing with their mucus strands, casting them out into the water and swallowing them once they've trapped enough passing food particles (Walsby et al. 2009).

So what about the shell?

A hard outer shell has been an invaluable asset to many a mollusk—some successful extant lineages may owe their survival to this feature. Mollusk shells have even influenced the fate and evolution of non-mollusks, of which hermit crabs may be the best example. So despite the fact that shells are not a requirement for molluskhood, they're still worthy of discussion.

Mollusk shells are made up of chitin (the chief component of crustacean shells) and proteins, reinforced with calcium carbonate. This mineral occurs naturally in a couple of different crystal structures, aragonite and calcite. Mollusk shells rely chiefly on aragonite, possibly because this was the crystal more easily precipitated from sea water at the time when mollusks first started calcifying their shells (Porter 2007). Aragonite is also used by scleractinian corals for their skeletons, so it's not surprising that sand in many productive marine regions consists largely of aragonite; it's mostly the broken, ground up shells and skeletons of mollusks and corals past.

Their aragonite preference may leave both corals and mollusks especially vulnerable to ocean acidification. At its present pH level, the ocean is well supplied with the minerals needed for all organisms that use calcium carbonate to build their shells or skeletons. It has been estimated that by the year 2050, rising acidity will begin to deplete the available ions below optimal levels for aragonite building in the cold waters of the Southern Ocean (Orr et al. 2005). Species that can build with calcite, like sea urchins and some sponges, will be slightly less sensitive to the change.

Masquerade and mistaken identities

If any of these mystery mollusks fooled you, you're in good company. When the name "Mollusca" was first coined, it also included barnacles (later discovered to be crustaceans), brachiopods (a separate phylum) and sea squirts (which are actually chordates, like you and me!) (Tudge 2000). Among the currently recognized mollusks, aplousobranchs have historically been classified as sea cucumbers, as well as sipunculans, priapulids and other worms (Heath 1868). Nudibranchs frequently appear in identification guides together with flatworms since observers have trouble distinguishing them. The animals can take part of the blame for this last confusion—there are convincing cases of mimicry between the two groups. The exact details of most cases are not known, but overall it's not surprising; mimicry is common in cases in which a toxic or unpalatable organism uses visual cues, such as striking color patterns, to help predators learn to recognize and avoid it. Many nudibranchs carry distasteful chemicals from the sponges they feed on, and advertise their identity with bright colors and patterns; other nudibranchs as well as flatworms have evolved similar color patterns in order to take advantage of this warning (Seifarth 2002). Mimicry aside, the widespread confusion of mollusks with other animals is testament to their incredible diversity of form.

This wide range of shapes and sizes may help explain how Mollusks have become such a globally cosmopolitan success. There are nearly 100 000 known species and this is likely to be a gross underestimate of the total number, considering how many mollusks we've already found in remote habitats, like the deep sea, that we have as yet only barely sampled. There are mollusks crawling through leaf litter and climbing in trees, clinging to rocks in lakes and rivers and on shorelines, and gliding along or burrowing under the ocean floor at every depth and latitude; there are winged mollusks soaring through the sunlit waters of the epipelagic zone, giant mollusks grappling with sperm whales in the abyssal

depths, and countless tiny interstitial mollusks living between grains of sand (Giere, 2009), which we have scarcely begun to catalog (eg: Burghardt et al, 2006).

Major molluscan groups

Aplacophorans

Aplacophorans, the mollusks that never had a shell, are now known to be two separate groups, the caudofoveates and the solenogastres. Though they lack shells, they do have calcified spicules on their skin, which give them a fuzzy appearance. Both groups lack eyes and tentacles, but at least some of them are equipped with a radula, which varies widely in shape, depending on the diet and feeding method of the animal (Bunje 2003). Most are just a couple of centimeters long, but a few measure as long as 30 cm. Caudofoveates burrow in the seafloor, throughout the global oceans, at all depths (Salvini-Plawen, 2008), and feed on microbes and detritus; they are well adapted for burrowing. They are slender and vermiform, and protected from abrasion by a tough cuticular head shield. Solenogastres are broader bodied and equipped with a long, grooved foot and pedal gland, good for gliding over hard substrate, and over the corals and other cnidarians they feed on (Heath 1911, Salvini-Plawen 1980). They probably locate their prey by smell (Scheltemaa and Jebb 2007). Some species have shown regenerative capabilities—if the posterior end is cut off, it will grow back. This occasionally results in a forked tail (Baba 1940). Caudofoveates have separate sexes but solenogastres are hermaphrodites, starting life as males and become females when they're older.

