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REVIEW

Structure and function of the digestive system in molluscs

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Abstract

The phylum Mollusca is one of the largest and more diversified among metazoan phyla, comprising many thousand species living in ocean, freshwater and terrestrial ecosystems. Mollusc-feeding biology is highly diverse, including omnivorous grazers, herbivores, carnivorous scavengers and predators, and even some parasitic species. Consequently, their digestive system presents many adaptive variations. The digestive tract starting in the mouth consists of the buccal cavity, oesophagus, stomach and intestine ending in the anus. Several types of glands are associated, namely, oral and salivary glands, oesophageal glands, digestive gland and, in some cases, anal glands. The digestive gland is the largest and more important for digestion and nutrient absorption. The digestive system of each of the eight extant molluscan classes is reviewed, highlighting the most recent data available on histological, ultrastructural and functional aspects of tissues and cells involved in nutrient absorption, intracellular and extracellular digestion, with emphasis on glandular tissues.

Keywords Digestive tract · Digestive gland · Salivary glands · Mollusca · Ultrastructure

Introduction

The phylum Mollusca is considered the second largest among metazoans, surpassed only by the arthropods in a number of species. However, the number of mollusc species is far from being accurately known, with a lower estimation of 70,000 named living species (Rosenberg 2014). The real figure is probably significantly higher because many species are still being discovered. Nonetheless, the number of described living species is still considerably lower than the upper estimation of 200,000 for the total number of extant mollusc species (Lindberg et al. 2004).

This phylum is not just huge in number of species, but it also encompasses a large morphological diversity, ranging in size from the tiny worm-like aplacophorans to giant squids. Despite this diversity, several features characterise the mollusc soft body, which is typically divided into head (not present in bivalves), foot used for locomotion (absent in caudofoveates) and visceral mass. The visceral mass is dorsally covered by the mantle tissues that frequently extend outwards to create a flap around the body forming a space in between known as pallial or mantle cavity. The gills of most aquatic species are located in this cavity, and in terrestrial snails and slugs, the pallial cavity functions as a lung. The mantle is also responsible for the formation of the shell (or sclerites in the shell-less aplacophorans). Although typical of molluscs, the shell can be reduced and internal in some or even entirely absent in others, and in these cases, the mantle becomes the dorsal surface of the body (Lindberg et al. 2004). Another unique feature of molluscs is the radula, a ribbon of chitinous material with teeth supported by the odontophore, a cartilaginous structure associated to a complex system of muscles responsible for radular movement during feeding (Katsuno and Sasaki 2008). In many molluscs, the chitinous organic matrix of radular teeth is mineralised with silica, iron oxides, calcium and other metallic elements. The radular teeth of chitons and limpets that feed by scraping algae from rock surfaces being also able to extract endolithic microorganisms from rocks are heavily mineralised for extra strength (Okoshi and Ishii 1996). The radular teeth of the common limpet *Patella vulgata*, having a composite structure of goethite nanofibres (an iron oxide) within a softer protein phase to provide mechanical integrity during feeding, were considered the strongest known biological material (Barber et al. 2015). The class Bivalvia, in

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which the head is absent, is the only class of molluscs in which the radula is lacking in all species.

Phylogenetic and morphological studies support the monophyly of the Mollusca and its traditional extant eight classes, but despite recent advances, the phylogenetic relationships between classes still present some unsolved questions (Sigwart and Lindberg 2015; Vinther 2015). Phylogenomic analysis indicates an early split in the phylum resulting in the clade Aculifera formed by shell-less aplacophorans (Caudofoveata + Solenogastres) and polyplacophorans with eight shell plates (chitons) and the clade Conchifera (Fig. 1). The last one includes all other living and fossil species descendent from an ancestor with a single plated shell, which became divided into two plates in Bivalvia or was secondarily lost in octopus and in several slugs (Wanninger and Wollesen 2019). Molluscs have a long evolutionary history, probably with an origin dating back to late Precambrian (Vinther 2015). According to Parkhaev (2017), the classes Polyplacophora, Monoplacophora, Gastropoda and Bivalvia appeared near the Precambrian–Cambrian boundary, Cephalopoda emerged in the late Cambrian and Scaphopoda in the Ordovician or later from still uncertain ancestors (Fig. 1). The oldest known aplacophoran-like fossils date from the Silurian (Parkhaev 2017), with a molecular clock estimated divergence from other molluscs in the late Ordovician, about 450 million years ago (Vinther 2015).

Molluscs are very successful invertebrates that have colonised all aquatic environments, from tropical to polar waters, being also found in most terrestrial habitats (Lindberg et al. 2004). More than half of the known species are marine, living from deep ocean to intertidal areas, about one third are terrestrial and more than 5000 species live in freshwater (Rosenberg 2014). Mollusc diets and feeding modes are highly diverse requiring particular morphophysiological adaptations in each case. Mollusc diets include detritus, bacteria, microalgae, protozoans, macroalgae, plants, several invertebrates and fish. According to their diet, most species are classified either as herbivores or carnivores, but true omnivory can be more common than previously thought particularly in non-selective grazers (Camus et al. 2009).

Despite all anatomical variations and specialisations that were reported, the digestive tract of molluscs can be divided into foregut, midgut and hindgut (Fig. 2). The former comprises the mouth, buccal cavity and oesophagus. The mouth opens into an oral tube usually with a pair of jaws, and the buccal cavity contains the anterior portion of the radula coming out from the radular sac where it is formed. Buccal glands and a pair of salivary glands are usually present. The oesophagus can include a dilated crop and, in some gastropods, a muscular gizzard with hard plates. Oesophageal glands can also be present. The midgut corresponds to the stomach, in some molluscs with a style sac and gastric caecum. Usually, two or more ducts

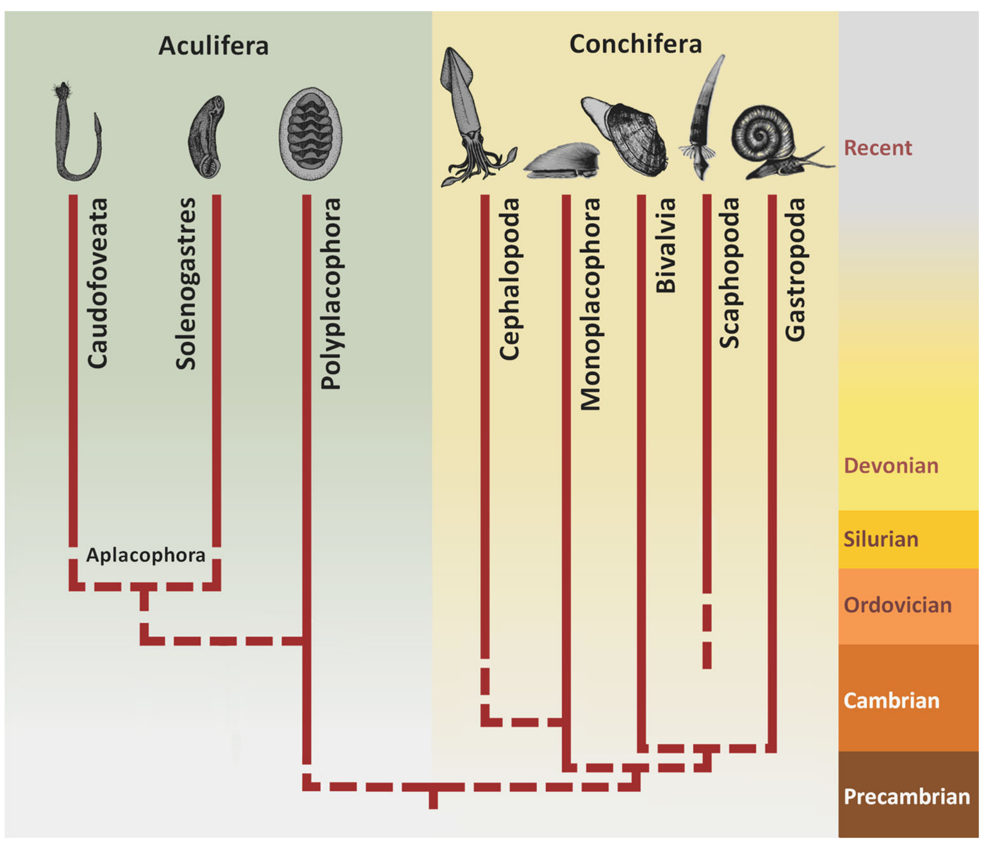


Fig. 1 Molluscan interclass evolutionary relationships according to recent hypotheses (Parkhaev 2017; Wanninger and Wollesen 2019). Fossil lineages without recent representation were not included

connect the stomach with the digestive gland. This major gland of the digestive system is typically formed by multiple tubules and has several functions, such as secretion of digestive enzymes for extracellular digestion; absorption of nutrients; intracellular digestion; and storage of lipids, glycogen and calcium, in addition to an important role in detoxification (Fig. 2). The hindgut can be divided into intestine and rectum ending in the anus. The intestine is usually long and coiled with anal glands present in some species (Fretter 1937; Voltzow 1994; Morse and Zardus 1997; Luchtel et al. 1997).

Reviews on the anatomy, histology and physiology of molluscan digestive system were previously published, some many years ago others concerning specific taxa or organs (Owen 1966, 1974; Salvini-Plawen 1981, 1988; Morton 1983; Boucaud-Camou and Boucher-Rodoni 1983; Purchon 1987; Dimitriadis 2001; Ponte and Modica 2017). This review highlights the most recent data available on histological, ultrastructural and functional aspects of tissues and cells involved in nutrient absorption and intracellular and extracellular digestion in the eight mollusc classes, with emphasis on glandular tissues.

Aculifera

The clade Aculifera comprises the two traditional shell-less aplacophoran classes Caudofoveata (=Chaetodermomorpha) and Solenogastres (=Neomeniomorpha) and the Polyplacophora. According to the Aculifera concept, aplacophorans originated from a polyplacophoran-like ancestor, a hypothesis that has received support from molecular, embryological and palaeontological data. This implies that the vermiform shell-less body of aplacophorans resulted from a simplification, probably related to the adaptation to a life in interstices of marine sediments, not reflecting a basal molluscan condition (Sutton et al. 2012; Scherholz et al. 2013).

Digestive system in Caudofoveata

Caudofoveates are vermiform molluscs with the body covered by a cuticle and aragonite sclerites, without shell and foot, ranging in length from a few millimetres to 14 cm. Only about 130 species have been described so far living in oceans from the sublittoral zone to depths of 9000 m. These molluscs inhabit burrows in the upper layers of sediments feeding on detritus and microorganisms. Although with a limited number of known species, caudofoveates are abundant in some locations being an important part of those deep-sea ecosystems (Todt et al. 2008; Ivanov and Scheltema 2008; Señarís et al. 2014). An overview of the digestive system is frequently included in descriptions of Caudofoveata species, but few publications provide specific information about the digestive system of these molluscs, and the existing ones are not recent (Salvini-Plawen 1981, 1988; Scheltema 1981; Scheltema et al. 1994).

Caudofoveates have a characteristic thick cuticularised oral shield entirely or partially surrounding the mouth. The buccal cavity contains the radula and only in one family a pair of jaws, and it is lined by an epithelium that in some species is covered by a cuticle and in others is ciliated. The folded buccal cavity is expansible and can be protrusible during feeding in some species. Epithelial and subepithelial glandular cells are generally scattered through the buccal cavity. A cluster of secretory cells open on a small papilla in front of the radula, and one or two pairs of multicellular tubular glands of uncertain homology with the salivary glands of other molluscs open close to the radula as well. Dorsal glands above the radula or behind it were also reported (Salvini-Plawen 1981, 1988). The short or moderately long oesophagus with a more or less folded wall is lined by an epithelium including ciliated areas and secretory cells. The stomach, in general lined by epithelial cells with a brush border, is crossed by one or two ciliated ridges that continue through the intestine. In some species, a style sac lined by cells with a dense cover of short cilia containing a mucoid or proteinaceous rod is present at the posterior end of the stomach (Scheltema 1981). A single dilated ventral digestive diverticulum opens at the posterior end of the stomach near the connection between the stomach and intestine (Fig. 3a). Two types of digestive cells were reported in the digestive diverticulum. The epithelium of the dorsal wall is formed by cells containing membrane-bound mineralised granules with concentric layers. Apocrine secretion was reported in these cells. The epithelium of the lateral and ventral walls is formed by club-shaped cells that in addition to numerous mineralised granules also contain a large apical vacuole enclosing a large basophilic granule that is released into the lumen by rupture of the cell apex (Salvini-Plawen 1981; Scheltema et al. 1994). The intestine is long and ciliated. Digestion was considered extracellular (Salvini-Plawen 1981), but the classic histological studies need to be complemented by additional research for a better understanding of the digestive system in caudofoveates.

Digestive system in Solenogastres

Solenogastres are also shell-less molluscs covered with sclerites, but unlike the caudofoveates, they have a narrow ventral foot. These aplacophoran molluscs are found across all oceans, living from the continental shelf and slope to depths below 5000 m. The clade includes almost 300 valid species, mostly feeding on cnidarians. Generally, Solenogastres are small measuring from less than a millimetre to 3 cm in length; nevertheless, larger species are known with a recorded maximum of 30 cm in *Epimenia babai*, and some are colourful (Todt et al. 2008; Bergmeier et al. 2017).

The mouth opens inside a vestibular pouch with sensory cells and preoral glandular cells, or directly on the body surface posteriorly to the vestibule. Preoral gland cells may contain electron-dense secretory vesicles, many rough endoplasmic reticulum cisternae and several Golgi stacks, therefore showing the ultrastructural features of protein-secreting cells. In other species, these cells have vesicles with lower electron density and were classified as mucocytes (Todt and Salvini-Plawen 2004a). The foregut can be divided into buccal cavity, pharynx and oesophagus (Fig. 3b). Depending on the species, the epithelium of the buccal cavity can be folded or almost smooth, more or less cuticularised, containing glandular cells. Sensory cells with bundles of cilia-forming cirri are also often present in the buccal cavity. A strong sphincter separates the buccal cavity from the pharynx, in which the epithelium can be similar to the one of the buccal cavity or distinct from it. Most species have radula, and at least in some, the pharynx is evertable. In those that do not have radula, the pharynx is surrounded by strong muscles functioning as a suctorial pump (Scheltema et al. 1994; Sasaki and Saito 2005).

