

The molluscan foot

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Abstract

The mollusks' singular foot is examined from an evolutionary perspective, starting with a peri-oral pedal shield in Caudofoveata. It evolves into a ventral pedal groove in Solenogastres, further developing into a sucker-crawling structure in Testaria, which is present in Polyplacophora, Monoplacophora, and the majority of Gastropoda. Within Diasoma, the foot takes on a digging form that extends forward, featuring an umbrella-like fold at the tip. This particular model is observed in Scaphopoda and protobranch bivalves. Bivalves have notably modified this model into the pelecypod model, a reduced byssal model, and even complete loss in some sessile groups, but not all. Non-benthic cephalopods, on the other hand, have adapted the foot into arms in the anterior region and a siphon in the posterior region.

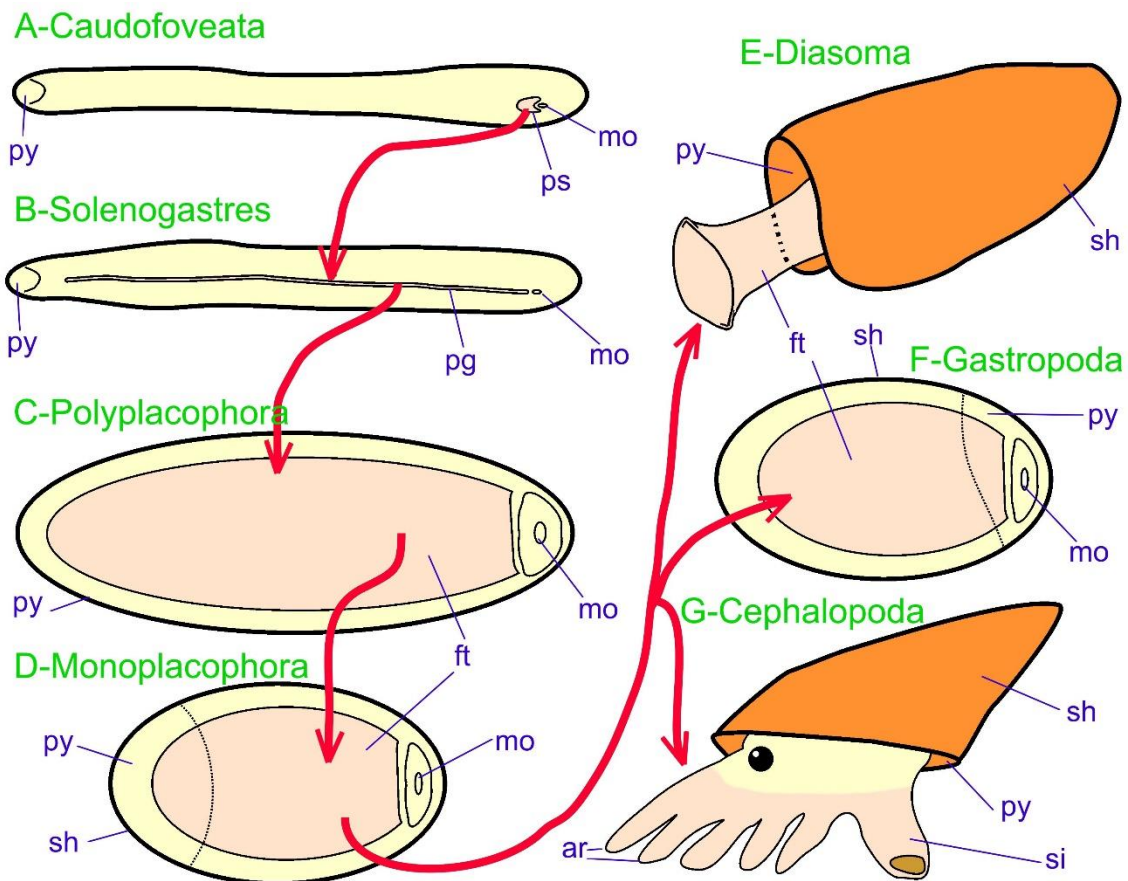
Keywords: anatomy, adaptation, taxonomy, phylogeny, evolution.

Introduction

Interestingly, arthropods, the most diverse group of multicellular organisms, achieved this status with a multitude of feet. Mollusks, the second most diverse group, achieved it with a single foot. The characteristic molluscan foot is a substantial structure used by the animal for locomotion, typically by crawling. Naturally, given the variety of molluscan body shapes, the foot has undergone various modifications, from multiplying into arms to disappearing altogether. Therefore, this article focuses on the foot and outlines its principal modifications along different branches within a phylogenetic framework.

The first step is the evolution of the foot at the class level. Subsequently, the article provides insights into the evolution of the foot within specific branches of the major classes.

