

The high classification of the Gastropoda, with emphasis on Caenogastropoda

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Abstract

The higher classification of Gastropoda, with a special focus on Caenogastropoda, is presented as an alternative to the relatively unresolved classification currently available in MolluscaBase. This proposed classification has been developed over three decades through several successive papers, primarily based on phenotypic characteristics and classical phylogenetic approaches. Each major taxon is concisely presented and justified.

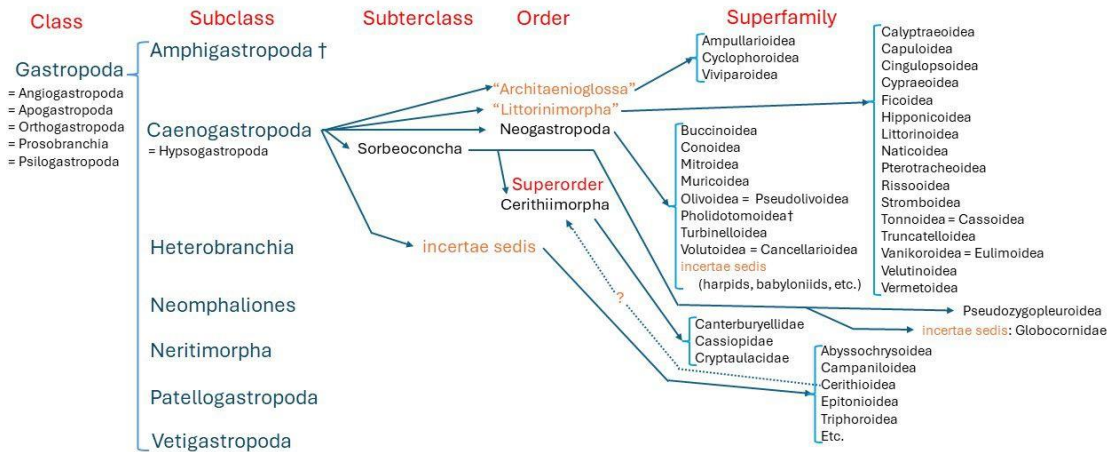
Keywords: anatomy, classification, taxonomy, phylogeny, evolution, phenotypy.

Introduction

The previous issue of Malacopedia (Simone, 2024) serves as an introduction to this one. In that issue, the reasons for the instability of mollusk higher classification, compared to that of vertebrates and arthropods, are discussed in the context of molecular inferences. One of the main reasons is that Malacology lacks the comprehensive morphological framework present in other zoological branches. This framework provides more stability in classification and phylogeny, allowing zoologists to better interpret any incongruence or disparity between morphological and molecular approaches. The detailed argumentation is presented in that paper.

Over the past three decades, nearly all phylogenetic papers published on Mollusca have been based on molecular approaches. I have provided some of the few phenotypic counterpoints, mainly on gastropods (e.g., Simone, 2011) and bivalves (e.g., Simone et al., 2015; Simone & Amaral, 2021). This paper addresses the higher classification of Gastropoda, with an emphasis on Caenogastropoda, a branch for which more detailed information is available. The main intention is to publicize this classification and demonstrate that a morphological framework exists that can be utilized, analyzed, and compared with studies from other approaches.

How is the Gastropoda and Caenogastropoda high classification in MolluscaBase?



1: Synopsis of the high classification of the Gastropoda present in MolluscaBase (2024) with emphasis on Caenogastropoda. Some paraphyletic or problematic taxa highlighted in beige; taxonomic ranks in red. More details in text.

MolluscaBase has been widely used by malacologists worldwide, as it is a very comprehensive, quickly updated, easily accessible, and reliable database. However, its classification is primarily, if not exclusively, based on molecular approaches, reflecting the prevailing methods in current studies.

Focusing on the higher classification of Caenogastropoda (Fig. 1), despite its completeness and prominence, several issues can be identified. There are multiple "incertae sedis" branches, as well as the use of some known non-monophyletic taxa (e.g., Architaenioglossa, Littorinimorpha). The subdivisions can sometimes be difficult to understand, such as the case of Sorbeoconcha, which is considered at the "subterclass" rank but is placed among taxa at the order rank. Additionally, it has a "superorder" (Cerithiimorpha) that is directly divided into families. Despite its name, the superorder Cerithiimorpha does not contain Cerithioidea, which is placed in another branch – incertae sedis (dotted line).

However, the given classification has few hierarchies, resulting in highly branched divisions and a lack of internal organization. For instance, Caenogastropoda is directly divided into five branches, Neogastropoda into nine, and Littorinimorpha into sixteen branches (Fig. 1).

Recent literature, however, presents more resolved classifications with fewer uncertainties and polytomies, where all proposed branches are justified and phylogenetically based. It is difficult to understand why these more accurate and coherent classifications are not preferred over the current one, which possesses numerous uncertainties, incongruencies, and low resolution.

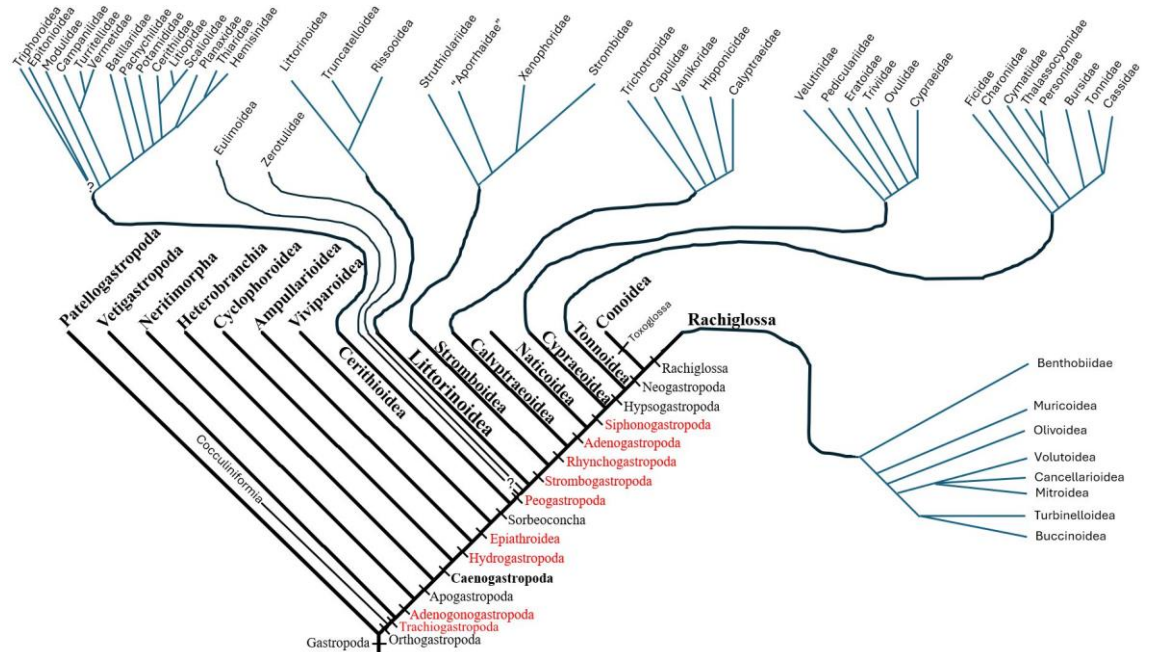
Some of these better-resolved classifications will be explained in upcoming issues of Malacopedia. This issue focuses on the higher classification of Gastropoda, focusing Caenogastropoda. Future issues will address other gastropod branches and classes.