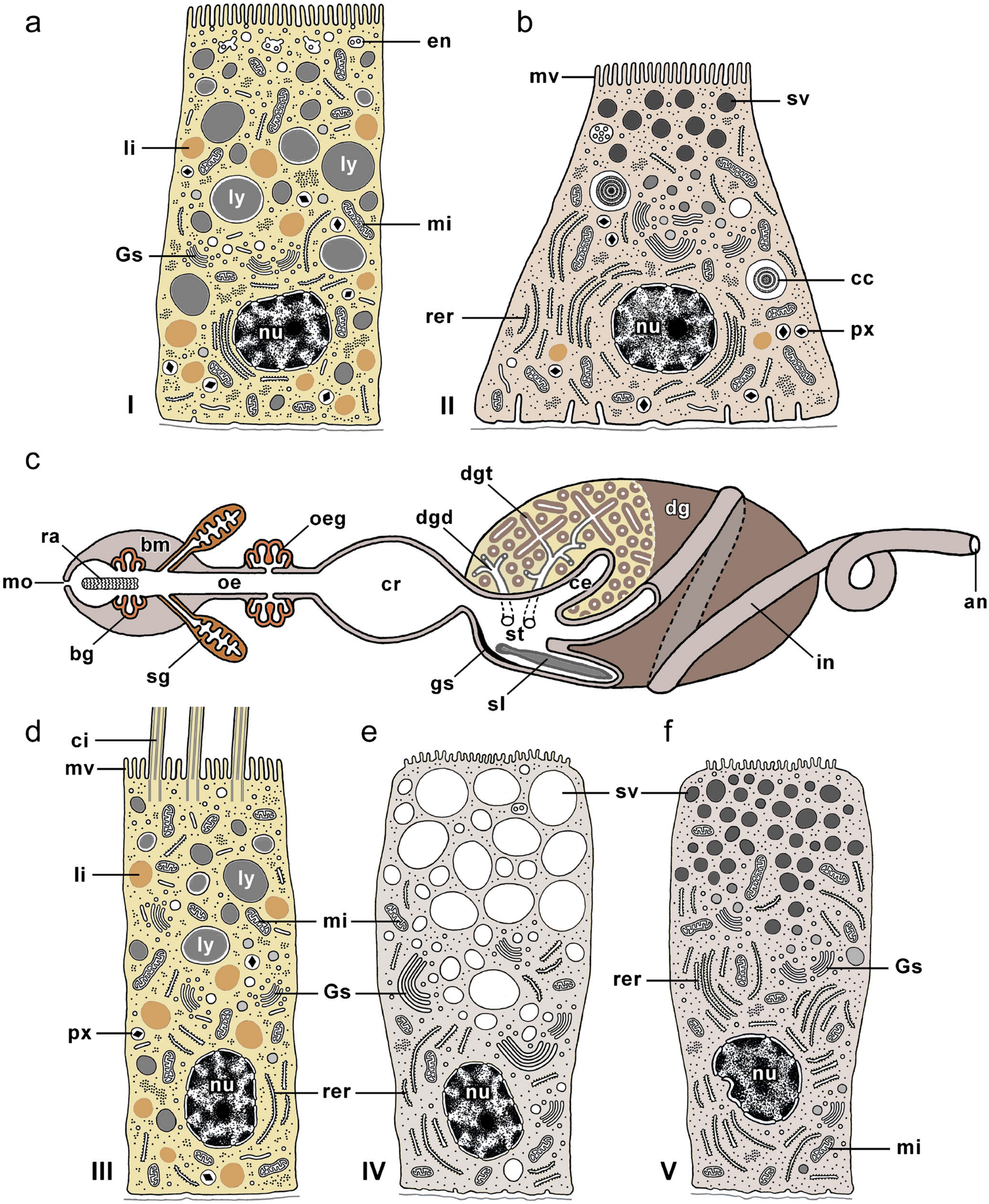
Foregut glands differ among Solenogastres and their features have been used for taxonomic purposes. Secretions are produced by multicellular glands and by more or less isolated cells distributed along the foregut epithelium mainly formed by cells with a microvillus border, both gland types coexisting frequently. In some species, such as *Wirenia argentea* and *Genitoconia rosea*, multicellular foregut glands are absent and all foregut secretion is produced by isolate glandular cell that occurs in larger numbers in the region around the radula. Close to the mouth, these cells are pear-shaped with a substantial part of the cell body protruding below the base of the supporting epithelial cells. Towards the posterior region of the foregut, glandular cells become highly elongated and subepithelial, with the cell body containing the nucleus and most cytoplasm well below the epithelium and a long narrow neck crossing the muscular layer and the epithelium to release secretory products into the lumen of the foregut. These cells were classified into different types according to size, shape and electron density of secretory vesicles. All were considered serous cells due to an ultrastructure typical of protein-secreting cells. Their cytoplasm is rich in rough endoplasmic reticulum cisternae and developed Golgi stacks, especially in cells not yet fully matured still containing a moderate number of secretory vesicles (Todt and Salvini-Plawen 2004a).

Additionally, multicellular glands are frequently present being classified according to their location into dorsal or ventrolateral glands. A single dorsal foregut gland was reported in a few species, consisting of densely packed subepithelial cells with a very long neck that releases secretory products through the roof of a pouch connected to the pharynx lumen by a duct-like passage. Four secretory cell types were reported in this gland characterised by the shape, size and electron density of their secretory vesicles. The three cell types with electron-dense secretory vesicles were classified as serous and the fourth cell type with electron-lucent vesicles was classified as mucous (Todt 2006). Paired ventrolateral foregut glands

Fig. 2 Generalised representation of the digestive system of molluscs and ▶ its major cell types (**a**–**f**). I—digestive cell of the digestive gland, II—basophilic cell of the digestive gland, III—ciliated cell of the digestive tract, IV—mucous cell of digestive tract and glands, V—protein (glycoprotein) secreting cell of digestive tract and glands. an—anus, bg—buccal glands, bm—buccal mass, cc—calcium concretions, ci—cilia, cr—crop, dg—digestive gland, dgd—digestive gland ducts, dgt—digestive gland tubules, en—endosomes, Gs—Golgi stacks, gs—gastric shield, in—intestine, li—lipid droplets, ly—lysosomes, mi—mitochondria, mo—mouth, mv—microvilli, nu—nucleus, oe—oesophagus, px—peroxisomes, ra—radula, rer—rough endoplasmic reticulum, sg—salivary glands, sl—style within the style sac, st—stomach, sv—secretory vesicles

opening into the pharynx in front or on both sides of the radula are much more common among Solenogastres, being histologically diversified (Handl and Todt 2005). Two or three different types of secretory cells were reported in ventrolateral glands of species that were investigated with transmission electron microscopy. These are subepithelial cells with a long neck, and the main differences between each type are the dimensions, shape and electron density of the secretory vesicles. In general, these cells were classified as serous due to the amount of rough endoplasmic reticulum and high electron density of their secretory vesicles. According to Todt (2006), the diversity of secretory cell types in the foregut of Solenogastres most likely reflects specific adaptations to feeding habits and digestion. Although the exact compositions of these foregut gland secretions are unknown, the predominance of serous cells suggests enzyme secretion to initiate prey digestion in the pharynx. On the other hand, the secretions of mucous cells will have a lubricating function (Todt 2006). To improve the characterisation of all these cell types, the application of histochemical techniques for protein and polysaccharide detection could be useful, given that at least some cells could be seromucous producing a glycoprotein secretion.

A short oesophagus is present in some species, but in many, it is practically inexistent due to an almost direct connection between the pharynx and the midgut (Scheltema et al. 1994). Unlike other molluscs, the midgut of Solenogastres is not differentiated into stomach and digestive gland but instead forms a sac that fills a major part of the animal (Fig. 3b). Especially in larger species, muscle bundles in serial arrangement along the body constrict the midgut sac creating lateroventral pouches (Todt and Salvini-Plawen 2004b). Ciliated cells forming a narrow dorsal tract and tall digestive cells were reported in the single-layered midgut epithelium. Digestive cells are attached to the basal lamina and laterally to one another in the basal region. Although with variations according to the phase of cell activity, the basal region contains the nucleus, numerous mitochondria, rough endoplasmic reticulum cisternae, Golgi stacks actively producing vesicles, lysosomes, electron-dense secretory vesicles, peroxisomes, lipid droplets and glycogen (Fig. 4). A belt desmosome and a septate zone are located at the top of the basal zone, and



above these junctional complexes, cells are no longer attached to each other. The enlarged apical portion bears a border of microvilli and bulge into the midgut lumen. The apical region contains clathrin-coated vesicles, endosomes and large lysosomes with pieces of prey tissue at different stages of digestion. When lysosomal digestion is completed, the content of the residual bodies is released into the midgut lumen by exocytosis (Fig. 4) or a large portion of the apical cytoplasm

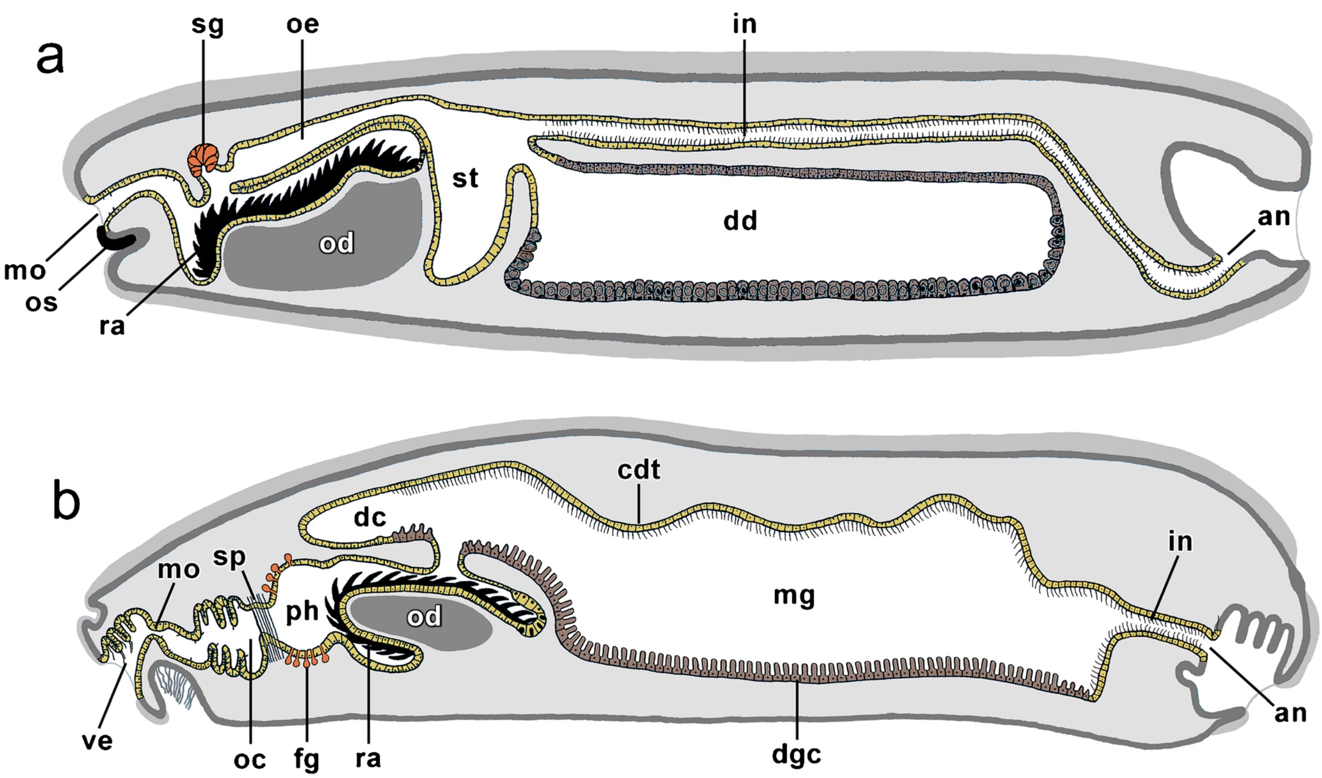


Fig. 3 Digestive system of aplacophorans. **a** Caudofoveata (=Chaetodermomorpha). **b** Solenogastres (=Neomeniomorpha). an—anus, cdt—ciliated dorsal tract, dc—dorsal caecum, dgc—digestive cells, fg—foregut glands, in—intestine, mg—midgut, mo—mouth, oc—oral cavity, od—odontophore, oe—oesophagus, os—oral shield, ph—pharynx, ra—radula, sg—salivary gland, sp—sphincter (circumpharyngeal muscle), st—stomach, ve—vestibule. Adapted from Scheltema et al. (1994)

containing several residual bodies is discarded into the lumen. Some digestive cells seem to undergo apoptosis after this last phase of digestion (Todt and Salvini-Plawen 2004b, 2005). In solenogasters that feed on cnidarians, intact nematocytes are fagocyted by midgut digestive cells, meaning that the discharge of these cnidarian defence cells was inhibited during feeding. This inhibition may be caused by secretory products released by foregut glandular cells. Moreover, in addition to intracellular digestion, the digestive cells also produce electron-dense secretory vesicles probably containing enzymes for extracellular digestion in midgut lumen (Todt and Salvini-Plawen 2004a). Therefore, these cells seem to accumulate all functions that in other molluscs are divided between digestive and basophilic cells of the digestive gland. A ciliated epithelium without secretory cells lines the short intestine, with the anus opening in the pallial cavity on the rear of the animal (Todt and Salvini-Plawen 2004b, 2005).

Digestive system in Polyplacophora

Polyplacophorans, commonly known as chitons, are dorsoventrally flattened molluscs, characterised by the presence of eight dorsal aragonite shell plates and a broad ventral foot. Surrounding the eight articulated shell plates, or even completely engulfing them in some species, there is a thick marginal girdle covered by a chitinous cuticle that can bear calcium carbonate sclerites. It is the largest class of the Aculifera, with almost 1000 known living species, most in intertidal or sublittoral coastal zones and some in deep ocean floors. In length, polyplacophorans range from less than 1 cm to more than 30 cm. Chitons are usually grazers with a broad and exceptionally long radula. Their diets consist mainly of detritus, algae and encrusting colonial animals. Exceptionally, a few species became predators of free-swimming crustaceans and others especially at great ocean depths are xylophagous (Eernisse and Reynolds 1994; Todt et al. 2008). Surprisingly, the digestive system of chitons is still poorly investigated. Apart from a couple of ultrastructural studies published years ago (Boyle 1975; Lobo-da-Cunha 1997), electron microscopy studies are markedly lacking. The classical article by Fretter (1937) is still a major source of information about the anatomy and histology of polyplacophoran digestive system.

In *Lepidochitona cinereus*, the mouth opens into a narrow oral tube leading to a wider buccal cavity. The massive odontophore supporting the radula protrudes into the buccal cavity and beneath it lies the subradular sac with a mucus-secreting epithelium. A bilobed subradular organ is located dorsally near the distal end of the subradular sac. This organ is lined by an epithelium mainly formed by cells with an apical microvillous border, containing electron-dense vesicles in the cytoplasm. Ciliated cells and some mucous cells are also

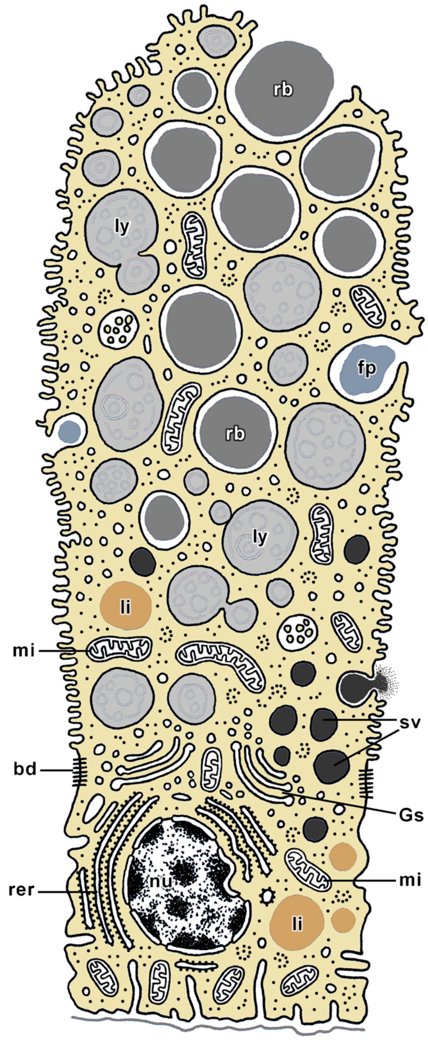


Fig. 4 Schematic representation of a digestive cell from the midgut epithelium of a solenogaster. bd—belt desmosome, fp—food particle, Gs—Golgi stack, li—lipid droplets, ly—lysosomes, mi—mitochondria, nu—nucleus, rb—residual bodies, rer—rough endoplasmic reticulum, sv—secretory vesicles. From Todt and Salvini-Plawen (2005)

present, and the dense innervation at the base of the epithelium suggests a chemosensory function (Fretter 1937; Boyle 1975).