Foot evolution in Class level



1: schematic representation of basal representatives of living molluscan classes or superclass, with emphasis in the foot (no scales or proportions). A, Caudofoveata, ventral-slightly right view; B, Solenogastres, ventral-slightly right view; C, Polyplacophora, ventral view; D, Monoplacophora, ventral view; E, Diasoma, left-slightly anterior view; F, Gastropoda, ventral view; G, Cephalopoda, left view. Homologous structures with same colors. Only topology of pallial cavity (py) indicated. Red arrows showing possible evolutive pathway. Lettering: ar, arms; ft, foot; mo, mouth; pg, pedal groove; ps, pedal shield; py, pallial cavity; sh, shell; si, siphon.

The evolution of the foot at the class level is depicted in Fig. 1, with conchiferan taxa represented by basal species. It is evident that there is a clear trend toward the enlargement of the foot from aculiferan to conchiferan branches, as well as notable specialization within conchiferan branches (indicated by red arrows).

In caudofoveates, the foot is limited to a peri-oral pedal shield, which, in some species, consists of only two small circular areas. In most species, it is a small heart-shaped ventral structure, as shown in Fig 1A. This structure is rich in adhesive glands and serves to anchor the animal to the substrate. It is not used for locomotion, as these animals move in a manner similar to worms, through peristaltic contractions.

The next stage of evolution is seen in solenogastres, which, as the name suggests, have a "sole in the belly" (curiously, the same meaning as Gastropoda). Although considerably larger than in Caudofoveata, the solenogaster's foot is essentially a narrow groove running along the ventral region, extending from the mouth region to the area close to the pallial cavity (Fig. 1B). Similar to caudofoveates, the foot of solenogastres is primarily used for anchoring the animal to the substrate rather than for locomotion.

A notably developed foot, occupying most of the ventral surface of the animal and serving both as a suction cup for attachment to the substrate and for crawling through it, is found in the next phylogenetic branch – the Polyplacophora (Fig. 1C).

This "sucker-crawling" model of the foot is so effective that it is retained in subsequent phylogenetic branches, including monoplacophores (Fig. 1D) and gastropods (Fig. 1F). In the case of gastropods, the most successful class of mollusks, this crawling foot model undergoes only a few specialized modifications, as discussed below.

The crawling foot model underwent significant modifications within the other two branches of conchiferans. Bivalves and scaphopods, collectively referred to as the superclass or subphylum Diasoma (Simone, 2009), exhibit these modifications. This is made possible by the fact that the basal bivalves, known as protobranchs, have a foot similar in function and appearance to that found in scaphopods, as shown in Fig. 1E. This foot operates like an inverted umbrella: the animal inserts it into loose substrate, unfolds it, thus anchoring itself and facilitating burial. The foot has a flattened tip surrounded by a complete or incomplete circular fold, sometimes equipped with tentacles. This configuration allows penetration into the substrate when contracted and functions as an anchor when expanded. Gadilida scaphopods and protobranch bivalves share a remarkably similar foot tip, operating in the same manner and are likely homologous. Dentaliida scaphopods have slightly modified this foot configuration, featuring a beak at the center of the foot tip (Simone, 2009), which gives the class its name – literally 'boat-foot' – due to its resemblance to a boat's bow. Bivalves, as discussed below, have continued to modify the foot further.

Another intriguing feature of the Diasoma's foot is that it points forward, unlike most other mollusks where it is oriented ventrally. This unique characteristic has been considered a distinctive Diasoma synapomorphy (Simone, 2009).