Below, the classification is represented as a branched tree – a cladogram (Fig. 2). Each branch (node) and terminal has its own taxonomic name. However, the name does not necessarily correspond to a Linnaean category. As shown, there are many more divisions between the class (Gastropoda) and the families (most of the terminals) than available Linnaean categories (orders and superfamilies), even if more prefixes were invented to accommodate all of them. Therefore,

there is no concern about this; the taxa are named and belong to subdivisions between class and family, but they are not necessarily orders or equivalent categories.

The arrangement of Fig. 2 is concisely described below. Each taxon, branch, or terminal is briefly explained, with at least one synapomorphy (novel character) highlighted and often illustrated. The internal arrangement of each superfamily is generally not discussed, but references for further details are provided.

The intention is to offer a more stable classification that has been consistently supported by numerous studies and papers over more than three decades.



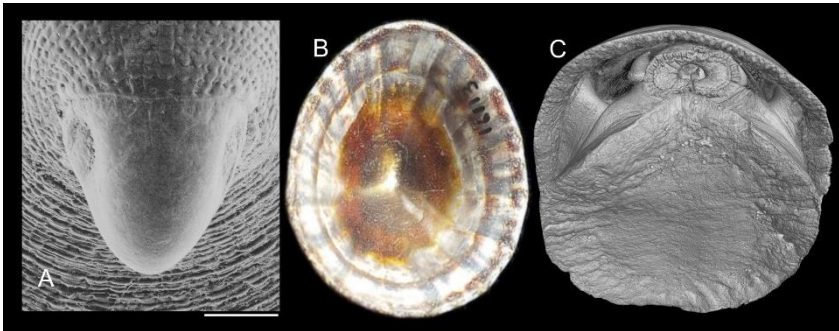
2: Synopsis of the high classification of the Gastropoda mostly based on Simone (2011) with emphasis on Caenogastropoda. More complex superfamilies are extended and an additional cladogram of its internal organization of families of superfamilies is shown (blue lines). These are also based on other complementary papers reported along the text. Taxa in red are those introduced by Simone (2011). Question marks and polytomies indicate still under analyses groups.

The classification of Gastropoda, with emphasis on Caenogastropoda (Fig. 2)

Gastropoda:

As a class, they are the only mollusks with torsion, meaning the pallial cavity is positioned anteriorly. Consequently, all pallial structures, such as gills, osphradia, rectum, and anus, are oriented towards the front. Torsion will be a dedicated subject in a future Malacopedia issue, along with the various ways some gastropod branches have resolved the issue of auto-pollution. It is important not to confuse torsion with shell coiling, as these are distinct and independent phenomena. In addition to torsion, there are other gastropod synapomorphies, such as the operculum (at least in the larval phase), the pair of cephalic tentacles, the snout (Figs. 3C, 10A, 14: sn), and over 30 other features (Simone 2011: 213, 153).

Patellogastropoda



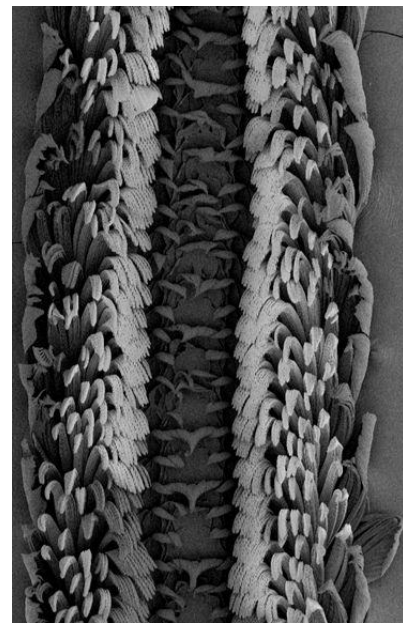
3: Characters of some Patellogastropoda. A, *Propilidium curumim*, detail of shell apex, SEM, dorsal view (from Leal & Simone, 1998), scale= 50 μ m; B, *Nacella magellanica* (MZSP 316113, Chile) shell, ventral-inner view (L 25 mm); C, *Lottia subrugosa*, head-foot and mantle, tomography, anterior-slightly ventral view (L 15 mm) courtesy Daniel Cavallari.

This is the most basal branch of Gastropoda. Patellogastropods exhibit several primitive characteristics, such as a symmetrical protoconch (Fig. 3A), indicating they never developed a coiled shell; their limpet condition is thus primary

(Simone, 2018a). Other primitive traits include the radula, which is docoglossan and mineralized, resembling conditions seen in other mollusks but modified in other gastropod branches. Key synapomorphies of patellogastropods include a distinct type of nacre in the shell (Fig. 3B) and the partial or complete loss of primary gills: the acmaeid-lottiid subgroup has lost at least one gill (Fig. 3C), while the patellid-nacellid subgroup has entirely lost primary gills.