The epithelium lining the buccal cavity is covered by a chitinous cuticle in some areas, and in others, it contains mucous cells. At the back of the buccal cavity, buccal glands that have also been called salivary glands open into buccal pouches in a region also known as pharynx. In *L. cinereus*, these glands are a simple sac directly opening into the buccal pouches without a duct. The epithelium of these glands is composed of large mucous cells interspersed with smaller wedge-shaped cells. In larger species, the salivary glands are branched and linked to the buccal cavity through a short duct (Fretter 1937).

The oesophagus is relatively short, possessing ciliated cells and scattered mucous cells. The ducts of the two "sugar glands" open on the middle of the oesophagus. The walls of these glands form numerous villi that fill the internal space. Villi epithelium consists mainly of two cell types. The first are voluminous gland cells with a large basal nucleus containing a prominent nucleolus and many secretory vesicles filling the cytoplasm; the others are smaller wedge-shaped cells. A third cell type was reported only on the tip of the villi, characterised by a vacuole in the apical cytoplasm (Fretter 1937). The function of these glands seems to be the secretion of polysaccharide-digesting enzymes (Meeuse and Fluegel 1958). The stomach epithelium contains ciliated bands and non-ciliated areas, mucous cells and other types of secretory cells. A bilobed digestive gland surrounds a great part of the stomach. The numerous ducts of each lobe unite to form two main channels which fuse before opening on the stomach (Fretter 1937; Greenfield 1972).

Digestive gland tubules are formed by typical basophilic and digestive cells, being among the few cells of polyplacophora digestive system of which ultrastructural data are available. The former are characterised by large amounts of flattened rough endoplasmic cisternae, several Golgi stacks, clear vacuoles and large almost spherical electron-dense secretory vesicles (Fig. 5a, b). The digestive cells have a sparse border of microvilli, a large number of vesicles in the apical region, vacuoles containing variable amounts of electron-dense material resembling endosomes and large electron-dense lysosomes. Golgi stacks and mitochondria are also present, but the endoplasmic reticulum is less developed than in basophilic cells (Fig. 5c, d). Both cells types contain many peroxisomes (Lobo-da-Cunha 1997).

Departing from the stomach, the long intestine is coiled around the digestive gland forming many loops. The two ciliated strips of the stomach epithelium continue through the anterior intestine, in which a few mucus-secreting cells are also present. A valve separates the anterior from the posterior intestine. The posterior intestine is lined by a ciliated epithelium containing secretory cells distinct from the mucous cells of the anterior intestine. The short rectum is also ciliated, ending in the anus located at the posterior end of the ventral surface of the animal (Greenfield 1972; Eernisse and Reynolds 1994).

Conchifera

The clade Conchifera encompasses a much higher number of species than the Aculifera, being also much more diversified anatomically, physiologically and ecologically. The last common ancestor of all five extant conchiferan classes, Monoplacophora, Cephalopoda, Bivalvia, Gastropoda and Scaphopoda, supposedly was an univalved monoplacophoran-like limpet (Vinther 2015). However, despite recent advances, the phylogenetic relationships between these five classes still require further investigation (Wanninger and Wollesen 2019). The three largest conchiferan classes, Cephalopoda, Bivalvia

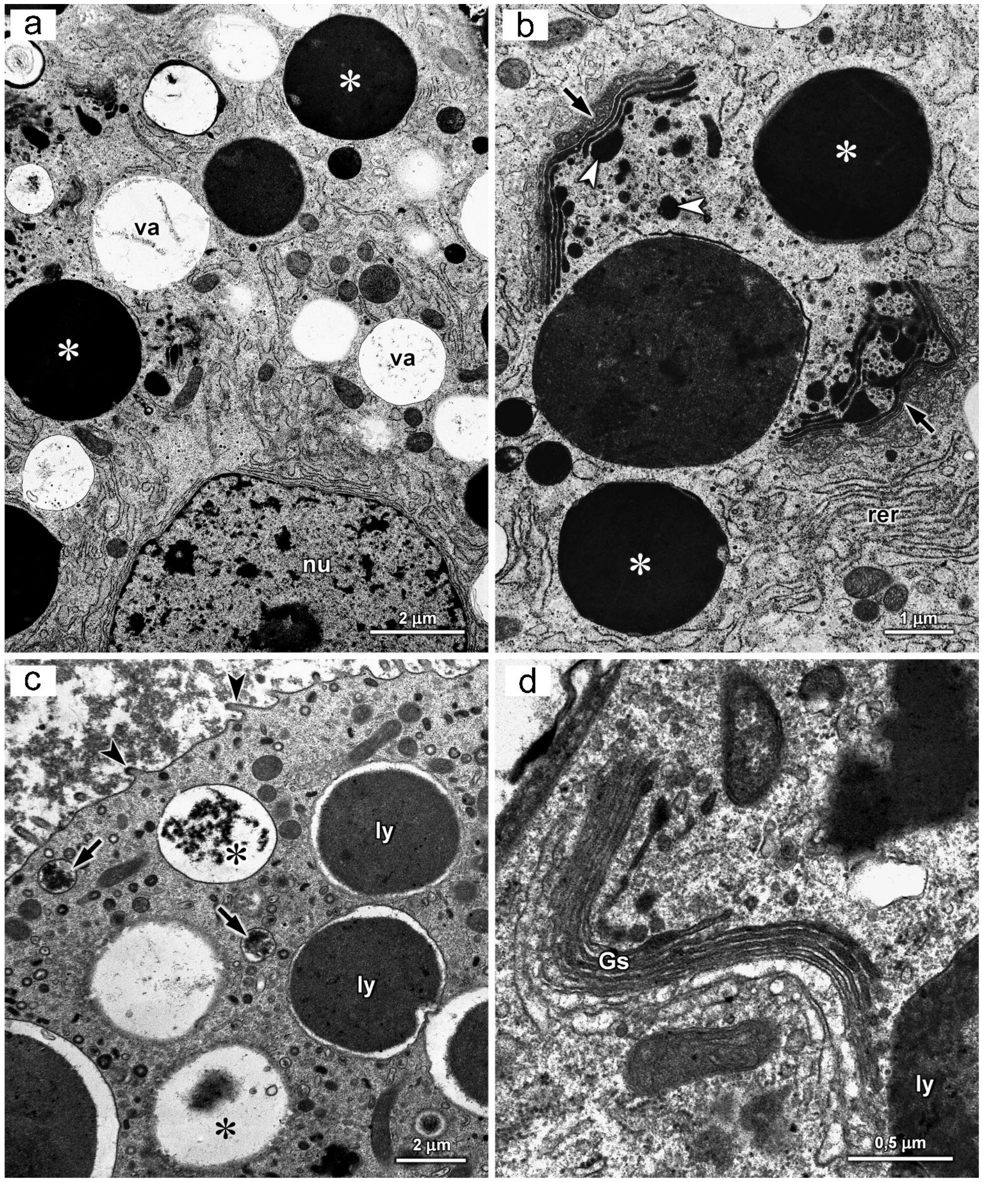


Fig. 5 Ultrastructure of *Acanthochitona crinita* (Polyplacophora) digestive gland cells. **a** General view of a basophilic cell showing the nucleus (nu), large electron-dense secretory vesicles (asterisks) and clear vacuoles (va). **b** Rough endoplasmic reticulum (rer) and Golgi stacks (arrows) in a basophilic cell. The *trans* face cisternae of the Golgi stacks and the vesicles associated with the *trans* Golgi network (arrowheads) have an electron-dense content identical to the content of the secretory vesicles (asterisks). **c** Apical region of a digestive cell with short microvilli (arrowheads), several vesicles (arrows), lysosomes (ly) and vacuoles that can correspond to endosomes (asterisks). **d** Golgi stack with a unusual S-shape (Gs) in a digestive cell

and Gastropoda, are the most studied among molluscs, whereas much less information is available on the other two.

Digestive system in Monoplacophora (=Tryblidia)

The first living representatives of this class were collected from deep ocean sediments in 1952 but were only formally described in 1957. Before that, these molluscs were known from the fossil record and thought to have become extinct during the Devonian, although a few recent shells collected earlier were erroneously classified as limpets of the class Gastropoda. Presently, more than 30 extant species have been recognised, living in ocean floors from less than 200 m down to 7000 m depth, where they are detritivorous browsers ingesting a variety of microorganisms. The more or less flattened single plate shell has a limpet-like shape, with an oval or round margin and an anterior apex, ranging in size from a few millimetres to 4 cm. Monoplacophorans differ from other extant molluscs by having a serial repetition of gills, nephridia and gonads along the body. Since the discovery of living representatives, monoplacophorans have been a focus of interest in the debate about the origin and evolution of molluscs but are now regarded as a basal conchifera branch rather than the most basal of all molluscs (Lindberg 2009; Haszprunar and Ruthensteiner 2013).

Despite the rarity of specimens, the digestive system of *Laevipilina antarctica* was investigated using transmission electron microscopy. Near the mouth aperture, part of the buccal cavity epithelium is covered by a cuticle. Buccal glands (also called salivary glands) with a pouch-like morphology open directly into the most anterior region of the buccal cavity without evident ducts. The distal epithelium of these glands comprises thin ciliated cells and broad mucous cells, while the proximal portion is formed only by mucous cells. These secretory cells have a basal nucleus with a large nucleolus, and the cytoplasm is rich in endoplasmic reticulum and Golgi stacks. The apical zone contains several large electron-lucent vesicles and a vacuole with a mass of heterogeneous material resembling the content of a lysosome. A single jaw is located at the dorsal wall of the buccal cavity. The buccal cavity forms a subradular pouch with a glandular epithelium, ending in a large subradular organ whose ultrastructure was not reported (Haszprunar and Schaefer 1997; Schaefer and Haszprunar 1997). In chitons, the subradular organ was considered a chemosensory organ for food tasting (Boyle 1975), and in monoplacophorans, the function is probably similar.

The oesophageal epithelium of *L. antarctica* is formed by cells with microvilli and cilia, containing several lysosome-like electron-dense bodies in the cytoplasm. In the middle oesophagus, two pairs of pouches are present. The epithelium of these pouches is sparsely ciliated and its cells have a dense microvillus border and many lysosome-like bodies of various sizes in the cytoplasm, which became less abundant in the most posterior part of the pouches. The oesophagus leads to a triangular stomach with a long caecum. The epithelium of both stomach and caecum is formed by elongated thin cells with a morphology typical of mucus-secreting cells. The nucleus is situated at midheight and the cytoplasm poor in organelles is mainly filled with electron-lucent secretory vesicles located above and below the nucleus, with some electron-dense bodies in the apical region. The stomach epithelium has a prominent border of microvilli and cilia (Haszprunar and Schaefer 1997; Schaefer and Haszprunar 1997).

The connection between the stomach and the digestive gland is widely opened. The epithelium of this lobed gland consists of secreting cells and absorptive cells. The former are characterised by a round nucleus and a dense system of tubular rough endoplasmic reticulum. The absorptive cells have a nucleus of variable shape and large food vacuoles in the cytoplasm. Large food particles, such as intact diatoms, dinoflagellates or foraminiferans, were found inside the digestive gland lumen. Usually only very fine partially digested particles enter in the digestive gland of molluscs, but the wide aperture between the stomach and digestive gland could explain the entrance of larger particles in the digestive gland of monoplacophorans. The long looped intestine receives the undigested residues coming from the stomach and, according to Haszprunar and Schaefer (1997), appears to be more specialised for transport rather than for absorption. The intestinal epithelium is generally composed of ciliated cells containing an ovate nucleus, low amounts of endoplasmic reticulum and some electron-dense bodies near the cell apex. Few mucous cells occur in the first part of the intestine. In the posterior loops of the intestine, the ciliated epithelial cells do not show the electron-dense inclusions and mucous cells are absent. The rectum is histologically similar to the intestine. According to the available data, the anatomy of the digestive system is similar among monoplacophorans, only with minor variations reported in the few species studied so far (Haszprunar and Schaefer 1997; Ruthensteiner et al. 2010).

Digestive system in Gastropoda

The class Gastropoda is by far the largest and most diverse among molluscs, with many thousands of species including whelks, snails, limpets and slugs living in marine, freshwater and terrestrial ecosystems. In size, they range from about a millimetre to almost a metre in *Syrinx aruanus* and *Aplysia vaccaria*. According to diet, the species can be herbivorous, carnivorous and omnivorous, and their feeding strategies are also very diversified including grazing, suspension-feeding, predation and even parasitism (Kohn 1983). Typically, the body is protected by a conical or coiled shell, but in terrestrial and marine slugs, the shell is substantially reduced and internal or even entirely lost. The foot is ventral and the head is usually distinct bearing one or two pairs of tentacles and eyes (Aktipis et al. 2008). However, the 180° torsion of the visceral mass during larval development is the feature that best distinguishes gastropods from other molluscs, causing the intestine to rotate forward and terminate above the head on the anteriorly directed mantle cavity (Voltzow 1994), although most heterobranchs are secondarily detorted. In partially detorted species, the mantle cavity containing the anus opens laterally on the right side, and in completely detorted species, the anus is situated at the posterior end of the animal (Gosliner 1994). In the last years, significant advances were made on the phylogeny of gastropods (Fig. 6), allowing a more accurate insight on the evolutionary paths followed by these molluscs (Colgan et al. 2007; Jörger et al. 2010; Zapata et al. 2014; Kano et al. 2016). In what concerns the digestive system, research has been mostly focused on caenogastropods and heterobranchs that together comprehend the large majority of gastropod species.