Bivalves

Bivalves' shells are divided in two halves, hinged by an elastic ligament. Within mollusks, bivalves are second only to snails in number of known species, and are incredibly diverse in size, shape, and mode of life. One of the major subgroup of bivalves, the Protobranchia, contains burrowing species that commonly feed on deposited sediment, using tentacles that extend from their mouth (called palp proboscides). Another major subgroup, the Pteriomorphia, includes species that suspension-feed and most live above the sediment, in various ways. They may attach to rocks or other hard substrata using proteinaceous threads (called byssus), cement their shell to exposed surfaces, bore into rock or coral, or simply recline on the sea bottom. Pteriomorphians comprise some of the most familiar and economically important bivalves, such as scallops, oysters, and marine mussels. Most members of the third and last major bivalve subgroup, the Heteroconchia, are burrowers that suspension-feed by filtering water circulated through their mantle cavity via a pair of siphons. However, Heteroconchia also includes species that live above the sediment, such as the wood-boring shipworms or the giant clams. Freshwater clams, manila clams and quahogs are among the most familiar heteroconchs.

Cephalopods

Cephalopods are one of the smaller mollusk groups at around 800 known species, but they are the most familiar group to many of us thanks to their elaborate, well documented behavior. Cephalopods are found throughout the world oceans at all depths. In this group, only the Nautiluses have a substantial outer shell. In other cephalopods it has been reduced to a small internal structure, the “pen” in squid or the “cuttlebone” in cuttlefish. The un-armored cephalopods rely for safety on an array of strategies including camouflage, constructed shelter, and flight. In a pinch, digging works too. Cephalopods are intelligent and highly visual. They're great visual communicators; elaborate posturing and skin pigment displays accompany social behavior, including aggressive behavior. All cephalopods can get around using jet

propulsion; however, all but the Nautilus rely chiefly on their fins except when high speed is urgently needed. Fins are attached to the mantle and vary from a continuous encircling skirt to a pair of stubby (but effective) flappers. Some cephalopods show parental care; eggs may be brooded by the mother or attached in a sheltered nook on the seafloor, where in some species they are tended until hatching.

Chitons

Chitons (Polyplacophora) are protected on their dorsal side by eight overlapping shell plates, which provide protection while allowing flexibility, as the animal crawls over curved and uneven surfaces, including other mollusks. The underside is unprotected, but the animal may have additional armament around the shell plates, on the girdle. This can be in the form of spicules or spikes. Chitons scrape food from rock or other hard surfaces with a well-developed radula; their diet can include algae, bacteria, and small sessile animals such as sponges or bryozoa. The largest known species, the Giant Pacific Chiton, can grow to about a foot long.

Snails

Snails (Gastropoda) are the largest Mollusk subgroup, with about 400 living families and tens of thousands of species. Snails are globally distributed in nearly every habitat, on land and under water. Most marine and aquatic snails are benthic, but a few are swimmers. Snails encompass a myriad of lifestyles, from predators to algae grazers, as well as an incredible diversity of form, most obviously in the shape and position of the shell- or its absence. When present, the shell is usually coiled, and usually, but not always, in a right-handed direction. Sometimes an operculum is also present, a door which fits in the opening of the coiled valve, shutting the animal inside for defense. In some snails the entire shell is internal, covered with skin. In groups lacking the protection of a shell, like the nudibranchs, many species are elaborately colored, either to blend with a similarly colored background, or to warn predators of noxious taste. Some pelagic snails, both shelled and shell-less, are transparent.

Monoplacophorans

Monoplacophorans bear a single shell and if you were looking at one shell-side up you might confuse it with a bivalve. Modern Monoplacophorans live in the deep sea, though fossil relatives once lived in shallow water also. We first discovered living representatives of this group only sixty years ago.

Tusk shells

Tusk shells (Scaphopoda) can be 3–15 cm long and are protected by a curved, tubular shell shaped like an elephant's tusk. The shell is open at both ends, and both the head and foot of the animal are at the broader end. The animal creates a current through the shell using its cilia and occasional contractions of its muscles to bring in water for respiration, which exits the narrow end of the shell. They live in the sediment and most feed chiefly on foraminiferans, but detritus, microbes, and other small prey are also taken by their fine, cilia-covered tentacles.

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