Orthogastropoda

This branch encompasses the remaining gastropods and is primarily characterized by significant modifications in the radula (Fig. 4). The typical orthogastropod radula is rhipidoglossan, consisting of a central rachidian tooth, usually five pairs of lateral teeth, and numerous (10–100) pairs of narrow marginal teeth per row (Fig. 4). Unlike the mineralized docoglossan radula of patellogastropods and other mollusks, the orthogastropod radula is flexiglossan, with teeth rows aligned more linearly, enhancing flexibility. Another notable modification is observed in the positioning of the odontophore horizontal muscle (m6), which is external to the cartilages rather than between them (Simone, 2011). Additionally, there is the appearance of a posterior pair of odontophore cartilages, resulting in the odontophore possessing four cartilages in total. Thirteen synapomorphies support the classification of Orthogastropoda (Simone, 2011: 312, 309).



4: Typical rhipidoglossan radula. *Calliostoma* sp (W 1.5 mm)

Cocculiniformia

This group remains understudied, with some organisms initially thought to be cocculiniforms later identified as belonging to other groups, such as vetigastropods. However, most members appear to form a cohesive group (Haszprunar, 1987; Simone, 1996; Leal & Simone, 2000). They are orthogastropods, possessing the rhipidoglossan radula and other modifications mentioned earlier. Their shells resemble primary limpets, characterized by a symmetrical protoconch, and all members exhibit limpet-like morphology. Cohesion within the group arises from shared distinctive characteristics, including an apparent hyper-torsion where the gill is located entirely on the right side, and the modification of the right tentacle as a copulatory organ.

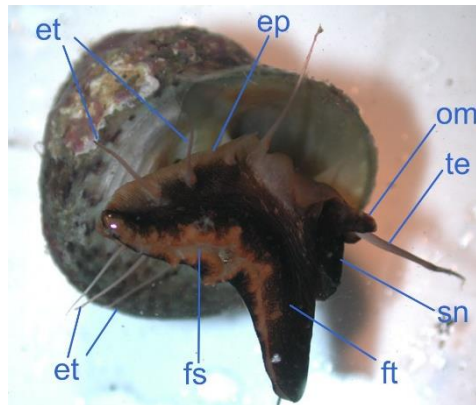
Trachiogastropoda

This name was introduced by Simone (2022b) to designate a node in the cladogram presented by Simone (2011) that had previously remained unnamed. The prefix "trachio-" is derived from the Latin word "trachia," meaning "throat." It alludes to the fact that in trachiogastropods, the esophagus serves a more complex role beyond being a simple connection between the oral cavity and the stomach, as observed in other mollusks and the first two branches of gastropods (Patellogastropoda and Cocculiniformia). Trachiogastropods possess chambers, diverticula, glands, papillae, a gizzard, and other structures. These adaptations indicate that the esophagus plays a significant role in processing food before it reaches the stomach, delivering partially processed material. This topic is explored in greater detail elsewhere (Simone, 2022b).

In addition to the complexity of the esophagus, another significant attribute of trachiogastropods is their shell coiling, or spiralization, which is a prominent synapomorphy. All other gastropods either have coiled shells or are descended from coiled forms, as evidenced by their ontogeny and/or phylogeny. The phylogenetic and anatomical implications of shell coiling were extensively discussed in another issue of Malacopedia (Simone, 2022a). Trachiogastropoda is supported by a set of 13 synapomorphies identified by Simone (2011).

Vetigastropoda:

This is a widespread group characterized mainly by heavy, nacreous shells. While the internal arrangement is not fully understood, some basal branches still retain paired pallial organs. Similar to higher gastropod branches, several inner groups of vetigastropods have convergently lost their right pallial structures. One of the primary synapomorphies is the presence of the epipodium (Fig. 5: ep), typically bearing several epipodial tentacles (et). These tentacles vary from a few to a considerable number, as seen in haliotids. In addition to the epipodium and its tentacles, vetigastropods share a unique microscopic receptacle within them (Haszprunar, 1987; Simone, 2011). A total of 12 synapomorphies support the classification of Vetigastropoda (Simone, 2011: 213, 309).



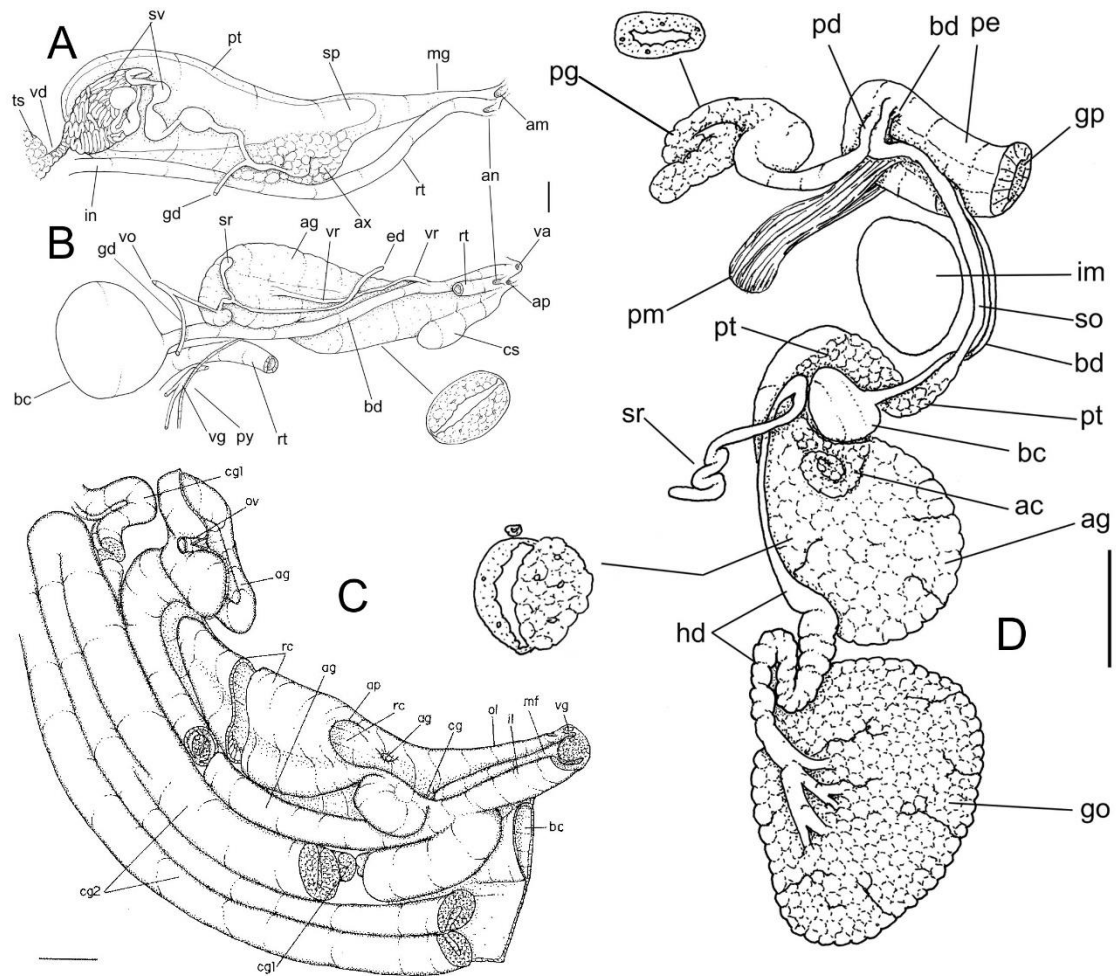
5: Living *Tegula virigula* (W 20 mm), ventral view, animal with head-foot extended showing epipodium and its tentacles. Lettering: ep, epipodium; et, epipodial tentacles; ft, foot; fs, foot sole; om, ommatophore; te, cephalic tentacle

