MOLLUSCA

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Summary

The Mollusca are the second largest phylum next to Arthropoda, with about 200,000 living species. They exhibit a great range of body form and physiological, behavioral and ecological adaptations. Their soft body is typically partially or entirely covered with a protective shell, although this is secondarily lost in some groups (e.g., slugs,

octopuses). Mollusks have an excellent fossil record extending back some 560 million years to the early Cambrian. They are divided into three major classes, Gastropoda (snails, slugs, limpets), Bivalvia (scallops, clams, oysters, mussels) and Cephalopoda (squid, cuttlefish, octopuses, nautilus) and three to four minor living classes (Aplacophora - which are often divided into two separate classes) (spicule worms), Polyplacophora (chitons) and Monoplacophora (a small group of deep sea limpets with a long fossil history). A few extinct groups, often treated as classes, are also recognised.

Several groups within the gastropods have become adapted to live on land (land snails and slugs) and several groups of gastropods and a few groups of bivalves (various groups of freshwater mussels or clams) are found in freshwater. All other mollusks are marine, with the greatest diversity seen in tropical seas. Mollusks range in lifestyle from pelagic to infaunal burrowers and inhabit virtually every marine, terrestrial and freshwater environment from high mountains to the deepest sea.
Many mollusks are economically important as food, ornaments, pests and disease carriers. Some non-marine faunas, particularly the endemic snails on oceanic islands and faunas in some freshwater systems, are currently undergoing a major extinction crisis. Despite only a small fraction of the world's faunas being adequately assessed, there are more recorded extinctions of mollusks than of birds and mammals combined.

1. Introduction

Mollusks are bilaterally symmetrical eumetazoans that are very diverse in body form and size, ranging from giant squids 21 m in length to tiny snails about 0.5mm in size. Nevertheless, there are some common morphological features that enable the Mollusca to be characterized as a monophyletic group. These include having the body, which typically has a head, foot and visceral mass, being covered with a skin-like mantle that typically secretes the shell (or more rarely spicules). The calcareous shell is single and often coiled in gastropods, although it is sometimes reduced or even lost. The shell is internal in some slugs and squids and cuttlefish. In bivalves, there are two external hinged valves that comprise the shell and there are eight articulated valves in chitons. *Nautilus* is the only living cephalopod to have an external shell.

Typically, at least in the more primitive members of each group, there are one or more a pairs of gills (ctenidia) which lie in a posterior mantle (or pallial) cavity or in a postero-lateral groove surrounding the foot, into which the kidneys, gonads and anus open and which also contains a pair of sensory osphradia. The buccal cavity contains a radula - a ribbon of teeth supported by a muscular odontophore (lost in bivalves). A head-foot region can be recognized in most mollusks other than bivalves (which have lost the head). The head, bearing the mouth, is well-developed in most mollusks and is typically where the nervous and sensory functions are concentrated. Adjacent to the head is a usually large, muscular foot formed from the ventral body wall and used primarily in locomotion by way of muscular activity, mucous and cilia. The foot typically has a broad crawling surface in gastropods, chitons and monoplacophorans, but is modified in many bivalves as a laterally compressed (tongue-like) digging structure and as arms in cephalopods. It is reduced to a groove or absent in aplacophorans.

Mollusks are coelomate, although the coelom is reduced and represented by the kidneys,

gonads and pericardium, the main body cavity being a haemocoel. They lack segmentation, and have spiral cleavage. Trochophore and/or veliger larvae are found in many aquatic taxa, but direct development is also common.

Mollusks are an extremely diverse group of organisms. About 75 000 living species and about 35 000 fossil species have been named, making Mollusca second only to the Phylum Arthropoda in terms of the number of species known. With an estimated 200 000 living species, they are the most diverse group of marine organisms. The majority of mollusks are marine, but large numbers of species occupy freshwater and terrestrial habitats. Mollusks are also extremely diverse in their food habits, ranging from species that graze on or filter microscopic algae, those that eat fungi or the leaves of terrestrial plants, to predators that capture fish and other mollusks. Many species of mollusks are important to humans. A large number of bivalves and some snails are important sources of protein. Some bivalves, particularly pearl oysters, produce pearls. Other species are pests in gardens and to crops. Some are essential components in the life cycles of human parasites, including devastating diseases such as schistosomiasis. And a few, such as oyster drills, cause problems by preying on other mollusks that are important to us.