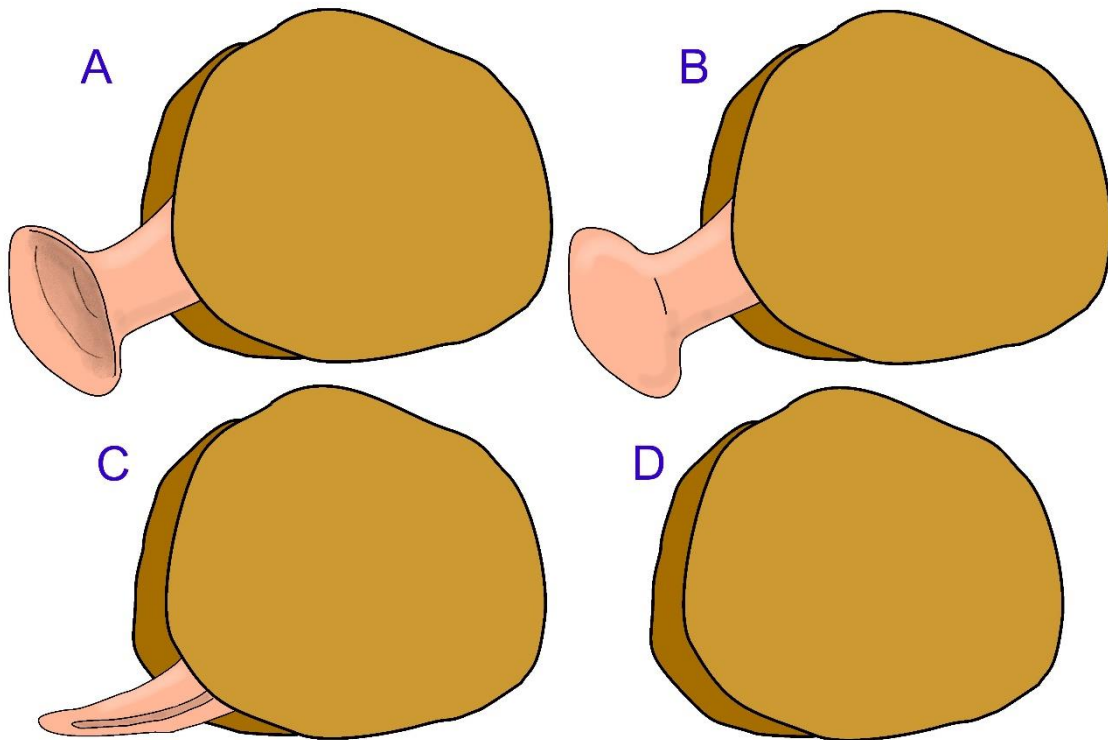
The other branch of conchiferans is Cephalopoda (Fig. 1G). This is the only class that has freed itself from a benthic lifestyle, venturing into a free-swimming existence. This pelagic adventure renders the crawling foot useless. In the most primitive cephalopods, as represented in Fig. 1G, the capacity for fluctuation and buoyancy is provided by the shell chambers (discussed in another issue of *Malacopedia*). Consequently, the foot is modified into two regions, with the posterior part forming the siphon (si). The siphon is a conical, tubular, muscular structure capable of directing the water expelled by the now muscular pallial cavity, enabling the animal to achieve jet-propelled locomotion. On the other hand, the anterior region transformed into tentacled arms, which elongate to facilitate prey capture. The fascinating subsequent evolutionary history of cephalopods significantly modified this initially simple scheme; the siphon almost became an independent structure, and the arms became elongated and complex, featuring various appendages and constitutions.

Main foot modifications in Bivalvia

The foot of the bivalves was likely responsible for the group's dominance over brachiopods, which were a more abundant group in the Paleozoic era and occupied a similar ecological niche. Over time, brachiopods gradually disappeared, seemingly outcompeted by bivalves. Without a foot, brachiopods cannot move in response to environmental disturbances. In recent times, the phylum Brachiopoda has lost much of its former glory.

As mentioned earlier, the earliest branches of bivalves are the protobranch grade (Simone et al., 2015; Simone & Amaral, 2021). All of these bivalves have a foot resembling an umbrella, as explained in the previous section as typical of the basal Diasoma (Figs. 1E, 2A). This type of foot was later succeeded by the pelecypod type, aptly named for its axe-like appearance. It resembles an axe when relaxed or when penetrating into the sediment. After penetration, through muscular

contraction, the tip of the foot takes on the shape shown in Fig. 2B, with a swelling at the tip. This swelling serves the function of anchoring the bivalve in the sediment, much like the "umbrella" in the basal diasome model. With the contraction of the longitudinal musculature, the animal can burrow inside the sediment. The foot can repeat this process as many times as the animal wants until it reaches its desired depth. The transition from an "umbrella" to a tumescent shape may provide advantages, as the majority of burrowing bivalves possess the latter type of foot.