Adenogonogastropoda

Adenogonogastropods, as the name suggests, are characterized by having gonoducts with glands, which is a notable synapomorphy. This distinguishes them from preceding branches, which consist predominantly of species with external fertilization, where gametes are released into the water for fertilization. Only the most basal patellogastropods, cocculiniforms, and vetigastropods exhibit external fertilization. In the latter two groups, several inner subgroups have independently evolved internal fertilization, including copulation and internal incubation of eggs, although these are convergent traits.

What defines adenogonogastropods is their internal fertilization and the preparation for spawning, which often includes laying eggs in protective capsules. This does not necessarily imply the presence of a penis for copulation. While many groups do possess a penis, several lack it entirely and instead transfer a spermatophore to the female through other means. Others have developed

alternative structures for mating, such as modifying the right cephalic tentacle. This topic was explored in detail in another issue of *Malacopedia* (Simone, 2020a).



6: Examples of gonoducts in the 3 main branches of Adenogonogastropoda: A-B, male and female pallial gonoducts of *Vitta zebra* from Brazil, Neritimorpha, scale= 1 mm (from Barroso et al, 2012); C, female pallial gonoducts of *Strombus pugilis* from Brazil, Caenogastropoda, scale= 2 mm (from Simone, 2005); D, genital system of *Siphonaria pectinata*, from Portugal, scale= 2 mm (from Simone & Seabra, 2017). Lettering: ac, albumen chamber; ag, albumen gland; am, male pore; an, anus; ap, female aperture; ax, annexed gland; bc, bursa copulatrix; bd, bursa copulatrix duct; cg, capsule gland; cs, reinforcement sac; ed, enigmatic duct; gd, gonopericardial duct; go, gonad; gp, genital pore; hd, hermaphrodite duct; il, inner lamina of pallial gonoduct; im, isolated portion of shell muscle; in, intestine; mf, middle fold of pallial oviduct; mg, male pallial gonoduct; ol, outer lamina of pallial gonoduct; ov, visceral oviduct; pd, penis gland duct; pe, penis; pg, penis gland; pt, prostate; py, pallial cavity; rc, seminal receptacle; rt, rectum; so, spermooviduct; sp, spermatophore; sr, seminal receptacle; sv, seminal vesicle; ts, testis; va, vaginal opening; vd, vas deferens; vg, visceral ganglion or vessel parallel to right margin of pallial cavity; vo, visceral oviduct; vr, vaginal duct connecting capsule gland with duct of bursa copulatrix.

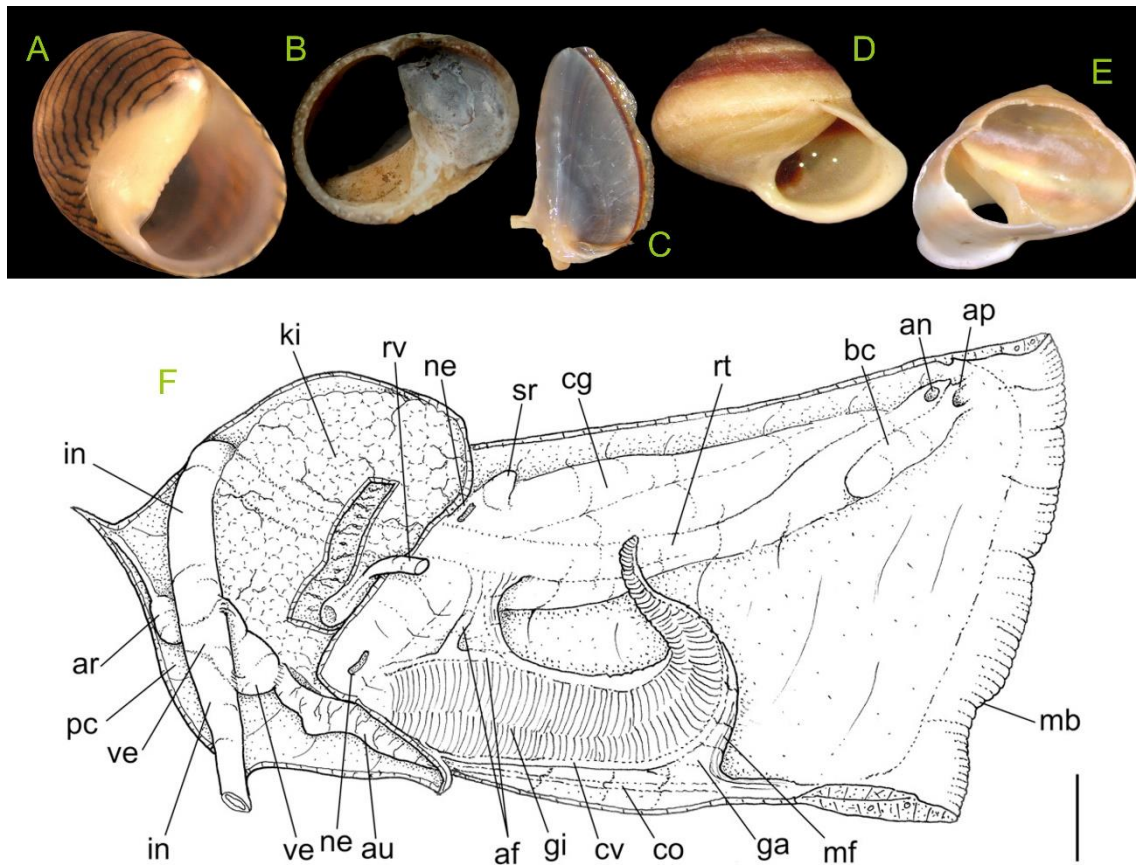
All adenogonogastropods exhibit anatomical adaptations for the production and processing of gametes and ova (Fig. 6). From the posteriorly located gonad to the genital pore, the genital system becomes distinct and specialized. This contrasts with preceding branches, where genital structures are associated with the kidney(s). There are theories suggesting that the genital system in taxa grouped under Adenogonogastropoda is a modification of the right kidney. However, neither ontogenetic nor phylogenetic evidence supports this hypothesis. Instead, it appears that there is a modification of the integument and pallial mucosa, leading to the development of specialized glands and tubes in certain regions (Simone, 2011).