The earliest undoubted mollusks are found in the Early Cambrian (approximately 560 mya) when several major groups (gastropods, bivalves, monoplacophorans, and rostroconchs) are known. The cephalopods are found from the Middle Cambrian, polyplacophorans from the Late Cambrian, and scaphopods from the Middle Ordovician. Studies on molluskan evolution are able to utilize this rich fossil diversity and can be particularly illuminating when combined with morphological, ultra-structural, embryological and molecular studies on Recent taxa. Studies on the genetics, diversity, phylogeny and ecology of mollusks have provided important insights into evolutionary biology, biogeography and ecology in general.

Mollusks occur in almost all possible habitats. Although most taxa live exclusively in marine or brackish habitats, there are several groups of bivalves and gastropods that occur in fresh water and some major groups of gastropods that have adopted a terrestrial life. Within each of these habitats, mollusks play a wide variety of essential ecological roles. As grazing herbivores or scrapers they can have a significant impact on the plant or algal species present in an area, especially in intertidal and shallow sublittoral habitats. As predators, they may have a similar effect on animals, especially other invertebrates including other mollusks. They are also food for a large number of organisms, including many vertebrates.

2. Relationships and Higher Classification

The living Mollusca are composed of three major classes, Gastropoda, Bivalvia and Cephalopoda, and four or five minor classes (see below), different classifications providing different interpretations of the status of the major groups. There are also several extinct classes of mollusks. The classes themselves can be arranged into several groupings; for example the Conchifera (Gastropoda + Monoplacophora + Bivalvia + Scaphopoda + Cephalopoda), the Visceroconcha (Gastropoda + Cephalopoda) and the Diasoma (= Loboconcha) (Bivalvia + Scaphopoda).

There continues to be debate as to what is the sister taxon to the mollusks. Ancestral flatworms have been proposed, while others favor sister relationships with Sipuncula or with Annelida. The latter relationship is supported, for example, by the shared possession of a trochophore larva, but annelids, unlike mollusks are segmented. Sipuncula also have a trochophore larva and are unsegmented.

3. General Morphology of the Mollusca

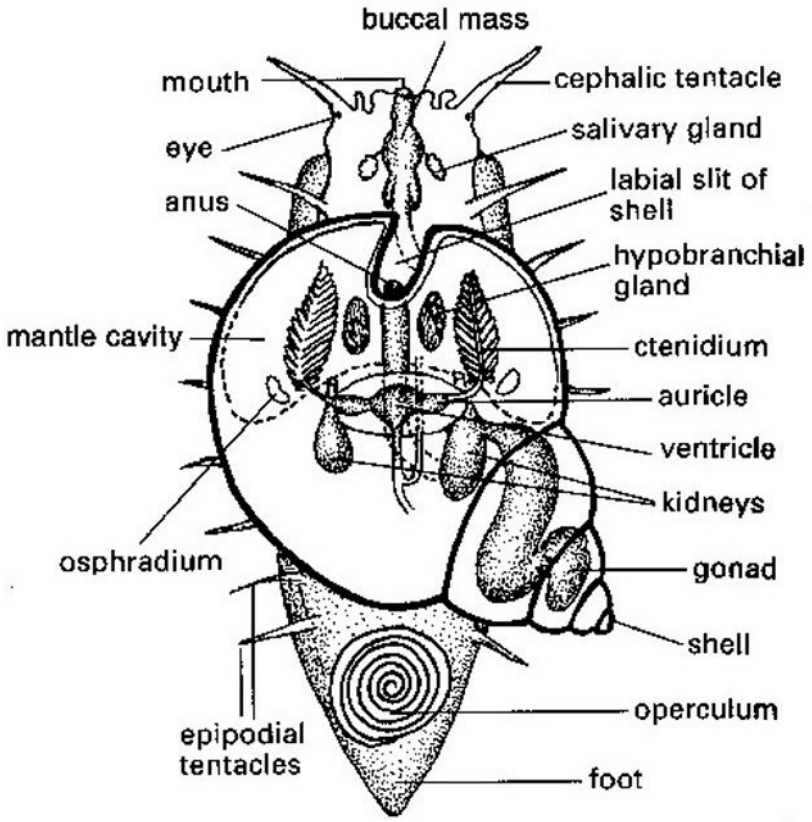
The digestive system of mollusks follows a common pattern, although in some of the more derived groups (cephalopods, bivalves, some gastropods) it is highly modified. The mouth opens to a buccal cavity that typically contains paired jaws and a muscular odontophore which bears the radula and, usually, a pair of salivary glands open to it. All of these structures, other than the mouth, are lost in bivalves. An oesophagus, sometimes with glandular pouches, opens to a typically complex stomach. The stomach contains ciliary sorting fields (muscular in cephalopods) and the ducts of the large digestive glands ("hepato-pancreas") open to it. Food particles are sorted from the waste material in the stomach and digestion occurs in the digestive gland. Waste is moved to the intestinal part of the stomach that typically starts as a style sac in which the waste string is rotated and bound with mucus before being passed into the intestine proper. In most bivalves and some gastropods, a crystalline style, a rotating rod of muco-protein that releases digestive enzymes, lies in the style sac. Faecal material is released through the anus that typically lies within the mantle cavity.