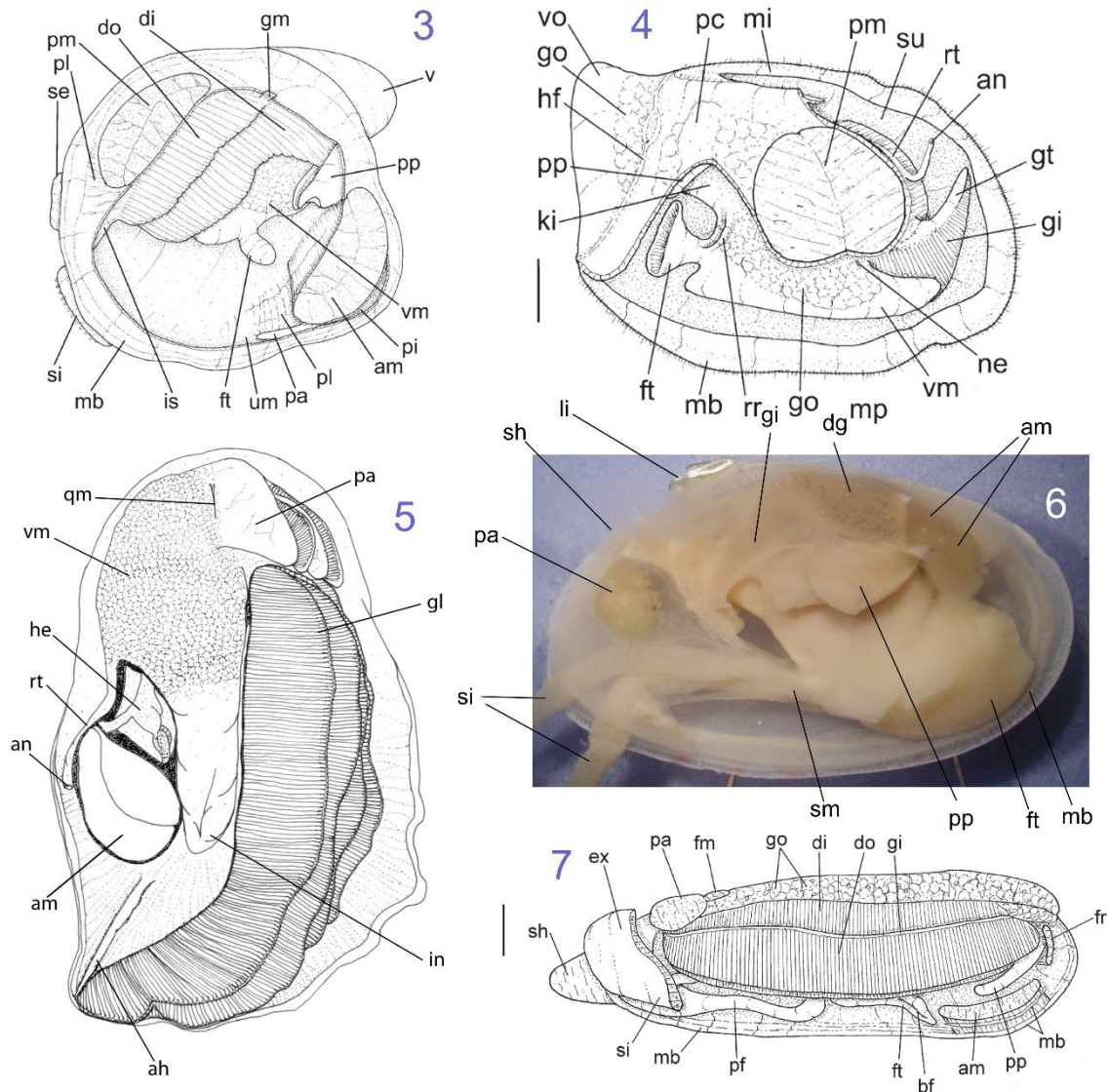


2: schematic representation main types of foot in bivalves (no scales or proportions). A, protobranch style, with umbrella-like fold at tip; B, pelecypod type in moment of anchoring, most common in autobranch burrowing species; C, byssal foot, reduced, being more concerned to byssus construction, common in pteriomorphians; D, loss of the foot, occurring in few sessile taxa.

Another significant group of bivalves evolved to attach themselves to hard substrates, accomplishing this through two main methods: 1) attaching one of the valves directly to the substrate, or 2) using a byssus. The bivalve byssus comprises bundles of resident proteins and chitin, the evolutionary intricacies and construction details of which will be the subject of another Malacopedia issue. What is relevant in this context is that the byssus is constructed by the foot through the byssal gland (Fig. 2C, the furrow running along the foot; Fig. 7: bf). The foot constructs the byssus and secures its tip to the substrate using another pedal adhesive gland, also present in that furrow. The byssus can range from a single hair-like stem (e.g., mytilids) to a broad, multifilamentary structure (e.g., arcids, anomiiids). In such cases, the foot does not need to be large; it is typically small, taking the form of an elongated, sharp-pointed appendage that the animal extends to find the optimal spot to fasten its byssal filament.

Mussels secured by their byssus are difficult to dislodge from their substrate; to remove them, the byssus must be either broken or extracted from its attachment point in the base of the foot. Some mussels kept in aquariums can easily scale the glass by using successive byssus filaments until they reach the top. Additionally, it has been observed that mussels can execute a defensive move against predatory snails by affixing a byssal stem to the dorsal region of the snail's shell.

When the mussel contracts rapidly, the gastropod suddenly finds itself in a vulnerable position with its aperture exposed. Mussels are not entirely defenseless in the face of threats.