As evident, the three primary branches of Adenogonogastropoda—neritimorphs (Figs. 6A, B), apogastropod caenogastropods (Fig. 6C), and heterobranchs (Fig. 6D)—exhibit complex genital

structures comprising tubes, glands, chambers, and other features that facilitate advanced gamete elaboration and egg laying.

Beyond gonoducts, Adenogonogastropoda boasts several other intriguing synapomorphies. Notably, they possess cephalic eyes with lenses, a feature convergent with higher vetigastropods and other mollusks (Simone, 2023). Another significant attribute is the loss of right pallial structures, such as the right gill, osphradium, and hypobranchial gland. While preceding branches show convergent losses with both kidneys present, adenogonogastropods definitively lack the right kidney. Ten additional synapomorphies substantiate the classification of this branch (Simone, 2011: 213, 309).

Neritimorpha



7: Examples Neritimorpha: A-C, *Vitta zebra* from Brazil (from Barroso et al, 2012); A, shell (W 18 mm); B, same with dorsal region broken and removed, showing absence of columella (W 17 mm); C, operculum, outer view (L 9 mm); D-E, *Helicina variabilis* from Brazil (from Simone, 2018b), shell (W 13 mm) frontal view and with dorsal region broken and removed; F, *Vitta zebra* pallial cavity and anterior end of visceral mass, ventral view, scale= 2 mm (from Barroso et al, 2012). Lettering: af afferent gill vessel; an, anus; ap, female aperture; ar, right auricle; au, left auricle; bc, bursa copulatrix; cg, capsule gland; co, collar vessel; cv, ctenidial vein; ga, gill suspensory membrane; gi, gill; in, intestine; ki, kidney; mb, mantle border; mf, muscle fibers; ne, nephrostome; pc, pericardium; rt, rectum; rv, efferent renal vessel; sr, seminal receptacle; ve, ventricle.

It is also a widespread group, but with an internal arrangement that remains obscure. The taxon is at least divided into an aquatic group, with neritids as the main representatives, and another terrestrial group, with heliciniids and proserpinids being more widely known. The aquatic forms appear more basal, retaining gills and an osphradium (Fig. 7F), along with two pairs of auricles (Fig. 7f: ar, au) (Barroso et al., 2012), thus classified as diotocardian. In contrast, terrestrial forms have lost both the gill and osphradium, and also lack the right auricle (Simone, 2018b). This condition, with a single auricle, is known as monotocardian.

The cohesion of neritimorphs is supported by a set of synapomorphies, among which the main ones include the globose shell (Figs. 7A, D), the absorption of inner shell whorls that widens the shell spire into a large, hollow chamber (Figs. 7B, E), divergent columellar muscles, and the presence of a calcareous operculum (Fig. 7C). These features are crucial despite variations or modifications within internal neritimorph branches. For instance, some genera like *Septaria* exhibit a limpet-like shell form, while certain *Helicina* species have a corneous operculum. The typical radula of neritimorphs is rhipidoglossan. A total of 12 synapomorphies support this branch according to Simone (2011: 213, 309).

Apogastropoda

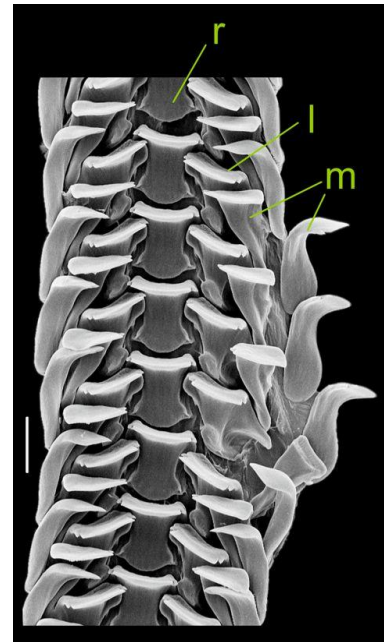
This taxon encompasses heterobranchs and caenogastropods and is also known as "Monotocardia," referring to the basal synapomorphy of losing the right auricle (Simone, 2011). Although this loss shows some convergences, such as seen in terrestrial neritimorphs mentioned earlier, it is a distinct basal characteristic unique to apogastropods. The type of shell coiling also differs from the preceding two branches (vetigastropods and neritimorphs), compressing the right side of the animal's structures, a topic explored elsewhere (Simone, 2022a). Apogastropods also exhibit other definitive losses, including one of the columellar muscles, the classic hypobranchial gland (replaced by hypertrophy of the local pallial mucosa), the posterior pair of odontophore cartilages and their pair of approximator muscles (m8), the gastric caecum, and the intestinal loops within the haemocoel. The gill in apogastropods is definitively monopectinate (while in preceding branches it is bipectinate), and the salivary ducts become more distinct and elongated.