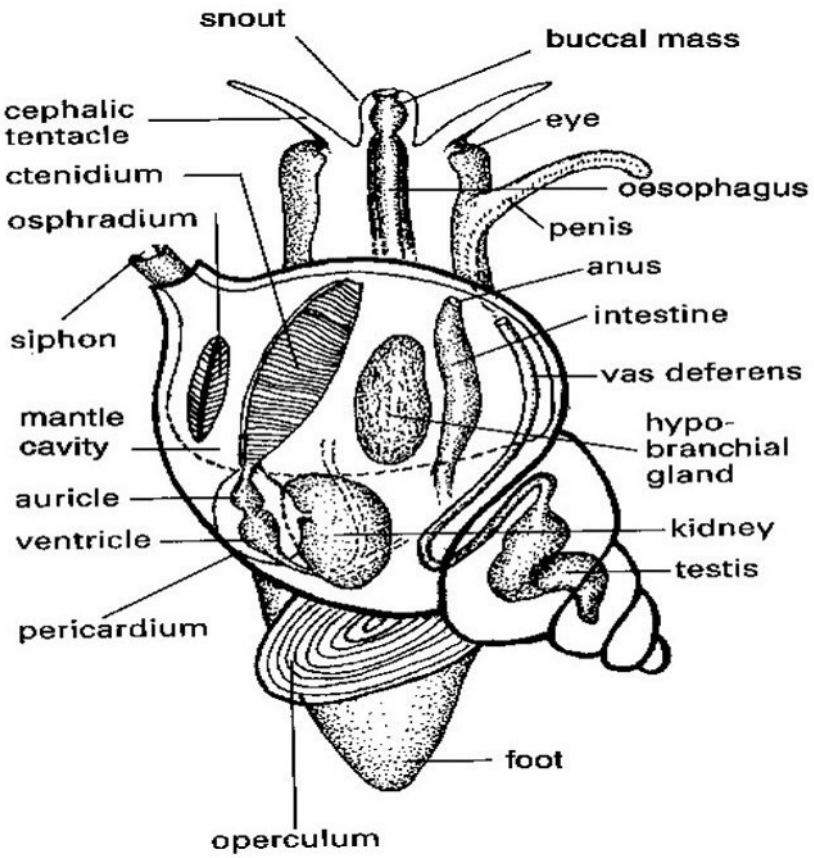
Mollusks, other than cephalopods, have an open circulatory system with blood sinuses, a heart, blood vessels, and respiratory pigment, usually haemocyanin. Cephalopods have a closed system with arteries and veins. Gas exchange is via gills, lungs, or the body surface. Excretion takes place by means of kidneys (nephridia) that excrete waste into the mantle cavity.

A fairly complicated nervous system is present, including several, mostly paired, ganglia and a system of nerves. Sensory and nervous systems are concentrated in the head region especially in gastropods and cephalopods. Highly specialized sense organs are on the head (eyes, tactile organs such as tentacles), as well as statocysts for balance and chemosensory osphradia, a pair of specialized patches in the mantle cavity. Light receptors are found on the dorsal surface of some mollusks (e.g., chitons) and on the mantle edge, particularly in some bivalves (where they may be structurally complex and eye-like). Many gastropods have small cephalic eyes and are rather complex in some groups. Most living cephalopods have large, very complex eyes that parallel those of vertebrates.