3-7: main foot types, drawings, and photos of bivalve specimens with a valve and mantle lobe removed to show inner structures of pallial cavity. 3-4, sessile bivalves that remain with a foot in adult phase (from Simone et al, 2015); 3, *Chama macerophylla* (W ~30 mm), right view; 4, *Spondylus americanus* (W ~60 mm), left view; 5, footless sessile species *Crassostrea rhizophorae* (W ~40 mm), right view (from Amaral & Simone, 2014); 6, pelecypod-bearing species *Temnoconcha brasiliana*, Tellinidae, Brazil (MZSP, L ~25 mm); 7, small foot for byssus of *Leiosolenus aristatus* (L ~15 mm), from Simone & Gonçalves, 2006). Lettering: ah, accessory heart; am, anterior adductor muscle (posterior in Fig. 5); an, anus; bf, byssal furrow; dg, digestive diverticula; di, inner demibranch; do, outer demibranch; ex, excurrent canal; fm, posterior foot retractor muscle; fr, anterior foot retractor muscle; ft, foot; gi-gl, gill; gm, gill muscle; go, gonad; gt, gill suspensory stalk; he, heart; hf, mantle hinge fold; in, intestine; is, siphonal septum; mb, mantle border; ki, kidney; li, ligament; mi, mantle border inner fold; ne, nephropore; pa, pallial aperture or palps or posterior adductor muscle; pc, pericardium; pf, pallial fold; pi, pallial chamber; pl, pallial muscles; pm, posterior adductor muscle; pp, palps; qm, Quenstedt muscle; rr, pedal protractor muscle; rt, rectum; se, excurrent siphon; sh, shell; si, excurrent siphon or siphons; sm, siphonal muscles; su, supra-rectal chamber; um, fusion between both mantle lobes; v, umbonal cavity; vm, visceral mass; vo, umbonal cavity.

The other bivalve strategy mentioned for attaching to hard substrates, which involves attaching one of the valves to it, renders the animal permanently sessile. In some cases, this strategy results in the loss of the need for a foot within certain taxa. This is observed in particular instances, such as ostreoides, dimyids, and plicatulids, where the foot is only present in larvae and very young specimens. Once they find a suitable location for attachment, they gradually absorb the foot, causing it to disappear in the adult stage.

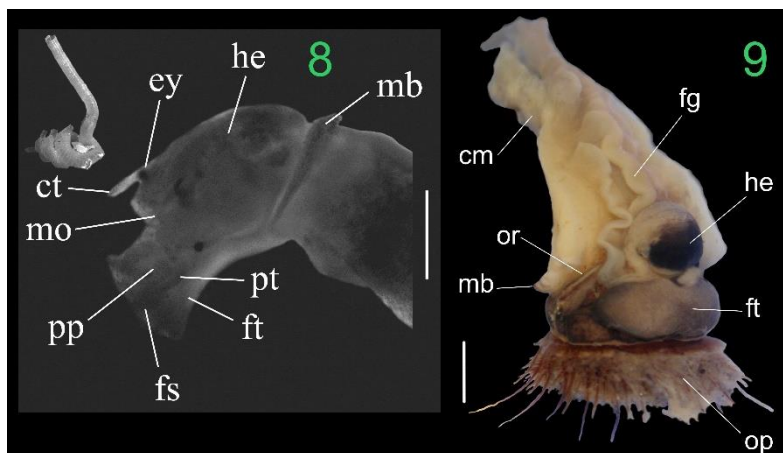
Surprisingly, however, there are several valve-attached taxa that retain a well-developed foot in the adult phase. Spiny oysters, the spondylids, for example, possess a well-developed, bell-like foot in their adult form (Simone et al., 2015) (Fig. 4: ft). The persistence, size, and form of this foot raise questions about their function. Other examples are the chamids, which have a small, tongue-like foot (Simone et al., 2015) (Fig. 3: ft). The continued presence of a foot in adult, entirely sessile bivalves undoubtedly has functional and ecological explanations. However, as far as our current knowledge extends, it remains an enigma. It is possible that the foot is used for cleaning the pallial cavity from dirt or invaders, defense against predators, or assisting in the maintenance of pallial structures, particularly the large gill. These, for now, are mere conjectures.

The aforementioned functions are the primary roles of a bivalve foot. However, some more uncommon functions have also been observed. For instance, there is the capacity for crawling. Certain bivalves, such as some galeommatids, are capable of crawling similar to gastropods (Simone, 2008). The ability to crawl has also been noted in giant clams of the Tridacnidae family (Jameson, 1976), as they search for better locations for habitation and even for spawning.

Bivalves are the only group known to have representatives that have lost the foot, as mentioned earlier. In all other classes of mollusks, including even the occasional sessile branches, the foot does not atrophy. Of course, this statement applies only to non-parasitic forms. Some eulimid gastropods that have evolved towards extreme endoparasitism do exhibit foot atrophy, along with the degeneration of other structures except for a few, such as the gonad. *Entoconcha* and some related species (Warén, 1984) serve as examples of this.