Buccal cavity

In many gastropods, the mouth surrounded by the lips is located at the end of a snout and opens into an oral tube that leads to the buccal cavity. Carnivorous caenogastropods usually have a muscular proboscis that may be introvertable or retractable, used to attack the prey (Golding et al. 2009). Single or paired chitinous jaws are usually positioned behind the mouth. Labial, buccal or oral glands with an elaborate structure or simple isolated goblet cells inserted in the epithelium that secrete mucus for lubrication were described in gastropods (Gosliner 1994; Voltzow 1994). These glands can also have a specialised function, as the highly branched oral dorsal

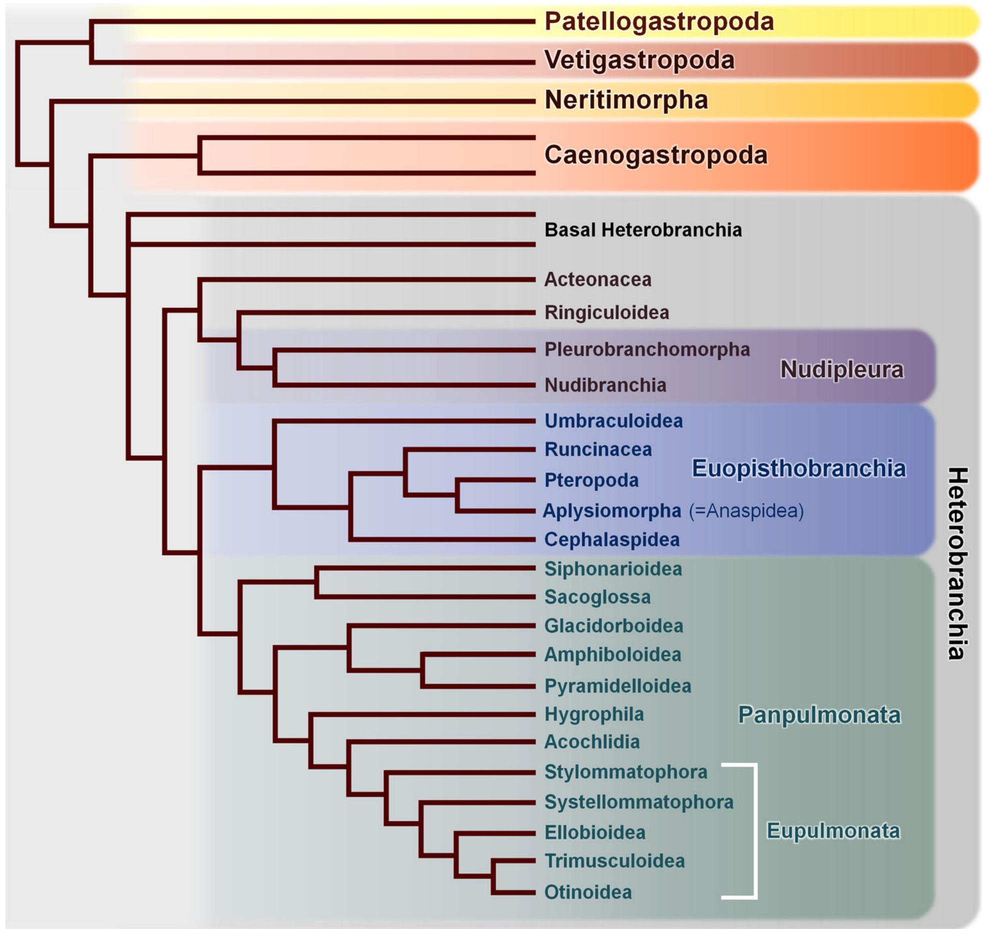


Fig. 6 Phylogenetic relationships between the five major gastropod taxa (Patellogastropoda, Vetigastropoda, Neritimorpha, Caenogastropoda, Heterobranchia), with the subdivisions of the Heterobranchia. According to Jörger et al. (2010), Zapata et al. (2014) and Kano et al. (2016)

gland of some Pleurobranchomorpha that secreted acid to attack prey or for defence gains predators (Morse 1984). Oral glands known as ptyaline glands were reported in some nudibranchs, and albeit not yet studied in detail, an important digestive function was attributed to them (Gosliner 1994; Brodie 2001). Although usually present, the radula was lost in some gastropods with a specialised feeding mode. The segment of the alimentary canal behind the radula is sometimes referred as the pharynx, a transition zone between the buccal cavity and the oesophagus. The muscles surrounding the buccal cavity and all associated structures form the buccal mass, that in some carnivorous heterobranchs without radula is modified becoming an enlarged muscular pump used to swallow the prey whole (Gosliner 1994).

Salivary glands

A pair of salivary glands linked to the buccal cavity by ducts is usually present in gastropods, secreting a mucus fluid for agglutination and lubrication of food particles during feeding and ingestion. Additionally, the detection of amylase, cellulase and protease activities in some species indicates that the saliva can also contributes to extracellular digestion in the foregut (Bolognani Fantin et al. 1982; Moura et al. 2004; Godoy et al. 2013). On the other hand, in nudibranchs with modified and specialised digestive systems, these glands can be greatly reduced or even absent (Gosliner 1994; Brodie 2001). The published studies show great histological diversity among the salivary glands of gastropods that can have tubular or acinar structure. In addition to ciliated cells, in some species, just one or two types of secretory cells were observed, while four or more were reported in others (Andrews 1991; Fretter and Graham 1994; Luchtel et al. 1997; Andrews et al. 1999; Lobo-da-Cunha et al. 2016). A diversity naturally correlated to differences in feeding modes and diets. A variety of designations were applied to these cells, but Serrano et al. (1996) proposed a more coherent classification based on ultrastructural features and light microscopy observations. Despite the differences among species, the names proposed by Serrano et al. (1996) for the five types of secretory cells found in salivary glands of terrestrial snails belonging to the superfamily Helicoidea (Heterobranchia: Stylommatophora) can also be applied to several salivary gland cells of other gastropod taxa.

The first of those five cell types was named swollen RER cistern mucocyte. These ones are characterised by extensive development of rough endoplasmic reticulum made up of swollen cisternae filled with thin tubular structures. Their Golgi apparatus is highly developed and the secretory vesicles show tendency to fuse with each other, which are ultrastructural features of mucus-secreting cells. Histochemical methods confirmed the presence of acid mucopolysaccharides in the secretory vesicles (Serrano et al. 1996). A second kind of mucocyte also occurs in the salivary glands of several gastropods. In these cells, rough endoplasmic reticulum cisternae and several Golgi stacks fill the cytoplasm around the secretory vesicles. These large vesicles frequently fuse with each other and contain filaments and granules arranged in patterns that differ among species. In some euopisthobranchs (Lobo-da-Cunha 2001; Lobo-da-Cunha and Calado 2008) and in the land slug *Arion ater* (Moya et al. 1992), for example, the secretory vesicles enclose peripheral masses of granular material (Fig. 7a, b). Using light and electron microscopy techniques, it was possible to show that the peripheral granular masses were made of protein while the remaining part of the vesicles contained acid polysaccharides (Lobo-da-Cunha and Calado 2008). These cells that stain metachromatically with methylene blue were called granular mucocytes (Serrano et al. 1996). A third type of secretory cell is characterised by large secretory vacuoles with electron-lucent or finely granular content. Flattened rough endoplasmic reticulum cisternae and Golgi stacks are abundant in these cells that were named vacuolated cells by Serrano et al. (1996). However, the detection of acid polysaccharides in the secretory vacuoles with low electron density indicates that this is another type of mucous cell (Lobo-da-Cunha 2002; Lobo-da-Cunha and Calado

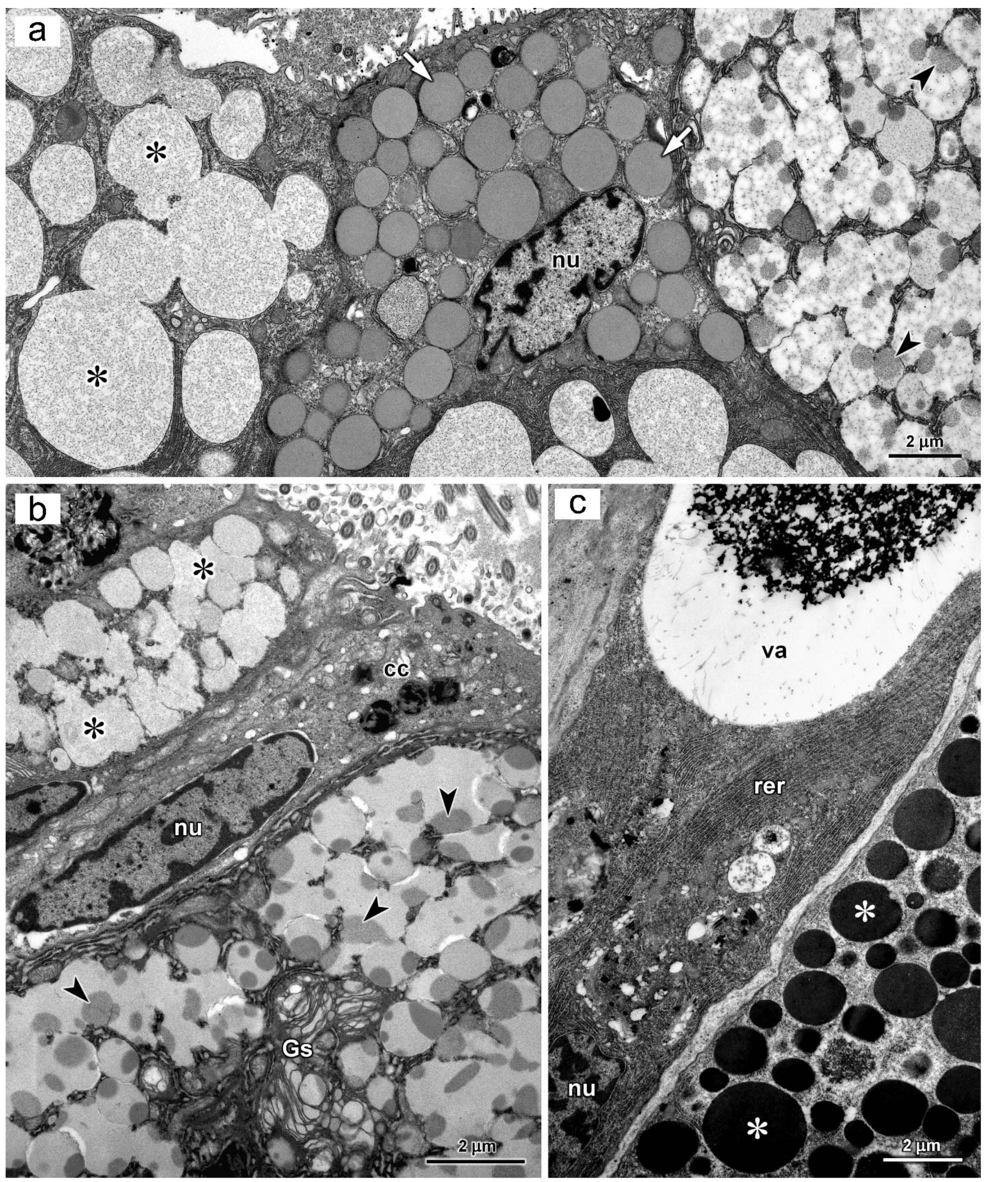


Fig. 7 Ultrastructural features of salivary gland cells in euopisthobranch gastropods. **a** *Aplysia depilans*. Vacuolated mucocytes contain vacuoles with finely granular material (asterisks); in granular cells, the secretory vesicle has a higher electron density (arrows) and granular mucocytes are characterised by secretory vesicles with peripheral masses of electron-dense material (arrowheads). **b** *Bulla striata*. A non-secretory ciliated cell (cc), a vacuolated mucocyte in which the secretory material has low electron density (asterisks) and a granular mucocytes with secretory vesicles containing peripheral electron-dense material (arrowheads). **c** *Philinopsis depicta*. Cell with a very large apical vacuole (va) enclosing a mass of secretory material and a granular cell filled with high electron-dense secretory vesicles (asterisks). Gs—Golgi stacks, nu—nucleus, rer—rough endoplasmic reticulum

2008). Therefore, it seems preferable to designate them as vacuolated mucocytes (Fig. 7a, b). The alveolar cells are similar to the previous ones, but their secretory vesicles are more electron-dense and stain more intensely with light microscopy methods (Serrano et al. 1996). Acid polysaccharides, PAS-positive substances and proteins were detected in the secretion produced by cell that can be included in this type (Moreno et al. 1982). Lastly, the basophilous or granular cells (Fig. 7a) are characterised by electron-dense vesicles that do not fuse with each other and contain a secretion rich in proteins (Serrano et al. 1996; Lobo-da-Cunha 2001).

In the salivary glands of aglajids, which are carnivorous cephalaspideans with a more derived digestive system, secretory cells diverge from the previous described types, all producing a highly electron-dense secretion rich in proteins (Fig. 7c) that also include acid mucopolysaccharides (Lobo-da-Cunha et al. 2009, 2016). Moreover, in addition to all this diversity of cell types, cell features may change over time. In the salivary glands of the euopisthobranch *Aplysia depilans* (Fig. 7a), the electron density of the secretory vesicles is low in immature granular cell and high in mature ones due to an increase in protein content (Lobo-da-Cunha 2001). In the pyramidellid *Sayella fusca*, three distinct phases of activity were reported in the secretory cells of the salivary glands (Peterson 1998).

In addition to a pair of acinous salivary glands, several carnivorous caenogastropods possess a pair of tubular accessory salivary glands (Schultz 1983; Ball et al. 1997). In the dogwhelk, *Nucella lapillus*, the acinous salivary glands contain two types of secretory cells, one secreting glycoproteins and the other secreting acid mucopolysaccharides with a small amount of proteins (Andrews 1991). The accessory salivary glands of this species comprise epithelial and subepithelial secretory cells, both with electron-dense secretory vesicles. The cell bodies of the subepithelial cells are arranged in cluster at the periphery of the gland and the long and thin necks cross the muscular layer and the epithelium to reach the lumen. The epithelial cells secrete proteins rich in tryptophan, while the subepithelial cells secrete a glycoprotein rich in cysteine (Andrews 1991). The secretion of the accessory salivary glands of *N. lapillus* contains serotonin (West et al. 1994) and induces muscular relaxation causing flaccid paralysis in mussels, which are the prey of these whelks (Andrews et al. 1991). In other species, the accessory salivary glands produce an acid secretion that may function in feeding and defence. In *Cassidaria echinophora*, the acinar salivary glands secret mucus, while the larger tubular accessory salivary glands produce a hyperosmotic secretion with a pH below 1 containing sulphuric acid and very low amount of organic components (Fänge and Lidman 1976). In these glands, there are many mitochondria and Golgi stacks in the basal region of secretory cells. The vesicles produced by the Golgi apparatus fuse to form very large vacuoles containing sulphate ions (Voltzow 1994).

Even without individualised accessory salivary glands, ranellids such as *Cymatium intermedius* produce an acid saliva. Their salivary glands are divided into two lobes: the anterior secretes mucus and proteins believed to be enzymes for external digestion of prey tissues, whereas the posterior lobe secretes sulphuric acid, a chelating agent to help dissolution of prey calcareous shell and probably a paralysing toxin (Andrews et al. 1999). Conversely, a strongly alkaline saliva with a pH around 10 is produced by the volutid *Odontocymbiola magellanica* (Bigatti et al. 2010). Toxins can also be secreted by ordinary salivary glands, at least in species lacking accessory salivary glands. The neurotoxin tetramine is produced in the salivary glands of the red whelk *Neptunea antiqua*, and other species without accessory salivary glands contain serotonin, histamine, choline and choline ester in the saliva (Endean 1972; Power et al. 2002).

Oesophagus and crop

The anatomy of the oesophagus and its associated glands is quite variable among gastropods. In many heterobranchs, the oesophagus presents a widen portion forming a crop to accommodate ingested food (Gosliner 1994; Luchtel et al. 1997). Additionally, some euopisthobranchs possess a muscular gizzard with hard plates for food maceration, dividing the oesophagus in anterior and posterior regions in relation to the gizzard (Gosliner 1994). A muscular gizzard can also be found in freshwater snails of the clade Hygrophila (Boer and Kits 1990).

In patellogastropods, vetigastropods and caenogastropods, the oesophagus is typically divided into anterior, middle and posterior regions (Voltzow 1994). In the common European limpet, *P. vulgata* (Patellogastropoda), dorsal longitudinal folds create a food channel that in the middle oesophagus has on either side numerous glandular pouches also called oesophageal glands. The epithelium around the food channel and the one lining the posterior oesophagus is formed by ciliated columnar cells bearing microvilli, which absorb glucose in a Na^+-dependent process. Subepithelial mucus-secreting cells occur in the food channel and posterior oesophagus (Bush 1989). The epithelium of the lateral glandular pouches of the middle oesophagus, in addition to ciliated columnar cells, contains cells that were considered responsible for both nutrient absorption and amylase secretion for extracellular digestion. These ones seem to undergo cycles of endocytosis and intercellular digestion followed by apocrine secretion. Residual bodies and electron-dense granules probably containing enzymes were found in the apical blebs that are released to the lumen of the oesophagus (Bush 1989).

Apocrine secretion was also reported in the oesophagus of the giant keyhole limpet *Megathura crenulata*

(Vetigastropoda). In this species, epithelial cells of the middle and posterior oesophagus form large apical blebs containing vesicles and granules with diverse electron densities. After detachment from the cell apex, the blebs eventually disintegrate and their content is released in the lumen. Some PAS-positive mucus-secreting cells also occur along the oesophagus (Martin et al. 2010). Using tissue homogenates, several enzyme activities were detected in the oesophagus of vetigastropods including acid and alkaline phosphatase, esterases, proteases and various glycosidases (Garcia-Esquivel and Felbeck 2006; Martin et al. 2011). Although some digestive activity seems to occur in this part of the digestive tract, the use of crude homogenates obtained with a mixture of oesophageal tissues does not allow a distinction between intracellular enzymes and enzymes that are secreted for extracellular digestion. However, lysosomes or residual bodies included in apical blebs shed into the lumen by apocrine secretion may contribute with enzymes for extracellular digestion (Martin et al. 2011).