The majority of mollusks have a shell of some kind that is secreted by the mantle and constructed with calcium carbonate - either aragonite, calcite or both. The outer surface of the shell is covered by the periostracum, a horny layer composed of conchiolin. The external parts of the shell may be smooth or sculptured with ribs, frills, nodules or spines. Some shells are very thick and heavy, others very fragile and even transparent. Shell shape, size, ornament and color are important characters in classifying species of mollusks, and their diversity and beauty have also made molluskan shells popular with collectors.

Most mollusks are dioecious (separate sexes), but some are monoecious (hermaphrodite). Some groups practice internal fertilization and produce various forms of jelly or capsule-covered eggs that contain the embryo for at least part of its development, others release their gametes into the water column and their development is entirely pelagic, passing through both trochophore and veliger stages. Some planktonic larvae feed on the plankton and other suspended particles (planktotrophic), and others feed on nutrients stored in the egg (lecithotrophic). Some species have direct development, with juveniles emerging from the egg capsule or from a brood pouch within the parent. Internal fertilizing taxa may transfer sperm during copulation involving a penis or, as in cephalopods and some gastropods, by transferring spermatophores - packets of sperm.





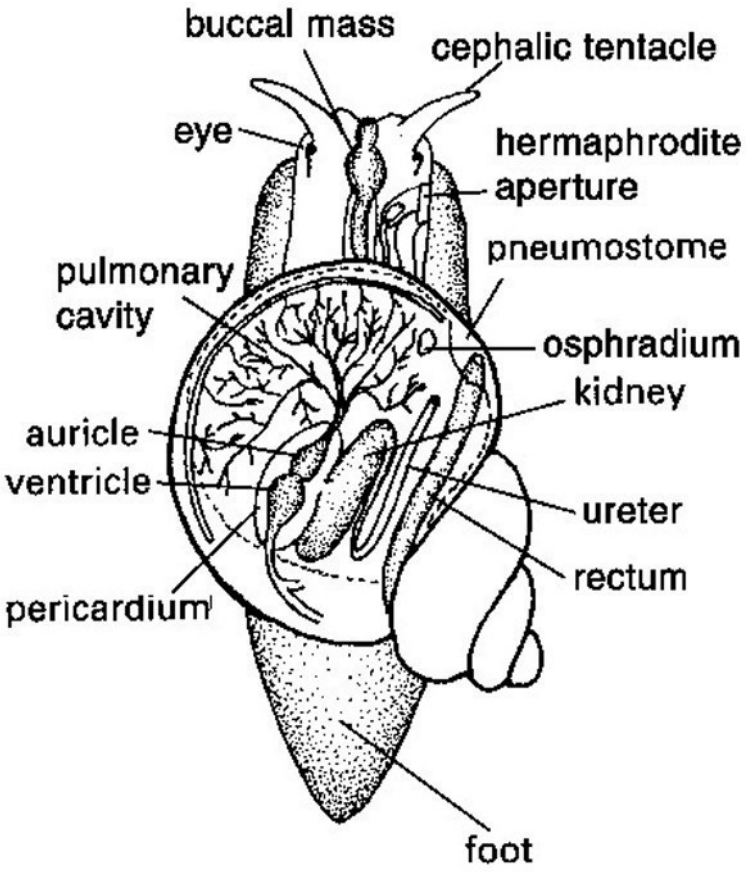


Figure 1. Structure of a vetigastropod (a), a higher caenogastropod (b) and a pulmonate (c). The diagrams emphasise the differences in the structures associated with the mantle cavity. The digestive and reproductive systems are only partially indicated (after Ivanov, 1940, taken (and slightly modified) from Healy in Anderson,1998).

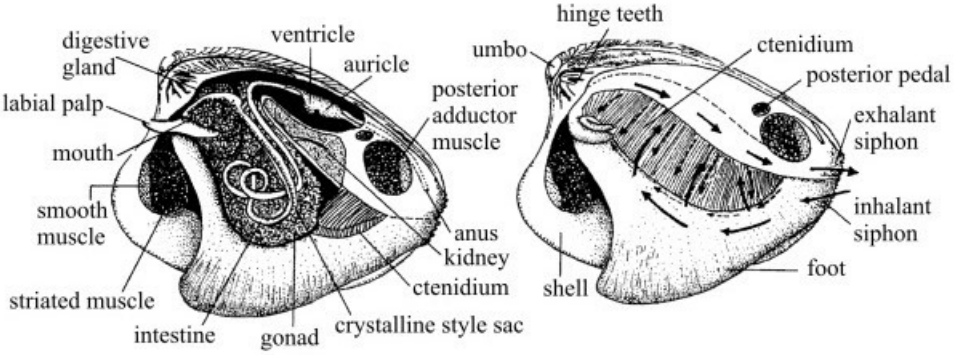


Figure 2. Structure of a typical heterodont (veneroidean) bivalve with the shell valve, mantle and ctenidia (gills) on the right side removed and the alimentary canal partially dissected (a) and with the right gills in place and showing the ciliary currents on the gills and mantle (after Barnes, 1980, copied from Healy in Anderson, 1998).