Main foot modifications in Gastropoda

Gastropods are the only class within the conchiferan group that inherited the broad crawling foot from the monoplacophore grade. Despite the extensive diversification within the class, the typical crawling and gliding model of the foot has been largely maintained in the vast majority of gastropods. Even as gastropods have transitioned into terrestrial environments through different lineages, they have preserved the usual crawling foot style.

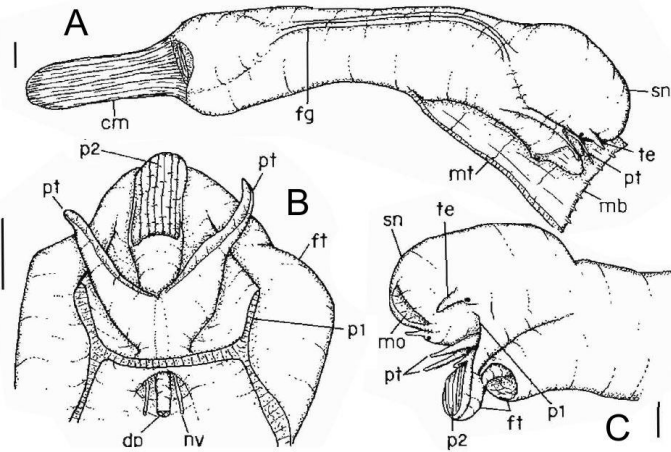


8-9: examples of sessile gastropods, but still having foot. 8, *Thylaeodus equatorialis* (Vermetidae), anterior region, left view, scale= 1 mm, shell (L ~15 mm) (From Spotorno & Simone, 2013); 9, *Stephopoma nucleogranosum* (Siliquariidae), head-foot, right view, scale= 1 mm (from Bieler & Simone, 2005). Lettering: cm, columellar muscle; ct, cephalic tentacle; ey, eye; fg, food groove; fs, foot sole; ft, foot; he, head; mb, mantle border, mo, mouth; op, operculum; or, opercular pad projection; pp, propodial pad; pt, pedal tentacles

The functioning, anatomy, and evolution of the gastropod foot within certain branches, as well as its possible anatomical subdivisions (such as propodium, epipodium, mesopodium, etc.), will be subjects of future Malacopedia issues. Just as the foot annexed structure, the operculum, has already been (Simone, 2020). In the current context, it's important to note that the gastropod foot varies significantly in

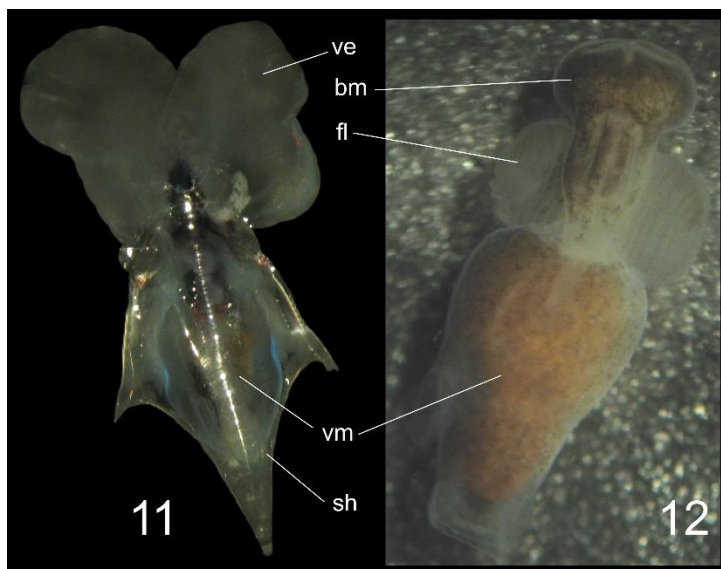
size among taxa based on their habitat. For instance, it is considerably large in species that inhabit unconsolidated substrates (e.g., volutids), as it is involved in digging. Conversely, it is relatively small in those that reside on hard substrates (e.g., muricids), where the foot plays a role in attachment and adhesion. However, in all cases, these modifications are quantitative. In a few select groups with pelagic, planktonic, and sessile habits, the foot underwent more significant adaptations.

A notable group of sessile gastropods includes the cerithioid caenogastropods Vermetidae and Siliquariidae (Figs. 8, 9) (Simone, 2001; Bieler & Simone, 2005; Spotorno & Simone, 2013). These gastropods are only free-swimming during their larval phase. After metamorphosis, they attach their shells to hard substrates and grow in an irregular manner while affixed to the rock. Siliquariids are filter feeders, yet their foot is well-developed (Fig. 9: ft), as is their operculum. In the case of *Stephopoma*, the operculum is covered in fine hair, which is produced by a lengthy projection from the opercular pad (Fig. 9: or), resembling the byssal foot of bivalves.