Another notable synapomorphy of Apogastropoda is the simplification of the radula to a taenioglossan type (Fig. 8). This type of radula typically consists of only seven teeth per row: a central rachidian (r) tooth, a pair of lateral (l) teeth, and two pairs of marginal (m) teeth. It appears that all heterobranchs and caenogastropods possess this type of radula in their basal branches or have evolved from it. In total, 20 synapomorphies support the classification of this taxon according to Simone (2011: 213, 309).

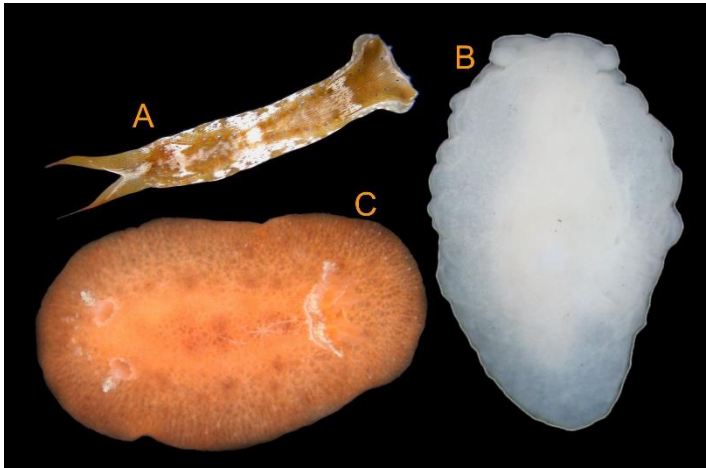
Heterobranchia

This highly diverse branch unites the former Pulmonata, Opisthobranchia, and various taxa that were previously classified among the prosobranchs, collectively known as Allogastropoda (Haszprunar, 1985). Its internal organization remains obscure, and current phylogenetic approaches, primarily molecular, have not yielded congruent results. A forthcoming Malacopedia issue will soon provide a morphological counterpart to complement these findings. This is why this extensive branch is only represented as a single terminal in the current fascicle.

Heterobranchia, as its name suggests, exhibits the loss of the primary gill as one of its main basal synapomorphies. This structure has largely been replaced by other types of secondary gills



8: Radula of *Laevilacunaria antarctica*, Antarctica, SEM, scale= 50 μ m, a typical taenioglossan radula (from Simone, 2017). Lettering: l, lateral; m, marginal.; r, rachidian (central).



8: Examples of living heterobranchs, taxa that is hard to determine the head's side in a first glance. A, *Navanax aenigmaticus* (Cephalaspidea, Aglajidae); B, *Phyllaplysia engeli* (Aplysiida, Aplysiidae); C, *Doris bovena* (Nudibranchia, Dorididae) (all ~15 mm. from Brazil. Courtesy A. Migotto, Ceibimar-USP)

is sinistral while the teleoconch is dextral. Another significant characteristic is simultaneous hermaphroditism; nearly all heterobranchs are simultaneous hermaphrodites, a rarity among other gastropods. Most other gastropod branches are typically gonochoristic, with hermaphroditism occurring mainly as protandric (e.g., calyptraeoidians), where the animal begins as male and transitions to female during its reproductive life cycle.

Another synapomorphy related to genital structures is their relatively "free" arrangement within visceral and haemocoelic cavities—they are not attached to the integument or mantle, except through minute jugal muscles and the genital pore(s). In contrast, other adenogonogastropods have genital structures attached to the mantle and/or integument. Heterobranchs also lack a distinct, protruded head with paired cephalic tentacles and eyes (Fig. 8). Instead, the anterior anatomy can be difficult to discern in some cases (Fig. 8). A total of 20 synapomorphies support this branch according to Simone (2011: 213, 309).

Caenogastropoda:

Also known as Pectinibranchia, encompasses most former Mesogastropoda and all Neogastropoda. It represents the largest taxon within Mollusca, comprising approximately half of all species in the phylum, and inhabits a wide range of suitable molluscan habitats. A total of 60 synapomorphies support this taxon (Simone, 2011: 213, 309). Notable among these are: Eyes positioned at the base of the tentacles, typically on ommatophores. Pedal gland immersed within the foot musculature, with a corresponding furrow along the entire anterior foot sole (Fig. 10A: pg). Septum that separates the haemocoelic chamber from the visceral mass, known as the diaphragmatic septum (Fig. 9: di), which was extensively discussed in a previous Malacopedia issue (Simone, 2021b). Elongated, ridge-like osphradium. Kidney with a hollow space, consisting of a pair of lobes, one of which surrounds the intestinal portion. Nephrostome isolated within a membrane that separates the renal chamber from the pallial cavity. Wide pair of longitudinal folds in the dorsal wall of the buccal cavity. Peribuccal musculature (mj) consolidated into two bundles. Reduction in the number of dorsal tensor muscles of the radula (m4) to two pairs. Reduction in size of the ventral pair of tensor muscles of the radula (m11). Elongated and thin accessory pair of

or respiratory organs (e.g., lung). However, some exceptions like amathinids and certain sacoglossans (e.g., *Ascobulla*) appear to retain a gill that may not be secondary in nature. Nevertheless, further analysis is required as this character could potentially represent a reversion to a primary gill structure.

Other synapomorphies of Heterobranchia (Haszprunar, 1985; Simone, 2011) include heterostrophy, where the protoconch exhibits a coiling direction 180° reversed compared to the teleoconch—meaning the protoconch