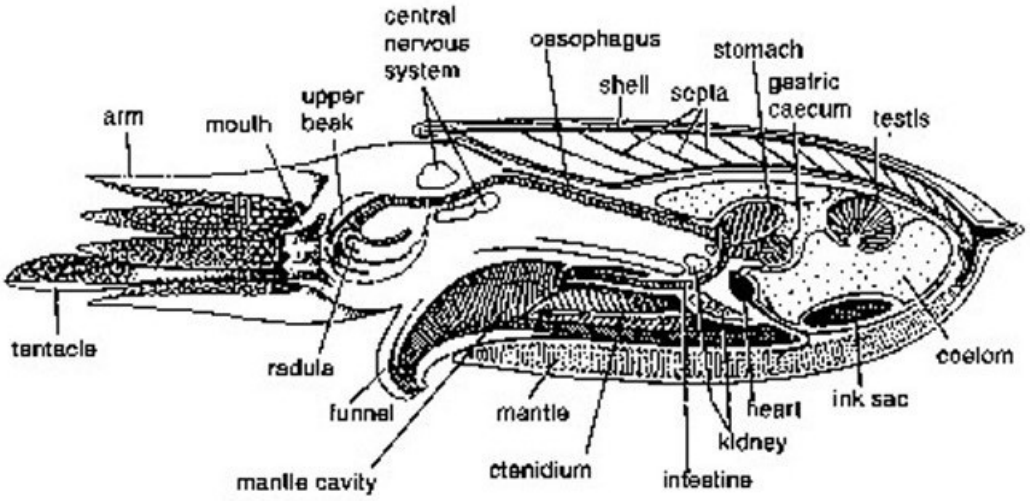
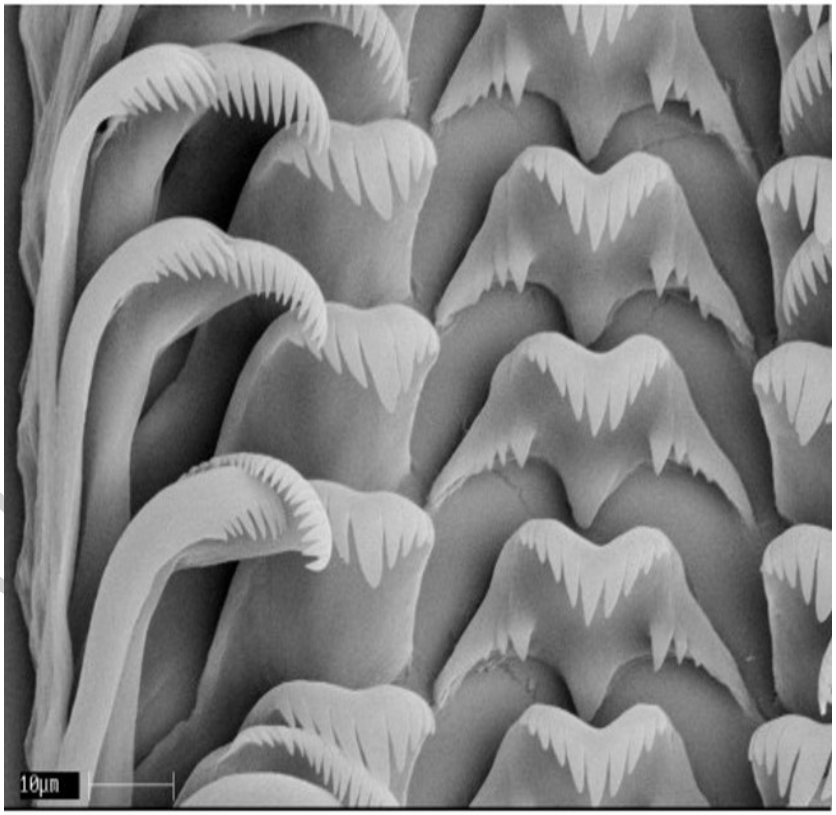


Figure 3. Structure of a decapod cephalopod (the cuttlefish, *Sepia*) (after Naef (1921-3), modified slightly from Schipp and Boletzky, in Harrison and Kohn, 1997).