In caenogastropods, the lumen of the oesophagus is also lined by and the epithelium formed by cells bearing microvilli and cilia, interspersed with secretory cells. Oesophageal glands of caenogastropods can consist of a dilated portion of the oesophageal wall with multiple folds of glandular epithelium that secrete digestive enzymes (Reid and Friesen 1980), or be a distinct gland connected with the oesophagus by a duct. In neogastropods, a highly diversified group of predatory caenogastropods, the anterior oesophagus extends from the posterior end of the buccal cavity to the valve of Leiblein. This is a pear-shaped structure that consists in a glandular chamber containing a posteriorly pointing cone-shaped valve that prevents regurgitation during proboscis extension. It is considered a significant adaptation to the carnivorous predatory feeding of neogastropods. Ciliated and secretory cells are present, the last ones containing granules with acid mucopolysaccharides and glycoproteins (Minniti 1986; Andrews and Thorogood 2005; Golding and Ponder 2010). Some neogastropods also possess a mid-oesophagus gland known as the gland of Leiblein. This complex gland with absorptive, storage and secretory functions contains some mucus-secreting cells and unciliated and ciliated epithelial cells. The columnar or club-shaped unciliated ones are filled with lysosomes, lipid droplets and glycogen granules, especially in well-fed animals. At the apex, these cells have coated and uncoated vesicles as well as cell membrane pits at the base of the microvilli, suggesting a strong endocytic activity. Both rough endoplasmic reticulum and Golgi apparatus are not particularly developed and secretory vesicles are not evident. These cells undergo a cyclic process of apocrine secretion, through which large cytoplasmic blebs containing lysosomes and their residual bodies are shed into the gland lumen. Therefore, enzymes still active in lysosomes and residual bodies seem to be the only contribution for extracellular digestion, after disintegration of the blebs in the alimentary canal. The ciliated cells can be columnar- or wedge-shaped with a wider apical surface bearing a dense border of microvilli. They also reveal signs of endocytosis and contain several lysosomes as well as many mitochondria. Calcium phosphate concretions with concentric layers are also present in these cells. Small apical blebs are formed, but large portions of cytoplasm are not shed into the lumen (Andrews and Thorogood 2005). Additionally, in Muricoidea, another gland occurs in the mid-oesophagus between the valve Leiblein and the connection with the gland of Leiblein duct. This gland known as *glande framboisée* contains ciliated cells that store lipids and protein-secreting cells (Martoja 1971; Voltzow 1994).

The oesophagus and crop of heterobranch gastropods contain secretory cells but lack the developed oesophageal glands reported in patellogastropods and caenogastropods. Generally, the oesophagus and crop have longitudinal folds lined by an epithelium formed by columnar cells with and apical border of microvilli, many of them also with cilia, and flask-shaped secretory cells that can be epithelial or subepithelial. Secretory vesicles with low electron density and many Golgi stacks are typical features of both epithelial and subepithelial secretory cells. The rough endoplasmic reticulum can also be developed, presenting dilated cisternae containing thin tubular structures. The histochemical and cytochemical assays show that these cells secrete neutral or acid mucopolysaccharides (Boer and Kits 1990; Dimitriadis et al. 1992; Lobo-da-Cunha and Batista-Pinto 2005; Lobo-da-Cunha et al. 2010a). However, protein secretion was not reported in either oesophagus or crop of heterobranchs. Therefore, although enzymes secreted by salivary glands can act in the foregut, extracellular digestion in the oesophagus and crop is mainly due to the digestive fluid that comes from the digestive gland (Fretter and Hian 1979). In some species, the crop is even a major site of extracellular digestion. For example, in *Philinopsis depicta* (Cephalaspidea), the prey is swallowed whole and retained in the dilated crop where the soft tissues are completely dissolved by the digestive juice, leaving the prey shell perfectly cleaned (Lobo-da-Cunha et al. 2011a). As in other gastropods previously mentioned, apocrine secretion was also reported in the anterior oesophagus of *Bulla striata* (Cephalaspidea), especially in the oesophageal pouch. In this species, the epithelial-supporting cells produce large apical blebs that are released into the lumen of the oesophagus (Fig. 8a). However, the functional meaning of this secretion is not clear because neither secretory vesicles nor lysosomes were not found in the blebs (Lobo-da-Cunha et al. 2010a).

Cell membrane invaginations, small vesicles, multivesicular bodies and lysosomes are present below the border of microvilli of oesophagus and cop epithelial cells of heterobranchs. Ultrastructural features indicate endocytic uptake of macromolecules or fine particles resulting from extracellular digestion and their intracellular digestion in

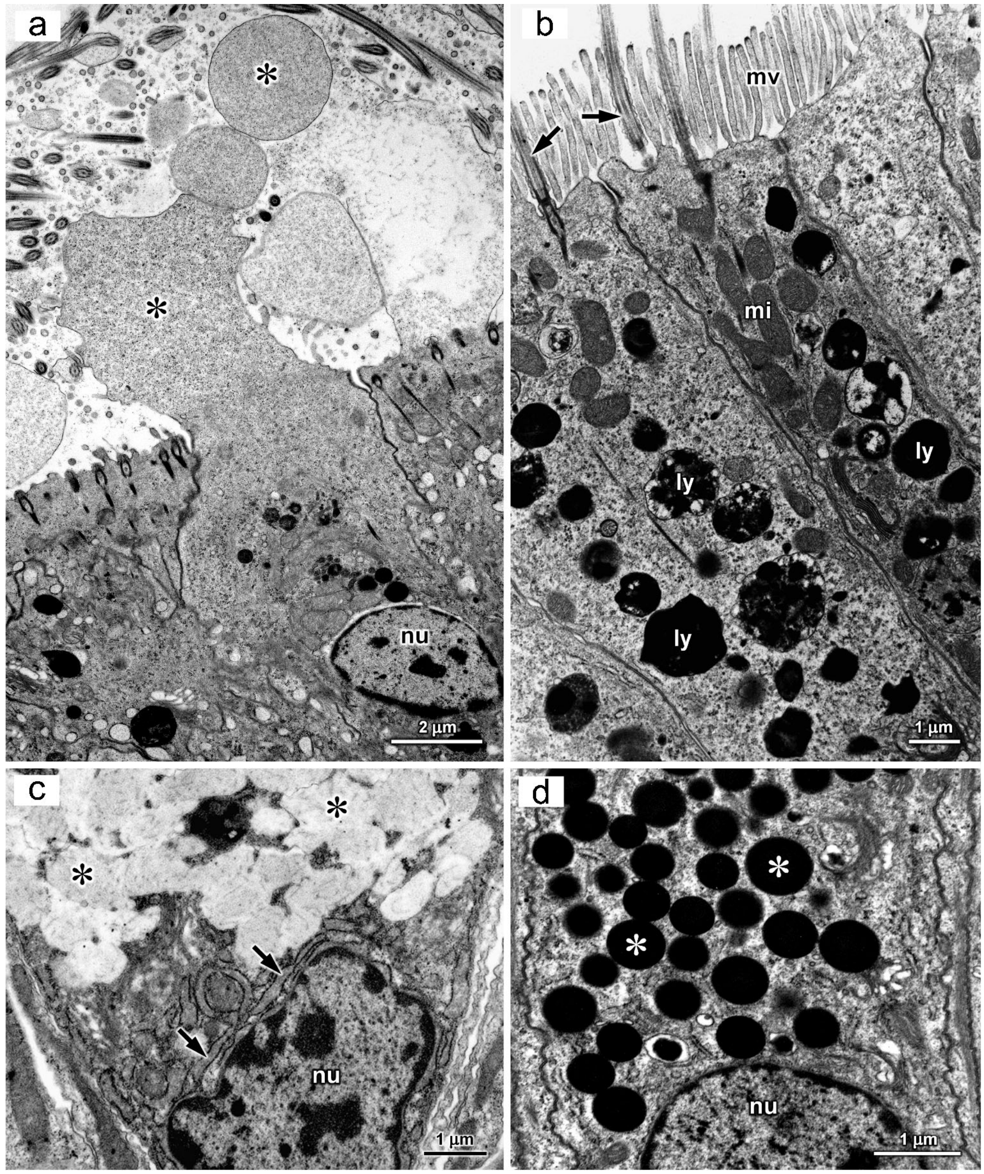


Fig. 8 Ultrastructure of crop, stomach and intestine cells in euopisthobranch gastropods. **a** Oesophagus of *Bulla striata*. Apical blebs (asterisks) being released by apocrine secretion into the lumen of the oesophageal pouch. **b** Stomach of *Aplysia depilans*. Cilia (arrows), microvilli (mv), mitochondria (mi) and lysosomes (ly) can be seen in epithelial cells. **c** Stomach of *Aplysia depilans*. Basal region of a mucous cell showing some rough endoplasmic reticulum cisternae (arrows) and secretory vesicles with low electron density (asterisks). **d** Intestine of *Bulla striata*. Basal region of a glandular cell containing electron-dense secretory vesicles (asterisks). nu—nucleus

lysosomes, as well as absorption of small molecules through the microvilli (Boer and Kits 1990; Dimitriadis 2001; Leal-Zanchet 2002; Lobo-da-Cunha and Batista-Pinto 2005; Lobo-da-Cunha et al. 2010a, b). Indeed, experiments made with land slugs proved that crop epithelial cells absorb soluble radioactive nutrients (Walker 1972), and endocytosis was demonstrated in these cells using horseradish peroxidase (Bourne et al. 1991). Considering the large size and abundance of lipid droplets in oesophagus and crop epithelium of marine, freshwater and terrestrial heterobranchs, it can be concluded that these cells are important fat reservoirs, at least in some species (Lobo-da-Cunha and Batista-Pinto 2005; Dimitriadis et al. 1992). Moreover, starvation experiments proved that these reserves are used during periods of food shortage (Dimitriadis et al. 1992). Using radioactively labelled palmitic acid, it was demonstrated that the crop is the major site for absorption and accumulation of fatty acids in a land slug (Walker 1972). Therefore, the peroxisomes present in these lipid-rich cells can have an important role in mobilisation of lipid reserves through β-oxidation of fatty acids, a well-known peroxisomal metabolic pathway that decompose fatty acids producing acetyl-CoA. Many mitochondria are also present in these cells, mainly in the apical cytoplasm and close to peroxisomes in the middle and basal regions (Lobo-da-Cunha and Batista-Pinto 2005).

Stomach

Stomach anatomy and histology were described in several gastropods (Fretter and Graham 1994; Luchtel et al. 1997).

In general, it is a sac-like compartment embedded in the digestive gland, whose ducts open on the stomach wall. Typically, two prominent ridges known as typhlosoles form a groove between them, through which waste coming from the digestive gland is carried to the intestine. In addition to sorting areas with a ciliated epithelium, the stomach of gastropods can include a caecum, gastric shield and style sac. The gastric shield corresponds to a portion of the stomach where the epithelium is covered by a cuticle. The style sac can be in wide communication with the intestine, be partially separated from the intestine due to the almost complete fusion of the two typhlosoles leaving only a narrow slit of communication along its length (Voltzow 1994; Martin et al. 2010) or be completely separated from the intestine (Alexander and Rae 1974). In microherbivores and suspension-feeders, a crystalline style is found inside the style sac (Voltzow 1994; Martin et al. 2010). This is a gelatinous rod formed by substances secreted by cells of the style sac (Alexander and Rae 1974). However, a crystalline style is rare in gastropods, being common in bivalves. In gastropods, the style sac more frequently contains a protostyle made from a string of undigested waste mixed with mucus. The stomach of vetigastropods and caenogastropods typically presents a more complex anatomy with gastric shield and style sac, which are absent in the more derived carnivorous caenogastropods (Fretter and Graham 1994; Voltzow 1994). In general, the stomach of heterobranchs is also simpler and without the style sac, although with a caecum in some cases (Fretter and Hian 1979; Boer and Kits 1990). In Nudipleura and cephalaspidean sea slugs as well as in stylommatophoran land snails and slugs, the stomach is a segment of the digestive tract with one or two typhlosoles but without other major anatomical features (Morse 1984; Dimitriadis 2001; Lobo-da-Cunha et al. 2011b).

Food coming from the oesophagus previously mixed with salivary and oesophageal secretions reaches the stomach where secretions released by the digestive gland and from stomach secretory cells are added. Although without a major role in digestion, the stomach of gastropods with its wall ridges and complex ciliary currents provides a sorting mechanism that conveys the finest food particles into the digestive gland ducts, whereas coarser particles are carried directly to the intestine (Voltzow 1994).

Stomach epithelium is formed by ciliate and unciliated columnar cells intersperse with secretory cells. Both ciliated and unciliated cells have a dense apical border of microvilli and many mitochondria in the apical cytoplasm. The observation of small vesicles, multivesicular bodies that are considered as endosomes, and lysosomes in the apical region of the stomach supporting cells suggests the intracellular digestion of substances collected by endocytosis (Fig. 8b). The accumulation of lipid and glycogen reserves is another function of the stomach epithelial cells (Boer and Kits 1990; Leal-Zanchet 2002; Martin et al. 2010; Lobo-da-Cunha et al. 2011b). Peroxisomes are also present, although with a smaller average diameter and less abundance than in the digestive gland. Nevertheless, considering the involvement of peroxisomes in lipid metabolism, these organelles likely play a relevant role in the metabolism of stomach cells that accumulate lipids (Lobo-da-Cunha and Batista-Pinto 2003).

Glandular cells containing secretory vesicles with lower or higher electron density were reported in the stomach epithelium of gastropods (Fig. 8c). In some species, just one secretory cell type was reported, but others possess two types of gland cells in the stomach, secreting polysaccharides and proteins. The basal region contains the nucleus, rough endoplasmic reticulum cisternae, several Golgi stacks formed by many cisternae and other organelles (Boer and Kits 1990; Leal-Zanchet 2002; Lobo-da-Cunha and Batista-Pinto 2003; Lobo-da-Cunha et al. 2011b). In some of these cells, the dilated rough endoplasmic reticulum cisternae are filled with thin tubules with diameter between 20 and 30 nm, which were also reported in the endoplasmic reticulum of the skin, salivary gland and crop mucus-secreting cells of some gastropods (Leal-Zanchet 2002; Lobo-da-Cunha and Batista-Pinto 2003). In the marine caenogastropod *Littorina littorea*, β-glucuronidase activity was detected not only in the lysosomes of columnar epithelial cells but also in the vesicles of stomach secretory cells (Pipe 1986).The detection of this and other digestive enzymes in gastric fluid reveals the capacity for extracellular digestion in the stomach, although the bulk of these enzymes comes from the digestive gland (Cockburn and Reid 1980; Tsuji et al. 2013, 2014). It was also suggested that the amebocytes present in the stomach wall could be involved in the digestive processes, collecting food particles by phagocytosis (Lobo-da-Cunha and Batista-Pinto 2003). The observation of nerve cells and terminals provides evidence of a neuronal control of stomach physiology (Boer and Kits 1990; Lobo-da-Cunha et al. 2011b).