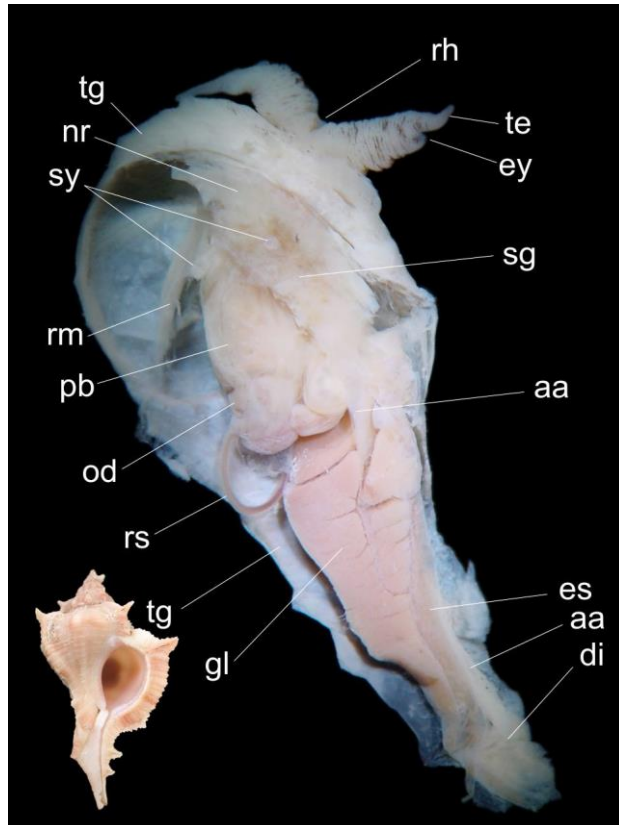
tensor muscles of the radula (m5), originating from the main dorsal tensor (m4) rather than from cartilages. Reduction in the length of the horizontal muscle (m6) relative to the length of the odontophore cartilages, with a broader and thicker form. Pair of muscles running inside the radular sac (m7). Pair of protractor muscles of the odontophore (m10) inserted in its anterior region. Subradular cartilage broad within the buccal cavity, covering its entire ventral wall. Single pair of lateral teeth on the radula, similar in shape to the rachidian. Loss of the longitudinal bundle on the inner surface of the esophagus and appearance of longitudinal pairs of folds. Reduction in the number of intestinal loops, primarily within the visceral mass. Formation of fecal pellets. Nerve ring positioned posteriorly at the middle level of the buccal mass. Well-defined buccal ganglia located close to the buccal mass.

Upon examining the odontophore of caenogastropods, incorporating the aforementioned modifications, it becomes evident that the radula does not glide on cartilages as observed in other gastropods. Instead, the intrinsic musculature of the odontophore is structured to securely grasp and manipulate the radula. The entire odontophore, through rhythmic movements, performs the scraping function. The significant diaphragmatic septum (Fig. 9), discussed by Simone (2021), holds profound implications for the evolution of the proboscis, gigantism, and other notable features within caenogastropods.

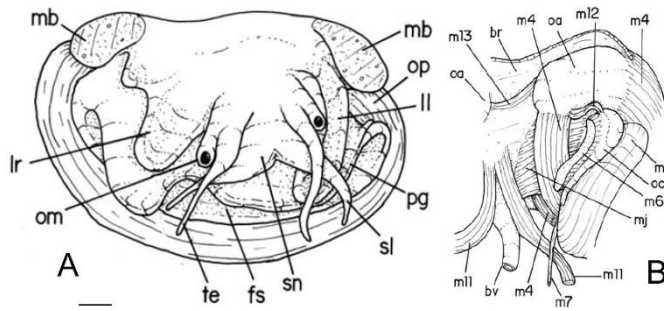
Cyclophoroidea

This represents the initial branch of caenogastropods, encompassing land snails characterized by their adaptation of the pallial cavity into a lung, highly vascularized and devoid of gills and osphradium (Simone, 2004a, 2011). In addition to these features, other synapomorphies include a discoid shell with a wide umbilicus, a calcareous and rounded operculum, separate salivary glands, and the esophagus inserting at the middle level of the stomach. The exophalic penis typically exhibits an open furrow, and the pallial oviduct houses the bursa copulatrix in its posterior region. While some cyclophoroideans lack a penis (e.g., certain diplommatinids), the unclear internal organization of the superfamily complicates determining whether this represents a basal trait or a case of reversion.

Hydrogastropoda:



9. *Siratus senegalensis* (Muricidae) (MZSP 33102), Shell (L 45 mm) and haemocoel (L ~30 mm), ventral view, foot and columellar muscle removed, inner structures as in situ. Lettering: aa, anterior aorta; di, diaphragmatic septum; es, esophagus; ey, eye; gl, gland of Leiblein; nr, nerve ring; od, odontophore; pb, proboscis; rh, rhynchostome; rm, proboscis retractor muscle; rs, radular sac; sg, salivary glands; sy, statocysts; te, tentacle; tg, integument



10. *Pomacearosseana* (Ampullariidae, Brazil) (From Simone, 2004a), with examples of synapomorphies of Hydrogastropoda. **A**, head-foot, frontal view, showing siphons, scale= 2 mm; **B**, odontophore, dissected up to its internal layer, right side, right cartilage deflected, showing m12, scale= 1 mm. Lettering: br, subradular cartilage; bv, blood vessel; ey, eye; fs, foot sole; ll, left siphon; lr, right siphon; m4-m12, odontophore muscles; mb, mantle border; mj, jaw and peribuccal muscles; oa, odontophore secondary cartilage; oc, odontophore cartilage; om, ommatophore; op, operculum; pg, pedal gland furrow; sn, snout; te, tentacle.

This branch derives its name from the predominantly aquatic (hydro-) environments inhabited by its members, including both freshwater and primarily marine habitats. Among the synapomorphies supporting this taxon, the most significant include the presence of left and right (incurrent and excurrent) siphons of head (nuchal) origin (Fig. 10A: ll, lr), the main dorsal pair of radular tensor muscles (m4) connected to tissue on the radular ribbon (to) and to its pair, and a pair of accessory muscles of the horizontal

muscle (m12) (Fig. 10B) with an obscure function. This taxon is supported by a set of 12 synapomorphies Simone (2011: 213, 310).

Ampullarioidea:

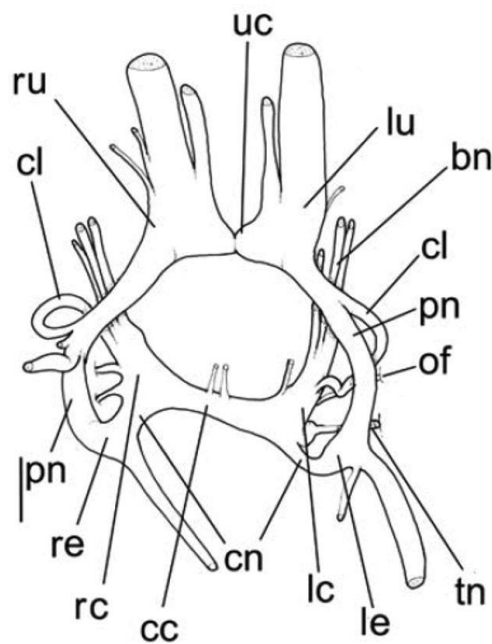
This superfamily of freshwater snails is characterized by 40 known synapomorphies (Simone, 2004a, 2011). Among these, the most interesting features include a globose shell, an operculum with an upper projection and subcentral nucleus, a pectinate osphradium located on a folded stalk, a sac-like lung positioned between the gill and osphradium with a pneumostome at the base of the incurrent siphon, and a heart with an ampulla at the anterior aorta.