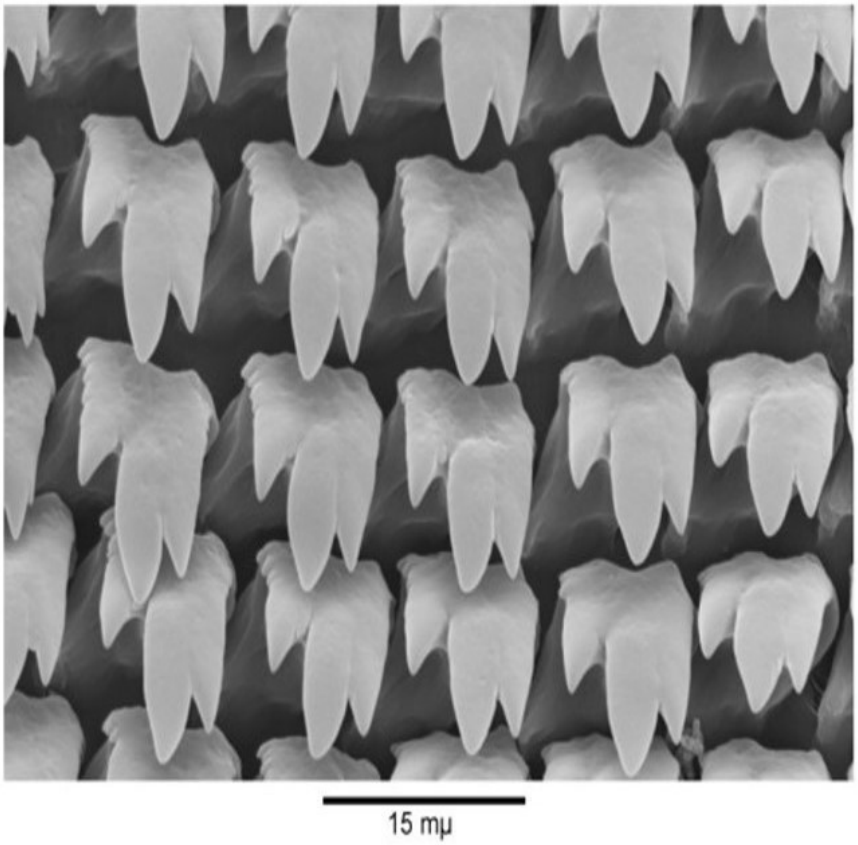


Figure 4. Scanning electron micrographs of portions of gastropod radulae. (a) several half rows of the radula of a caenogastropod (*Bithynia sp.*) that, like most caenogastropods, has seven teeth in each row, with clearly differentiated teeth. (b) a small portion of the radula of a freshwater pulmonate (*Kessneria papillosa*) with numerous rows of similar teeth.

During development, mollusks are one of several invertebrate phyla that undergo spiral cleavage. Embryological studies show that they have a true coelom (eucoelom), formed by the splitting of embryonic mesodermal masses (schizocoely) and that they have protostomous development (mouth develops before the anus), these characteristics also being shared with several other phyla.

Many mollusks pass through free-swimming larval stages called trochophore and veliger larvae. The trochophore larva, characterized by its apical tuft of cilia and ciliated bands, is found in primitive gastropods and many bivalves, as well as aplacophorans, scaphopods and chitons. Similar larvae are also found in several other marine invertebrate phyla. Veliger larvae are characteristic of gastropods and bivalves and have a bilobed, ciliated swimming organ known as the velum that, in feeding larvae, also collects food particles from the water.

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Biographical Sketch

Winston Ponder is a Principal Research Scientist in the Malacology Section of Invertebrate Zoology, in the Australian Museum, Sydney, Australia. He graduated from the University of Auckland, New Zealand and has since published more than 140 research papers. His research interests include systematics of mollusks, in particular the phylogenetic relationships of gastropod mollusks and their biology, and Australian-region freshwater mollusks. He is also active in the conservation of mollusks and other invertebrates.