Digestive gland

As in other molluscs, the digestive gland is the largest gland of gastropod digestive system. It is conceivably the best studied organ in the digestive system of gastropods, being formed by numerous blind-ending tubules linked by a system of branch ducts that communicate with the stomach. These tubules, named digestive diverticula, consist of a single-layer epithelium encircled by a very thin layer of connective tissue. The epithelium of the digestive diverticula is typically formed by two cell types, called digestive and basophilic cells (Voltzow 1994; Luchtel et al. 1997). Nonetheless, other types of cells were reported in particular cases (Kress et al. 1994), including thin cells that were regarded as undifferentiated precursors of the other cell types (Dimitriadis 2001). Mucous cells characterised by a developed Golgi apparatus and electron-lucent vesicles containing polysaccharides were noticed in the digestive gland of some gastropods (Franchini and Ottaviani 1993; Rebecchi et al. 1996; Dimitriadis and Andrews 2000; Lobo-da-Cunha et al. 2018). Due to their reduced size and scarcity in the digestive gland, mucus-secreting cells seem ineffective for coating or lubrication of the epithelium, which are usual functions of mucus in digestive organs. Thus, secretion of substances with defensive or regulatory activities is another possible function for these cells (Lobo-da-Cunha et al. 2018).

The digestive cells are the most abundant in the digestive gland. These columnar- or club-shaped cells are characterised by an intense endocytic activity and intracellular digestion (Voltzow 1994; Dimitriadis 2001). Substances collected from the lumen of digestive diverticula can be seen attached to cell membrane pits formed at the base of the microvilli (Franchini and Ottaviani 1993; Rebecchi et al. 1996). These observations suggest the attachment of macromolecules or fine particles resulting from extracellular digestion to cell membrane receptors in order to concentrate them in endocytic vesicles. After detachment from the cell membrane, the endocytic vesicles transport the collected material to the endosomes located at the cell apex. These substances end up in lysosomes where the final stages of digestion take place (Taïeb 2001; Lobo-da-Cunha et al. 2018). Light and electron microscopy images also indicate that lysosome fusion gives rise to very large vacuoles containing undigested residues. At this stage, the cells are filled with very large vacuoles surrounded by thin threads of cytoplasm. These highly vacuolated cells correspond to the excretory cells reported in some species, but seem to be a final excretory phase of digestive cell activity rather than a distinct cell type (Walker 1970; Dimitriadis and Konstantinidou 2002; Lobo-da-Cunha et al. 2018). At end of the intracellular digestion phase, these cells release the undigested substances in the lumen of the digestive diverticula, and through digestive gland ducts, waste products are conducted back to the stomach (Franchini and Ottaviani 1993; Rebecchi et al. 1996). Nutrition obtained by digestive cells can be stored in the form of glycogen reserves and lipid droplets that can be very abundant in these cells (Dimitriadis and Hondros 1992; Gonçalves and Lobo-da-Cunha 2013; Lobo-da-Cunha et al. 2018).

Basophilic cells also known as crypt cells typically have a pyramidal shape and present ultrastructural features of protein-secreting cells, namely, large amounts of rough endoplasmic reticulum, several Golgi stacks and electron-dense secretory vesicles (Franchini and Ottaviani 1993; Rebecchi et al. 1996; Taïeb and Vicente 1999; Dimitriadis and Andrews 2000). These cells are considered responsible for the secretion of enzymes for extracellular digestion. However, in addition to a positive reaction to protein detection by histochemical methods, the secretory vesicles of basophilic cells are also strongly stained by PAS reaction indicating a glycoprotein secretion (Lobo-da-Cunha et al. 2018). In many gastropods, these cells store mineralised granules with a typical concentric-layered structure located within vacuoles. In stylommatophorans, these cells are even called calcium cells due to the large amounts of calcium concretions they contain (Walker 1970). The supply of calcium for shell growth and repair, pH regulation and detoxification by sequestration of toxic metals are functions that have been attributed to these concretions containing calcium, magnesium, other metallic elements and phosphate (Luchtel et al. 1997; Gibbs et al. 1998). Additionally, it was recently demonstrated that calcium can also be present in vacuoles of basophilic cells lacking solid concretions (Lobo-da-Cunha et al. 2018). Peroxisomes are abundant in both basophilic and digestive cells and especially can have larger dimensions than in other tissues, indicating that these organelles have an important role in digestive gland metabolism (Lobo-da-Cunha et al. 1994, 2019).

Ultrastructural observations suggest a moderate endocytic activity in basophilic cells. The secretory activity of these cells implies the fusion of secretory vesicles with the cell membrane. In this process, the membrane of secretory vesicles is added to the cell membrane that would keep extending its surface area if this surplus of membrane was not compensated by membrane retrieval. This can be achieved through the formation of endocytic vesicles. Membrane internalisation and subsequent fusion between endocytic vesicles could explain the formation of vacuoles in the cytoplasm of basophilic cells. Accordingly, older basophilic cells, which have gone through several cycles of exocytosis and membrane internalisation, should contain more and larger vacuoles than younger basophilic cells, and this seems to be the case. Perhaps due to this accumulation of vacuoles, some researchers considered that basophilic cells were precursors of the "excretory cells". Moreover, calcium collected from the extracellular fluid by endocytic vesicles could be delivered to vacuoles of basophilic cells contributing to the accumulation of calcium in these structures (Lobo-da-Cunha et al. 2018).

The available data show that the fundamental morphological and functional aspects of the digestive gland are quite similar in most gastropods. Several enzymes were detected in this gland, namely, acid phosphatase, glycosidases, esterases and proteases, allowing the intracellular and extracellular digestion of a large variety of macromolecules (Foster et al. 1999; Taïeb 2001). Due to the large size of the digestive gland, the amount of basophilic cells makes this gland the major source of enzymes for extracellular digestion. Likewise, due to the intense endocytic activity and massive intracellular digestion in digestive cells, this gland is by far the major site of nutrient absorption (Luchtel et al. 1997). Nevertheless, in some gastropods, the digestive gland presents particular aspects. In sacoglossans, functional chloroplasts extracted from algae are retained in digestive cells, a process known as kleptoplasty (Martin et al. 2013). Furthermore, aeolid nudibranchs that feed on cnidarians retain the nematocysts of their prey within cnidophage cells of the digestive gland for their own defence, which means that the discharge of nematocysts is inhibited during feeding (Martin 2003).

Intestine and rectum

The intestine length varies among species, being more or less coiled in the visceral mass. The highly coiled intestine of the common limpet, *P. vulgata*, is about 8 times longer than the shell length, whereas in other gastropods, it runs straight from the stomach to the anus. In general, there seems to be a tendency towards a shorter intestine with less loops in carnivores. The intestine wall comprises one or two muscular layers, connective tissue and a ridged epithelium. The intestine can be divided into distinct sections, including the rectum, according to their histological traits (Bush 1988; Fretter and Graham 1994; Leal-Zanchet 1998; Dimitriadis 2001).

The intestinal epithelium is formed by columnar supporting cells and secretory cells. The former bear microvilli on the apical surface and most of them are ciliated. Many mitochondria, endocytic vesicles, multivesicular bodies and lysosomes, lipid droplets and glycogen deposits, a few Golgi stacks, rough endoplasmic reticulum cisternae and some peroxisomes are present in the cytoplasm of these cells. Ultrastructural features are typical of absorptive cells with endocytic and intracellular digestive activities (Franchini and Ottaviani 1992; Pfeiffer 1992; Leal-Zanchet 2002; Lobo-da-Cunha and Batista-Pinto 2007; Martin et al. 2010; Lobo-da-Cunha et al. 2011b). In *P. vulgata*, it was demonstrated that glucose is absorbed by a Na^+-independent process in the anterior intestine and through a Na^+-dependent process in the posterior intestine (Bush 1988). It was also demonstrated that other sugars, amino acid, fatty acids and water are also absorbed by the intestinal epithelium (Walker 1972; Orive et al. 1979; Bush 1988; Dimitriadis 2001).

Light and electron microscopy observations also revealed cells that secrete mucus and cells that secrete proteins (Fig. 8d). Intestinal secretory cells rich in rough endoplasmic reticulum cisternae and electron-dense secretory vesicles were implicated in the secretion of proteins to coat the faecal rods with a protective layer to prevent their disintegration (Bush 1988). However, secretion of digestive enzymes cannot be ruled out for intestinal cells of the serous type. Mucous cells are filled with large secretory vesicles in which neutral and acidic mucopolysaccharides were detected. The basal region includes the nucleus, several Golgi stacks and many rough endoplasmic reticulum cisternae (Boer and Kits 1990; Franchini and Ottaviani 1992; Leal-Zanchet 2002; Lobo-da-Cunha and Batista-Pinto 2007; Lobo-da-Cunha et al. 2011b).

A more or less developed anal gland consisting of a rectal diverticulum occurs in some gastropods. Ultrastructural studies of this gland in the neogastropod *N. lapillus* revealed cells with and apical border of cilia and microvilli. In these cells, formation of endocytic vesicles was observed not only at the base of the microvilli but also on the basal cell membrane that is considerably folded and associated with mitochondria. Collected substances are digested in lysosomes and the resulting large residual bodies are expelled by apocrine secretion. A large population of symbiotic bacteria was found in the lumen of this gland. Despite being linked to the rectum, neither faeces nor mucus enter the gland, which seems to have an excretory function rather than a digestive one. In other gastropods, the anal gland is just a small diverticulum that secretes mucus (Andrews 1992).

Enteroendocrine cells were observed in the basal region of the intestinal epithelium, never reaching the lumen. Their cytoplasm contains small electron-dense granules, rough endoplasmic reticulum cisternae, Golgi stacks, lysosomes, mitochondria and a few lipid droplets. Intraepithelial nerve terminals are abundant in the intestine establishing contact with the secretory and enteroendocrine cells, providing clues of a neuronal control of intestinal physiology (Bush 1988; Franchini and Ottaviani 1992; Lobo-da-Cunha and Batista-Pinto 2007; Lobo-da-Cunha et al. 2011b).

There are bacteria associated with the digestive system of gastropods, and at least some of them can secrete enzymes, but the exact role and relevance of these symbionts in the digestive process is not clear yet (Walker et al. 1999; Godoy et al. 2013; Dudek et al. 2014).

Digestive system in Bivalvia

Bivalves are very common molluscs, including mussels, clams, scallops and oysters, among others. Their body is laterally compressed and enveloped by mantle folds that secrete the two valves of the shell joined together by a hinge. The heads and associated structures such as the radula and salivary glands are absent. This class contains more than 10,000 species, being the second most diverse among molluscs. The large majority of them are marine occurring at all depths, and others live in estuaries or in freshwater. Species that borrow in sediments have a strong muscular foot for digging, mussels use byssal filaments for attachment on rock surfaces, some live freely on the surface of sediments and others bore in wood or soft rocks (Giribet 2008). Most are suspension-feeders that capture plankton and organic particles from water, while others are deposit-feeders obtaining nutritive particles from sediments, but some are carnivores feeding on small crustaceans and shipworms consume wood (Morton 1983; Voight 2015; Rosa et al. 2018).

In suspension-feeding bivalves, particles suspended in water enter through the inhalant aperture or siphon and are captured by the ctenidial filaments (gills). Subsequently, a pair of labial palps transport and select the particles to be ingested by the mouth, rejecting unwanted particles that aggregated by mucus from the pseudofeaces. In deposit-feeding bivalves, the labial palps are responsible for food collection and the gills have only a respiratory function (Morse and Zardus 1997; Rosa et al. 2018). The triangular or leaf-shaped labial palps comprise multiple lamellae lined by a ciliated epithelium containing mucus-secreting cells (Beninger et al. 1995; Morse and Zardus 1997). The mouth is typically a simple aperture bordered by fleshy lips (Morton 1983). Cells that secrete both acid and neutral mucopolysaccharides occur in buccal, peribuccal and oesophageal epithelia. The bucco-oesophageal glands of the mussel *Mytilus edulis* also secrete neutral and acid mucopolysaccharides, but a digestive role was not established for these glands. The mucus with food particles is transported along the oesophagus into the stomach by ciliary action (Beninger et al. 1991; Beninger and Le Pennec 1993; Thomas 1993).

The bivalve stomach is a complex organ that includes sorting areas, gastric shield and style sac (Fig. 2). Based on anatomical features, five main stomach types were recognised (Morton 1983; Purchon 1987). The stomach of the deposit-feeder nuculoid bivalves differs in some respects from the stomach of suspension-feeders. In the first, the globular portion of the stomach communicates with a conical style sac from which arises the first part of the intestine known in bivalves as midgut (Purchon 1987). In other bivalves, the style sac is completely separated from the intestine, or a slit in the sac makes a partial communication with the intestine (Morse and Zardus 1997). In less specialised carnivorous bivalves, the sorting areas are reduced, but a style sac and a gastric shield are present, whereas in more specialised carnivores, the stomach forms a powerful crushing gizzard with a thicker muscular wall and an inner layer of scleroprotein (Morton 1983; Purchon 1987).

The stomach-sorting areas, comprising several ridges lined by a ciliated epithelium, separate the finest particles that go through the digestive gland ducts from the larger particles that go directly to the intestine (Thomas 1993). Sorting areas also have glandular activity. In the scallop *Pecten maximus*, stomach cells that secreted amylase are rich in rough endoplasmic reticulum cisternae and Golgi stacks. These cells contain secretory vesicles with median or high electron density in the apical region, which are released to the stomach lumen by apocrine secretion (Henry et al. 1993). The gastric shield corresponds to an area of columnar cells with a border of microvilli covered by a cuticle. The style sac is an extension of the stomach that in deposit-feeder nuculoid bivalves contains a mucous protostyle, while in suspension-feeders, it houses a more solid crystalline style (Kristensen 1972). The ciliated epithelium of the style sac generates a rotational motion in the style whose tip protrudes from the style sac. The rotation of the protostyle inside the stomach pulls filaments of mucus loaded with ingested particles from the oesophagus and across the sorting areas of the stomach. The rotation of the more rigid crystalline styles grinds food particles against the cuticle of the stomach shield (Morse and Zardus 1997). Biochemical studies showed that in addition to α-amylase and chitinase activities, the style also has enzymes with the capacity to digest cellulose or at least soluble cellulose derivatives (Palais et al. 2010; MacKenzie and Marshall 2014). The polysaccharide-hydrolysing enzymes of the style may play a more important role in extracellular digestion in bivalves with a less robust style, in which the mechanical grinding action of the style against the gastric shield is less effective. Some bivalves possess a permanent hard crystalline style, whereas in others, the crystalline style is softer and transient dissolving and reforming often in synchrony with feeding tidal cycles (Kristensen 1972; Morton 1983; MacKenzie and Marshall 2014).

As in gastropods, the digestive gland of bivalves consists of numerous blind-ending digestive diverticula connected to the stomach through main and secondary ducts. Duct cells are columnar-shaped bearing microvilli, and some also have cilia. The abundance of endocytic vesicles, multivesicular bodies and lysosomes points to an endocytic activity and intracellular digestion. The cytoplasm is rich in other organelles, lipid droplets and glycogen deposits (Owen 1973; Henry et al. 1991). Some mucous cells were also reported in digestive gland ducts (Henry et al. 1991). The digestive diverticula contain digestive and basophilic cells with the general morphofunctional features already mentioned in gastropods (Cajaraville et al. 1992; Weinstein 1995; Robledo and Cajaraville 1996; Morse and Zardus 1997). More recently, glycosylation in the Golgi apparatus and sorting pathways of lysosomal enzymes were investigated in mussel digestive cells (Robledo et al. 2006). The observation of coated pits in the apical cell membrane of mussel basophilic cells showed that endocytosis also occurs in these cells, whose main activity is the secretion of digestive enzymes for extracellular digestion (Dimitriadis et al. 2004). Flagella were observed in basophilic and undifferentiated cells (Owen 1973; Henry et al. 1991; Weinstein 1995). Amylase, cellulase, esterase, acid phosphatase, peptidases and other enzyme were detected in digestive diverticula of bivalves (Henry et al. 1991; Palais et al. 2010). Seasonal variations in digestive gland activities related with phytoplankton abundance were reported in scallops (Le Pennec et al. 2001), but not in oysters (Weinstein 1995). Moreover, the digestive gland diverticula of bivalves living in intertidal environments undergo rhythmic changes correlated with the tidal-feeding cycle (Morton 1983).