10: *Thylacodes decussatus* (Vermetidae) head-foot. A, entire right view; B, detail of anterior region of foot, dorsal view, head removed; C, detail of anterior region, left view (from Simone, 2001) Scales= 1 mm. Lettering: cm, columellar muscle; dp, duct of pedal gland; fg, food groove; ft, foot; mb, mantle border, mo, mouth; mt, mantle; nv, nervep1, flaps uniting head with lateral region of foot; p2, glandular pad of foot; pt, pedal tentacles; sn, snout; te, cephalic tentacle.

In contrast, vermetids form a mucous net in the surrounding water, connecting with their



11-12: Examples of planktonic species collected in São Pedro e São Paulo Archipelago, Brazil (MZSP) living, dorsal view. 11, *Cavolinia inflexa*, Euthecosomata (L ~5 mm); 12, *Clione* (?) sp, Gymnosomata (L ~10 mm). Lettering: bm, buccal mass, fl, natatory flap; sh, shell; ve, velum, vm, visceral mass.

fellow colony members. Periodically, these specimens consume this net, ingesting whatever the mucous net has collected in the meantime. The gland responsible for producing this net is the pedal gland, which in vermetids is notably large (Simone, 2001). Vermetids are the only caenogastropods with such a gland, which is usually embedded in the pedal wall, extending into the haemocoel. Their foot exhibits a complex array of folds, pads, tentacle-like projections, etc., which are utilized by the specimens to construct the mucous net. Each vermetid genus has its own unique

arrangement of foot structures. The *Thylacodes* model is presented in Fig. 10.

Only a few gastropod branches are not benthic. Some heterobranchs and caenogastropods have adopted neuston, pelagic, planktonic, and even floating lifestyles. In all of these cases, they still possess a foot, which can range from a "normal" model to a highly modified one. However, it's important to note that none of them are considered excellent swimmers.

Prominent among the planktonic heterochanch groups are the pteropods. They can be divided into two categories: one group possesses shells, known as thecosomates (Fig. 11), presently consisting of Euthecosomata and Pseudothecosomata. These are the typical prey for the shell-less variety, the Gymnosomata (Fig. 12). It is important to note that these two groups may not be closely related.

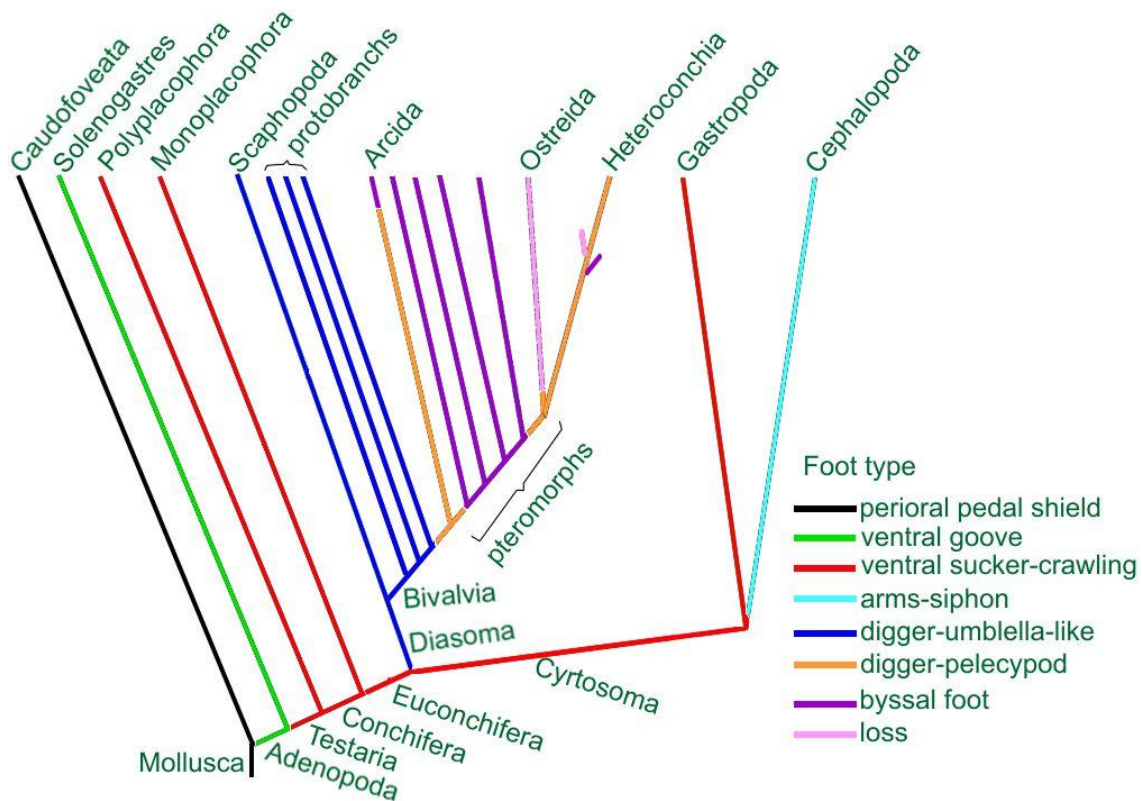
The thecosomates are a neotenic group, meaning that they look like adult veliger larvae, their foot transforms into a velum (Fig. 11: ve), also referred to as fins or wings. The velum consists of a pair of broad flaps that these animals use to swim, resembling wings. This characteristic gives them the common name "sea butterflies." In contrast, the gymnosomates are active predators and more agile swimmers. Their shell-less bodies exhibit greater flexibility, allowing them to rapidly move short distances, akin to a minute torpedo, when they detect prey. They employ an alien-like buccal apparatus to capture their food. Swimming in gymnosomates is facilitated by laterally positioned muscular natatory flaps (Fig. 12: fl), also known as swimming wings, giving them the common name "sea angels." These wings are certainly derived from the foot.