From the stomach, the intestine receives waste coming from the digestive gland as well as those particles that were rejected for being too large to go into the digestive gland ducts. The intestinal epithelium is formed by columnar cells bearing microvilli and cilia, which have endocytic vesicles, lysosomes, lipid droplets, endoplasmic reticulum cisternae and Golgi stacks in the cytoplasm. Mucus-secreting cells are also present. It was recognised that both extracellular and intracellular digestion take place in the intestine of bivalves, and the transport of nutrients from the intestine epithelium to developing oocytes was demonstrated in the scallop *P. maximus*. In addition to the role of the intestine and stomach epithelium in digestion and nutrient assimilation, haemocytes have also been implicated in these processes. It seems that these cells of the immune system can cross the digestive track epithelium to phagocyte nutritive particles, digest them and transport nutrients to other parts of the body (Le Pennec et al. 1991; Beninger et al. 2003).

Modifications of the digestive system occur in bivalves adapted to a particular environment or food sources (Morton 1983). Shipworms are bivalves with a deeply modified body that burrow tunnels in underwater wood using their specialised shell valves with toothed ridges. Wood particles resulting from burrowing activity are ingested and transported to the stomach by ciliary currents. In the stomach, wood particles are mixed with enzymes from the digestive gland and proceed to the large caecum that is considered the main site of extracellular digestion. The abundant expression of putative glucose transporters in cells of the caecum epithelium bearing cilia and microvilli indicates that they are able to absorb sugars resulting from extracellular wood digestion. In these bivalves, the basophilic cells of the digestive gland most probably secreted β-1,4 glucosidases responsible for extracellular breakdown of cellulose and hemicelluloses. The digestive gland also contains amoeboid cells that phagocyte wood particles that are digested in lysosomes (Sabbadin et al. 2018). Bacterial symbionts are abundant in the gills of these bivalves, but the caecum harbours only very sparse microbial populations that do not seem to play a major role in wood digestion. On the other hand, a higher density of bacteria was found in the intestine suggesting a possible role in intestinal digestion (Betcher et al. 2012).

Marine bivalves that live in sulphide- and methane-rich environments, either in littoral waters or in deep-sea hydrothermal vents and seeps, have different degrees of dependence on endosymbiotic bacteria for nutrition. The digestive system is completely absent in those species most dependent on symbiotic bacteria, being partially reduced in bivalves that maintain some suspension-feeding capability to complement the nutrition they receive from the endosymbionts living in bacteriocyte cells of the gills (Le Pennec et al. 1995; Roeselers and Newton 2012). Another case of symbiosis occurs in Tridacninae, the tropical giant clams that harbour symbiotic unicellular algae known as zooxanthellae, which provide additional nutrition to these bivalves living in nutrient-deficient waters (Morton 1983).

Digestive system in Cephalopoda

This class of molluscs with near 800 living species is divided into the clades Nautiloidea and Coleoidea. The first includes the genus *Nautilus* and *Allonautilus* the only extant cephalopod with external shell, and the second encompasses all other extant cephalopods. The Coleoidea are further divided into Octopodiformes, including the octopods and the vampire squid (*Vampyroteuthis infernalis*), and Decapodiformes comprehending the squids and cuttlefish (Uribe and Zardoya 2017). All are marine, living from shallow waters to deep ocean. Some reach a huge size, more than 10 m in the giant squid *Architeuthis dux* and colossal squid *Mesonychoteuthis hamiltoni* that are the largest living invertebrates. In cephalopods the foot is transformed into arms and tentacles bearing suckers that are used for prey capture, although the multiple tentacles of nautiloids have a ridged surface instead of suckers. All cephalopods are carnivorous, coleoids being typically active predators and nautiloids largely scavengers. Due to their active behaviour and high metabolic rate, cephalopods need to consume large amounts of food. They possess a highly developed and efficient digestive system that allows fast growth and a high rate of food conversion into body tissue (Boucaud-Camou and Boucher-Rodoni 1983; Budelmann et al. 1997; Mangold and Young 1998). However, despite some recent studies about digestive physiology (Gallardo et al. 2017; Ponte et al. 2017; Ibarra-García et al. 2018), compared with other areas of cephalopod biology such as the nervous system and behaviour, not so much research has been done on digestive system in the last decades (Ponte et al. 2018).

Positioned in the centre of the arms and tentacles, the buccal mass includes the mouth and lips, a pair of mandibles forming sharp beaks, strong muscles, the radula, scattered buccal glandular cells and a submandibular gland. The latter, also known as sublingual gland, is a single organ formed by several lobes, being well developed in the vampire squid and octopuses, but reduced to two small folds in *Nautilus* (Budelmann et al. 1997). In *Cirrothauma murrayi*, a finned octopus from deep ocean, this gland contains mucous and serous cells whose products are released through pores located in the buccal cavity (Aldred et al. 1983). A pair of anterior salivary glands is also associated with the buccal mass. These ones, composed of ramified tubules, produce a mucous secretion containing glycoproteins, dipeptidase and hyaluronidase (Budelmann et al. 1997).

With the exception of nautiloids, posterior salivary glands also known as venom glands are present in cephalopods. In octopus and cuttlefish, a pair of these glands lies behind the buccal mass being connected to the buccal cavity by a duct, but squids have just one venom gland (Fig. 9). These glands consist of numerous lobules with a tubular structure and produce a secretion containing a complex mixture of biologically active substances that rapidly paralyse the prey. Posterior

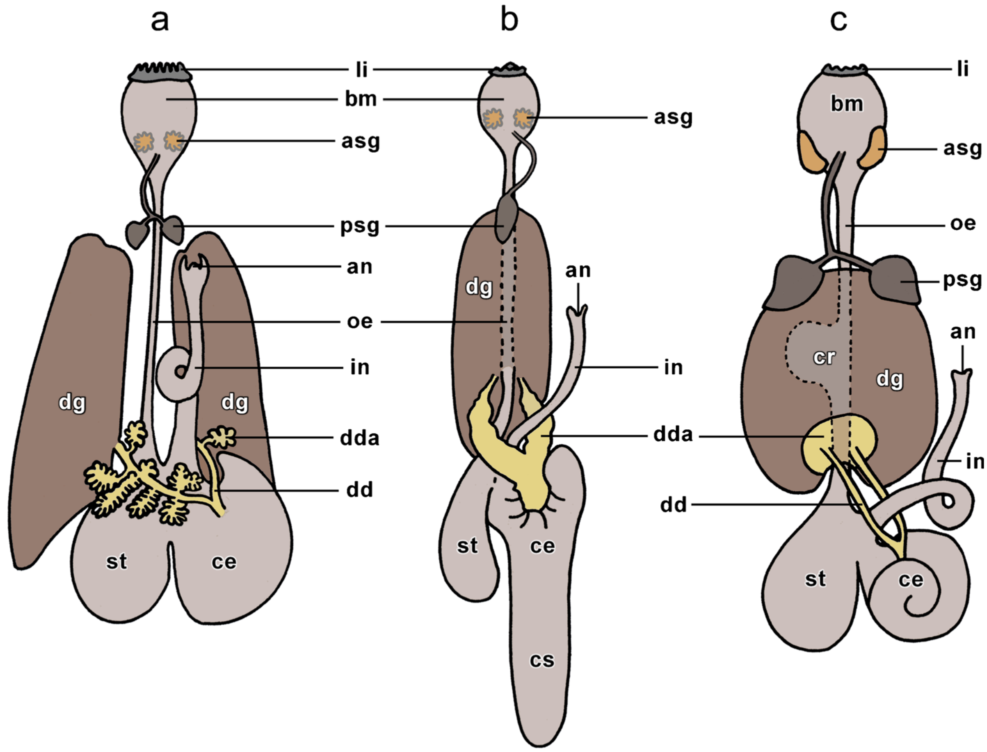


Fig. 9 Digestive organs of cephalopods. **a** Cuttlefish (*Sepia officinalis*). **b** Squid (*Loligo vulgaris*). **c** Octopus (*Octopus vulgaris*). an—anus, asg—anterior salivary glands, bm—buccal mass, ce—caecum, cr—crop, cs—caecal sac, dd—digestive ducts, dda—digestive ducts appendages, dg—digestive gland, in—intestine, li—lips, oe—oesophagus, psg—posterior salivary glands, st—stomach. Adapted from Boucaud-Camou and Boucher-Rodoni (1983)

salivary glands are known to secrete neutral and acid proteoglycans, toxins such as the polypeptide eledosin and the neurotoxic glycoproteins cephalotoxin and maculotoxin, cardioexcitatory and vasodilatory substances that allow a fast distribution of toxins through the prey circulatory system. On the other hand, the presence of hyaluronidase, chitinase and chymotrypsin in the posterior salivary glands of octopus indicates that digestion starts when the excreted enzymes reach prey tissues (Koueta and Boucaud-Camou 1986; Budelmann et al. 1997; Linares et al. 2015; Ponte and Modica 2017).

The elongated oesophagus constitutes the first part of the U-shaped digestive tract (Fig. 9). In *Nautilus* and most octopods, the oesophagus has a distended portion forming a crop where ingested food can be stored and digestion can start (Westermann et al. 2000). In *Nautilus*, the epithelium of the oesophagus and crop consists of columnar cells with a microvilli border, containing lysosomes and lipid inclusions. Mucous cells and cells with electron-dense secretory vesicles are also present (Westermann and Schipp 1998a, b). In coleoids, a cuticle covers the oesophageal epithelium. The oesophagus opens into a sac-like stomach in which the columnar epithelium is coated by a cuticle. Near the junction with the oesophagus, the stomach is connected to the vestibule where both caecum and intestine also open. However, in some squids, the vestibule is absent. Although no enzyme secretion was reported in the stomach, food is digested there by the conjugation of mechanical action of the thick muscular wall and enzymes coming from the digestive gland and possibly also from salivary glands (Boucaud-Camou and Boucher-Rodoni 1983; Mangold and Young 1998; Westermann and Schipp 1998b; Westermann et al. 2002).

The liquid chyme with fine particles that result from stomach digestion passes through the vestibule and enters the caecum, while larger undigested parts go to the intestine. The caecum is an organ with multiple primary folds, being bag-shaped in nautiloids and spiral-shaped in coleoids. The primary folds are lined by a ridged epithelium forming secondary folds and grooves (Fig. 10). Columnar ciliated cells and flask-shaped secretory cells were reported in the caecal epithelium. The ciliated cells have a border of microvilli, lipid droplets, some Golgi stacks and small lysosomes where fine particles collected by endocytosis are digested. The secretory cells contain numerous Golgi stacks, endoplasmic reticulum cisternae and secretory vesicles with glycoproteins, being responsible for the formation of mucus strings that transport discarded particles to the intestine (Boucaud-Camou 1977; Westermann and Schipp 1998a, b). Squids have a sac extending from the coiled region of the caecum. The epithelial folds of the caecal sac are lined by ciliated cells that bear a border of microvilli and accumulate lipid droplets. However, glandular cells are absent in this sac that contains a liquid with solid particles in some cases (Boucher-Rodoni and Boucaud-Camou 1987; Mangold and Young 1998). It can be concluded that in addition to an absorptive activity, the caecum also seems to act as a sorting organ separating undesirable residues from nutritive particles and molecules (Boucaud-Camou 1977; Westermann et al. 2000).

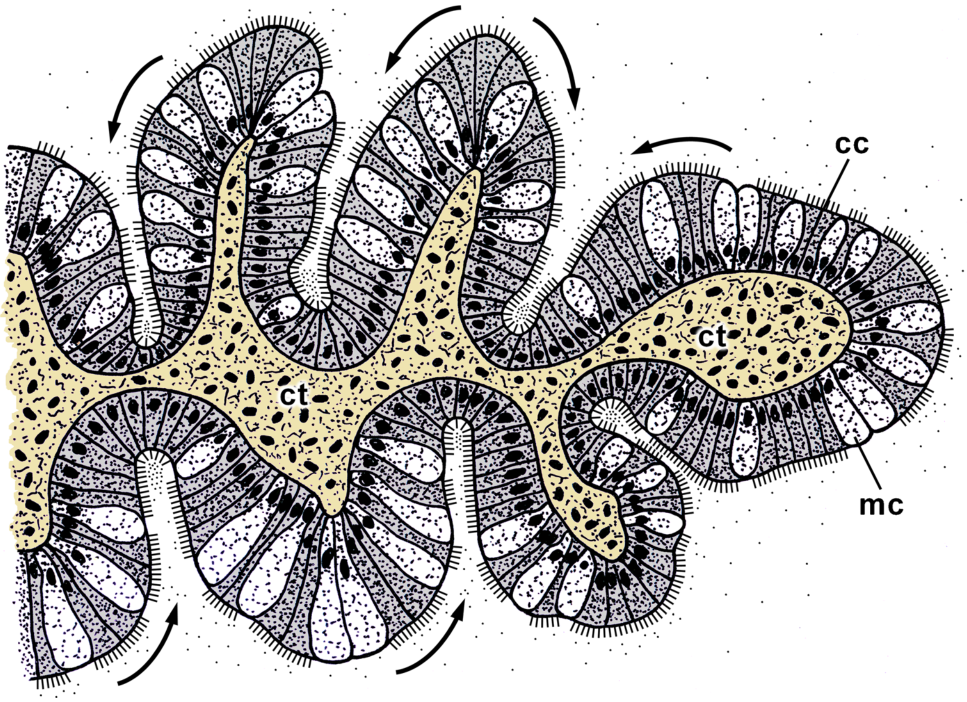


Fig. 10 Primary fold of the caecum. Arrows indicate the ciliary currents that gather undigested particles into mucous strings formed at the bottom of the epithelial secondary folds. cc—ciliated cells, ct—connective tissue, mc—mucous cells. According to Boucaud-Camou (1977) and Boucher-Rodoni and Boucaud-Camou (1987)

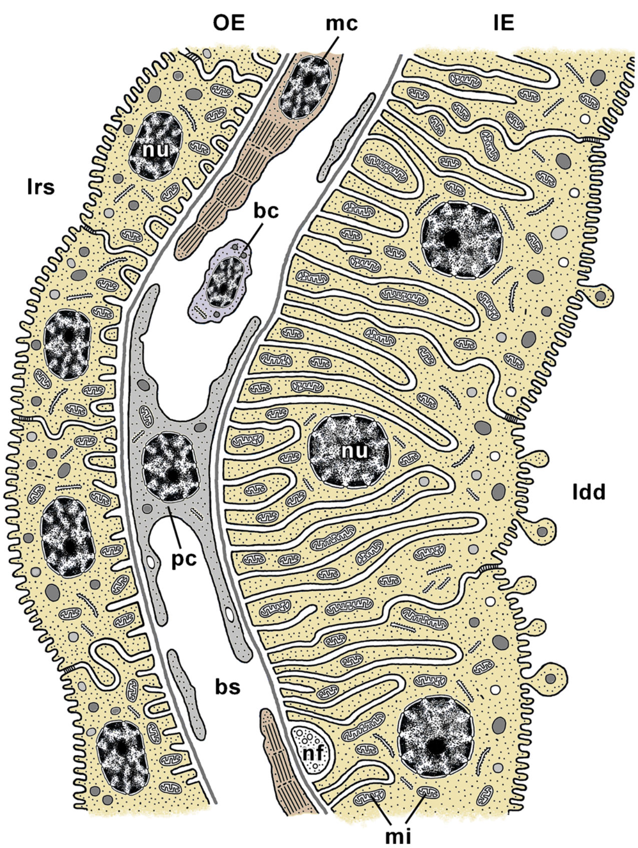


Fig. 11 Histology of digestive ducts appendages of the cuttlefish (*Sepia officinalis*). bc—blood cell, bs—blood sinus, IE—inner epithelium, ldd—lumen of digestive duct appendage, lrs—lumen of renal sac, mc—muscle cell, mi—mitochondria, nf—nerve fibre, nu—nucleus, OE—outer epithelium, pc—pilaster cell. From Schipp and Boletzky (1976)

In cuttlefish and squids (Decapodiformes), the two digestive ducts connecting the caecum with the digestive gland bear numerous branched appendages (Fig. 9a, b). These appendages, called pancreas in older texts, lie within the kidney sac and consist of two epithelia separated by a space enclosing a system of blood vessels and sinus (Fig. 11). The inner epithelium lines the lumen of the diverticula that are connected to the digestive ducts. The cells of this epithelium are characterised by very deep cell membrane invaginations that arise from the cell base and extend almost to the cell apex. A very large number of mitochondria fill the thin portions of cytoplasm flanked by the cell membrane invaginations indicating an intense active transport across the epithelium. Mitochondria are also abundant at the cell apex just below the border of short microvilli. Additionally, these cells show signs of endocytosis and contain electro-dense lysosomes, but the rough endoplasmic reticulum is not specially developed and secretory vesicles are not evident (Fig. 11). Therefore, this epithelium must have a mixed function being involved in absorption of small molecules and intracellular digestion of microscopic food particles as well as excretion or osmotic regulation. The outer epithelium of the digestive ducts appendages, which is in direct contact with the fluid of the renal sac, is formed by cells with long microvilli and basal cell membrane invaginations associated with mitochondria, suggesting excretory functions (Boucaud-Camou 1972b; Schipp and Boletzky 1976; Boucher-Rodoni and Boucaud-Camou 1987). In octopods, these appendages are enclosed in the digestive gland capsule (Fig. 9c), being absent in nautiloids (Boucaud-Camou and Boucher-Rodoni 1983).

The digestive gland is not only the largest organ of the digestive system but the largest in the visceral mass of most cephalopods. In many cephalopods, this gland is a unified solid mass, whereas in *Nautilus*, it is divided into three to five lobes, being bilobed in cuttlefish (Mangold and Young 1998). Through the digestive ducts, enzymes for extracellular digestion flow from the digestive gland to the caecum and stomach, while products of extracellular digestion that takes place in the stomach and caecum travel in the opposite direction to reach the numerous digestive diverticula that constitute the digestive gland. Two or three cell types were reported in the digestive diverticula of cephalopods (Boucher-Rodoni and Boucaud-Camou 1987; Budelmann et al. 1997), but in some species, just a single cell type was recognised (Swift et al. 2005). This gland was mostly studied in the cuttlefish *Sepia officinalis*, in which three cell types were recognised in the digestive diverticula. The basal or replacement cells that were considered precursors of the other types have a pyramidal shape and are found at the base of the epithelium not reaching the lumen of the diverticula. They contain large amounts of rough endoplasmic reticulum cisternae, a developed Golgi apparatus and small electron-dense bodies. Excretory or vacuolar cells characterised by a large apical vacuole with a clear content were also reported (Boucaud-Camou and Yim 1980; Budelmann et al. 1997; Costa et al. 2014). However, the most abundant are the column-shaped digestive cells, formerly called *boules* cells. At their apex, coated pits formed at the base of the microvilli collect substances from the lumen of digestive diverticula, giving rise to endocytic vesicles. The observation of numerous endocytic vesicles and lysosomes indicates that these cells are engaged in absorption and intracellular digestion of substances coming from the stomach and caecum, just like the digestive cells of other molluscs (Boucaud-Camou and Yim 1980; Budelmann et al. 1997). These cells accumulated lipid droplets and, at a later stage, form a large vacuole containing an internal mass that is excreted to the lumen of the digestive diverticula (Boucaud-Camou 1972a; Boucher-Rodoni and Boucaud-Camou 1987). Experiments with carmine and ferritin particles as well as with radiolabelled food showed that this gland is the major site for uptake of macromolecules and particles, although absorption also occur in the caecum, digestive duct appendages and intestine (Boucaud-Camou and Boucher-Rodoni 1983; Boucher-Rodoni and Boucaud-Camou 1987; Westermann et al. 2000). On the other hand, the digestive cells were also considered responsible for production and secretion of amylases, lipases and proteases destined for extracellular digestion (Budelmann et al. 1997; Swift et al. 2005; Gallardo et al. 2017; Ibarra-García et al. 2018), a function attributed to the basophilic cells of gastropods and bivalves.

The intestine is rather short in coleoids but longer in *Nautilus*. The indigested coarse residues go directly from the stomach to the intestine that also receives residues coming from the caecum and digestive gland. The internal folds of the intestine are lined by a ciliated epithelium containing glandular cells that secrete polysaccharides with minor protein components. Most species have an ink gland with a duct that opens into the intestine not far from the anus (Boucaud-Camou and Boucher-Rodoni 1983; Boucher-Rodoni and Boucaud-Camou 1987; Mangold and Young 1998; Westermann and Schipp 1998b).

Digestive system in Scaphopoda

The Scaphopoda are marine molluscs with a worldwide distribution that can be found from shallow waters to depths below 6000 m. The slightly curved tubular shell with a narrow apex is opened at both ends and looks like a tusk. These animals live in burrows with the head pointing down, feeding on foraminiferans and other microorganisms they collect from the sediments using special feeding tentacles, the captacula. This class contain about 400 living species, ranging in length from less than 1 cm to nearly 15 cm, being one of the less studied classes of molluscs (Reynolds 2002). The digestive system of some species was investigated many years ago (Sahlmann 1973; Thaib 1976; Steiner 1994), but there is a lack of recent publications.

The mouth is located at the tip of a short proboscis that at least in some genera seems not able to extend beyond the anterior aperture of the shell. Muscular action in the proboscis moves the collected food items trough the oral tube lined by a non-ciliated epithelium into a pair of buccal pouches where food can be stored. The secretory cells that were observed in the non-ciliated epithelium of these pouches probably secrete mucus. Food proceeds to the pharynx to be macerated by the massive radula. The single jaw present on the dorsal wall of the pharynx, probably made of chitinous material, may help food grinding being a hard surface against which the radula acts on. Alternatively, it may just serve to protect the underlying tissues from damage that could be caused by radular action. Salivary glands are absent, but secretory cells occur in oesophageal pouches (Shimek and Steiner 1997). According to Thaib (1976), the epithelial cells of these pouches form large apical projection typical of apocrine secretion, releasing mucoid substances, peptidases, proteases, glycosidases and lipase into the oesophagus lumen where these enzymes can start extracellular digestion.

Ciliary and muscular action along the oesophagus moves the macerated food embedded in mucus to the stomach. The ventral wall of the stomach contains ciliated cells, whereas other parts are covered by a cuticle. Some glandular cells and amebocytes are also present in the gastric epithelium. One or two digestive glands open laterally on the stomach.

These glands are divided into lobes, each one composed of blind-ending tubules lined by protein-secreting pyramidal basophilic cells and absorptive-secretive cells. Extracellular digestion proceeds in the stomach where food is exposed to enzymes coming from the digestive glands. Fine nutritive particles enter the tubules of the digestive glands where digestion continues. In there, absorptive-secretive cells collect the fine particles by endocytosis and carry out the intracellular phase of digestion in lysosomes. At the end of this phase, undigested wastes and lysosomal enzymes are released into the lumen of digestive gland tubules and are transported back to the stomach. In the stomach, undigested residues and particles too large to enter the digestive gland tubules are rolled up into a mucous string and conveyed to the intestine by ciliary action (Shimek and Steiner 1997).

The intestine forms two to five loops depending on the species. In deep-sea scaphopods, with four or five intestinal loops, the elongated hindgut can be an adaptation to poor nutrition as also suggested in other molluscs (Steiner 1994). The epithelium in the proximal intestine comprises ciliated cells and scattered gland cells secreting proteins, whereas the distal portion of the intestine lacks secretory cells. Intestinal musculature is well developed, performing strong peristaltic movements to conduct faecal matter. A rectal gland formed by blind-ending tubules is connected to the rectum through a broad duct. These glandular cells secrete an electron-dense substance most probably of lipidic nature. The function of this gland is uncertain, but lubrication of faeces is a hypothesis (Shimek and Steiner 1997).

Digestive system development in molluscs

Typically, molluscs pass through two larval stages: the trochophore and the veliger. The trochophore bears ciliary bands for locomotion and the veliger is characterised by the velum, a pair of lobes with long cilia along the edge, with which planktonic larvae can swim and gather food in those species with a planktotrophic larval stage (Fioroni 1982; Hadfield et al. 1997; Page 2009). Finally, the veliger sinks to the bottom and metamorphoses into the adult form. However, in some gastropods, larval stages occur inside the egg or egg capsules from which juveniles looking like miniature adults emerge (Hookham and Page 2016).

Trochophore larvae have a very simple digestive tract formed by mouth, oesophagus, stomach and intestine ending in the anus. In the scallop *Mizuhopecten yessoensis*, for example, the gut epithelium of the newly formed trochophore presents sparse short microvilli and some of its cells are ciliated. The cytoplasm of these cells contains the Golgi apparatus, a large number of flattened rough endoplasmic reticulum cisternae, mitochondria and yolk granules. At the late trochophore stages, gut epithelial cells became more differentiated with numerous microvilli forming an apical brush border. In veligers, the digestive system becomes more complex. Oesophageal cells have phagosomes and electron-lucent vacuoles. The gastric shield and style sac appear as differentiated zones of the stomach. The digestive gland starts to develop, but at this stage, is still part of the stomach epithelium, formed by small cells rich in rough endoplasmic reticulum cisternae (precursors of basophilic cells) and columnar cells containing numerous phagosomes (precursors of digestive cells). Intestinal cells bear cilia and microvilli (Kamenev et al. 2018).

In gastropods, several changes were reported in the digestive system during larval development and metamorphosis. In some caenogastropods, a complete remodelling of the larval foregut occurs to shape the highly complex foregut of the adults (Hookham and Page 2016; Page and Hookham 2017). In other cases, a structural simplification takes place. In siphonariids, for example, the veliger stomach is regionalised with a gastric shield and style sac, which are no longer present in the postmetamorphic stomach that is a uniformly ciliated sac (Page et al. 2019).

Contrary to other molluscs, cephalopods have a direct development without neither larval stage nor metamorphosis, hatching as a miniaturised form of the adult. Cephalopods have telolecithal eggs and present a discoidal cleavage unlike other molluscs in which a total and spiral segmentation occurs (Fioroni 1990; Nixon and Mangold 2006; Bonnaud-Ponticelli and Bassaglia 2014).

Recently, some efforts have also been taken to understand the role of regulatory genes in the development of the digestive system of molluscs. The expression of the three *ParaHox* genes (*Gsx*, *Xlox*, *Cdx*) during anterior–posterior development of the digestive system in the vetigastropod *Gibbula varia* suggests that these genes are involved in anterior–posterior differentiation of the gut in this species. In addition to their roles in the development of other organs, *Gsx* gene seems responsible for patterning the mouth and foregut, with *Xlox* patterning the midgut or digestive gland and *Cdx* patterning the hindgut. Additionally, during postlarval development of *G. varia*, *Gsx* transcripts were detected in the precursor cells of odontoblasts at the base of the radula sac. This was considered a molluscan novelty related to radula evolution (Samadi and Steiner 2010). Conversely, *Gsx* gene was not considered involved in patterning the foregut in scaphopods and cephalopods (Wollesen et al. 2015). Studies with the Pacific oyster (*Crassostrea gigas*) revealed a high expression of genes from the *Wnt* cluster in the digestive gland, stomach and intestine of adults and in the gut of larvae. Clustered *Wnt* genes play important roles in gut development of different animals, and the gene expression results suggest that they are also involved in gut formation in oyster (Liu et al. 2018).

Concluding remarks

Typically, digestion in molluscs proceeds in two phases. First, enzymes secreted by glands are responsible for the extracellular digestion in the lumen of the digestive tract, and afterwards, the products of this first phase of digestion are collected by absorptive cells where intracellular digestion occurs. Macromolecular products of extracellular digestion are uptaken by endocytosis for further breakdown in lysosomes, whereas small molecules such as simple sugars and amino acids can be transported across the cell membrane of the microvilli border of absorptive cells. Therefore, the digestive process of molluscs with a major phase of intracellular digestion in lysosomes differs substantially from that of vertebrates. Although an important physiological role was recognised for endocytosis in vertebrate intestinal cells (Zimmer et al. 2016), intracellular digestion and storage of reserves are not a major function of vertebrate enterocytes.

It is well established that the digestive gland is the major site of nutrient absorption in molluscs, but several studies demonstrate that the digestive tract epithelium also contributes to the absorptive capacity of the digestive system. Digestive tract epithelial-supporting cells of molluscs are remarkable cells that perform multiple tasks, such as endocytosis and intracellular digestion, absorption of small molecules, storage of glycogen and lipid reserves and transport of nutrients to the underlying tissues. The presence of cilia in many of these cells indicated that they are also implied in the movement of particles along the digestive tract. Therefore, these are metabolic active cells that need many mitochondria to provide the energy required for transports and ciliary motion. Epithelial-supporting cells with a similar ultrastructure are found in different molluscan classes along the digestive tract from the oesophagus to the rectum, but physiological differences probably occur between the epithelia of different parts of the digestive tract.

Many secretory cells occur in the digestive system of molluscs, some inserted along the digestive tract epithelium and others in glandular organs. Histochemical techniques revealed the presence of mucopolysaccharides and proteins in the secretory vesicles of these cells, and several digestive enzymes were also detected in the digestive fluid, but much remain to be discovered about the specific function of all those secretory products that are not well characterised at the molecular level. The digestive gland is a key organ in the digestive system of molluscs, in general with similar structure and functions in polyplacophorans, monoplacophorans, bivalves, gastropods and scaphopods. The similarities of this organ in aculiferan and conchiferan classes indicate that the fundamental morphofunctional features of the digestive gland have been well conserved during the evolution of most mollusc clades, and suggest an ancestral origin for this organ prior to the split that divided the phylum in Aculifera and Conchifera clades. A major deviation from the basic digestive system pattern of molluscs occurred in the aplacophoran clades Caudofoveata and Solenogastres, which are now considered to have a derived body plan that does not reflect a basal condition. Protein-secreting cells like the basophilic cells typical of molluscan digestive glands were not reported in the digestive diverticulum caudofoveates nor in the midgut sac of solenogasters, in which cells are of the digestive type. It is interesting to note that in the digestive gland of cephalopods, basophilic cells seem also to be absent, all functions being carried out by a single cell type. The foregut glands and buccal structures are much more diversified probably because they are more closely related to the adaptations to a specific diet or feeding mode.

Anatomy and histology of the digestive system, and even the ultrastructure of several cell types, are now reasonably investigated in gastropods, bivalves and cephalopods, which are the best studied molluscs. Conversely, in other classes, much more still remains to be investigated. A number of physiological and biochemical studies were also made, but some were done many years ago. Therefore, the use of modern equipment and techniques would allow a significant increase of information on the physiology and metabolism of mollusc digestive system, which is lagging far behind what is known about the mammalian digestive system.

Compliance with ethical statements

Conflict of interest The author declares that he has no conflict of interest.

Ethical approval This article does not contain any studies with human participants or animals performed by the author.

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