Another planktonic-floating taxon includes the glaucids, typically blue nudibranchs that have a diet of toxic jellyfish. Despite their preference for pelagic environments and their rare appearances in benthonic areas (usually after storms, near death), they still exhibit a vestigial foot sole in their ventral region.

Some highly interesting and modified caenogastropods also inhabit the water column. The floating Janthinidae possess the capability to produce bubbles using a modified mucus from their pedal gland, with their foot used to manage these bubbles. In the case of the free-swimming taxon *Atlanta*, they feature a flattened and narrow foot, often referred to as a "swimming fin," which allows them to make short displacements through quick repetitive movements. Another pelagic group consists of the Carinariidae, possibly among the most modified of non-benthonic snails. Despite still having a vestigial shell, their bodies are gelatinous. They are active predators, consuming other planktonic organisms, particularly small crustaceans. To pursue their prey, they use wing-like parapodia (also known as swimming fins), which may have evolved from the foot and are connected to other appendages like suckers, tails, etc.

Phylogenetic inferences

The phylogenetic relationships among molluscan classes and certain subdivisions are depicted in Figure 13. In this Figure, different types of feet in each branch are denoted by distinct colors. As mentioned earlier, the initial branch, Caudofoveata, is characterized by a small perioral pedal shield (depicted in black). This structure then evolves into a longitudinal pedal groove in the Solenogastres branch (shown in green). In the subsequent branch, Testaria, the foot further expands, becoming wide, occupying most of the ventral surface (illustrated in red). This characteristic



13: Morphology-based Mollusca phylogeny, mostly based on Simone (2009, 2011) and Simone & Amaral (2021), showing different types of foot as indicated by colors (see text for details). The survey is not exhaustive. Two paraphyletic taxa reported (protobranchs, pteriomorphs).

remains consistent in all known Polyplacophora, Monoplacophora, and the vast majority of Gastropoda.

For Cephalopoda, a modified foot is present, with arms anteriorly and a muscular siphon posteriorly (represented in light blue). It's worth noting that this taxon significantly alters the model, as will be emphasized in a future issue of Malacopedia.

The fundamental foot structure of Diasoma, characterized by an umbrella-like tip (shown by dark blue), is found in Scaphopoda and in protobranch Bivalvia. In the remaining bivalves, known as Autobranchia, the primary foot model is the pelecypod type (depicted in orange). However, it's important to note that the pelecypod model is relatively uncommon among the pteriomorphs, which represent the basal stage of bivalves. Notably, the Arcida is a prominent taxon that exhibits this characteristic.

A significant portion of pteriomorphs, in fact, possesses a byssal and reduced foot (colored in purple). By applying the principle of parsimony, it's suggested that the byssal foot emerged within some early branches of bivalve phylogeny, only to disappear in subsequent branches, as illustrated in Figure 13, eventually reverting to the pelecypod model. Some Arcida species also possess the byssal reduced foot (purple).

Considering the variations in the byssal foot structure within different pteriomorph branches, it is highly likely that it independently evolved multiple times from the pelecypod model.

In the pteriomorph branch Ostreida, the foot has been completely lost (indicated in pink). On the other hand, within the Heteroconchia, a branch that encompasses the majority of bivalve diversity, the predominant foot type is the pelecypod variety (depicted in orange). However, it's

worth noting that a few less common branches within this group have evolved different foot structures, including a crawling foot (e.g., galeommatids), no foot at all (small pink branch, e.g., some chamids), and a small byssal foot (small purple branch, e.g., dreissenids).

Acknowledgements

A special thank to Carlo M. Cunha for the photos 11 and 12.

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