Ampullarioideans are typically large in size and possess both gill and lung structures, enabling them to breathe amphibiously, in both water and air.

Epiathroidea

The taxon is characterized by a unique nerve ring configuration known as epiathroid. In this condition, the pleural ganglia are positioned dorsally, closer to the cerebral ganglia, contrasting with the hypoathroid condition found in other groups where the pleural ganglia are ventral and closer to the pedal ganglia (Fig. 11) (Haszprunar, 1988). This anatomical feature serves as a defining trait for the Epiathroidea within gastropod taxonomy (Simone, 2004a, 2011).

Other interesting synapomorphies of the Epiathroidea include a tall, slightly turriform shell shape. The osphradium is ridge-like, approximately equal in length to the gill. There are paired retractor muscles of the buccal mass (m2). The main dorsal tensor



11. Brain of *Viviparuscontectus* (Viviparidae, Hungary) (from Simone, 2004a), the first branch with epiathroid nerve ring, scale= 0.5 mm. Lettering: bn, nerves to buccal mass; cc, cerebral commissure; cl, cerebro-pedal connective; cn, cerebro-pleural connective; lc, left cerebral ganglion; le, left pleural ganglion; lu, left pedal ganglion; of, ophthalmic nerve; pn, pleuro-pedal connective; rc, right cerebral ganglion; re, right pleural ganglion; ru, right pedal ganglion; tn, tentacular nerve; uc, pedal commissure.

muscles of the radula (m4) are further simplified into single bundles, each connected to the radular ribbon via ligaments and directly to their counterparts. Salivary glands open in the anterior region of the buccal mass. The middle esophagus features a conspicuous pair of folds. There is a loss of esophageal lateral pouches and their respective vessels. The prostate is located in the pallial spermoduct. The nerve ring is positioned entirely posterior to the buccal mass, and the buccal ganglia are widely separated. In total, 19 synapomorphies support this branch according to Simone (2011: 213, 310).

Viviparoidea

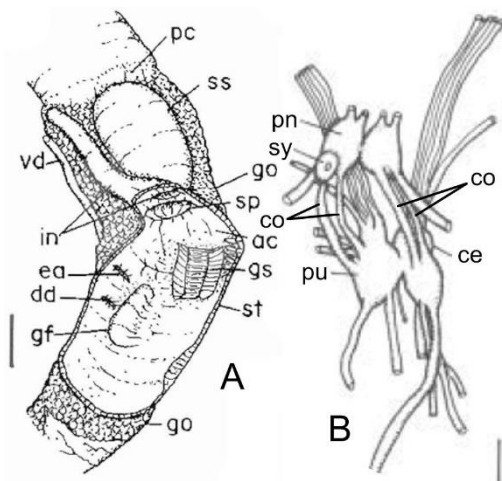
This is another branch of freshwater snails. They are sometimes grouped with ampullarioids in certain classifications, but were found to be separate in morphological analysis (Simone, 2004a, 2011). Among their synapomorphies, the most notable features are a multispiral shell with a tall spire and deep suture, long gill filaments for filter-feeding, and an endostyle on the right side of the gill. Additionally, they have a salivary gland divided into two separate masses and a right tentacle modified as a copulatory organ with a closed (tubular) vas deferens.

Sorbeoconcha:

The sorbeoconchs, a name introduced by Ponder & Lindberg (1997), represent a predominantly marine taxon, though some freshwater and even terrestrial branches exist. Their synapomorphies include several notable features: the loss of head-foot inhalant siphons, a reduced and shallow dorsal chamber of the buccal mass, and the insertion of the esophagus at the middle level of the stomach. Males possess a convoluted seminal vesicle and have reverted to an open pallial vas deferens. The bursa copulatrix is located at the posterior level of the pallial oviduct. There is an approximation between the cerebro-pedal and pleuro-pedal connectives, which run closely parallel to each other (Fig. 12B: co). Perhaps the most remarkable feature is the appearance of a stomach style sac containing a rotating crystalline style (Fig. 12A: ss). This complex structure is absent in preceding gastropod branches and is strikingly convergent with that of lamellibranch bivalves. A set of 17 synapomorphies supports this node in Simone (2011: 213, 310).

Cerithioidea

This large, predominantly marine superfamily includes two freshwater branches (Thiariidae and Pleuroceridae). From a morphological perspective, it also encompasses Vermetidae and Campanilidae (Simone, 2001, 2011), which are classified in a separate superfamily in some classifications (MolluscaBase, 2024). Additionally, it likely includes Triphoroidea and Epitonioidea, taxa with still obscure taxonomy and relationships. Despite having a proboscis and a different radula,



12. Two of the main Sorbeoconcha synapomorphies: A, Style sac in stomach (ss), e.g., *Modulus modulus* (Cerithioidea, Brazil), dorsal view, scale= 1 mm (from Simone, 2001); B, closure of connectives (co), e.g., *Strombus pugilis* (Stromboidea, Brazil), ventral view, scale= 1 mm (from Simone, 2005). Lettering: ac, anterior gastric chamber; co, cerebro-pedal and pleuro-pedal connectives; dd, duct to digestive gland; ce, cerebral ganglion; ea, esophageal aperture; gf, gastric fold; go, gonad; gs, gastric shield; in, intestine; pc, pericardium; pn, pedal ganglion; pu, pleural ganglion; sp, style sac aperture; ss, style sac; st, stomach; sy, statocyst; vd, vas deferens.

these two superfamilies appear to be specialized members of Cerithioidea, though this is still under investigation.

Among the cerithioidean synapomorphies, which are also shared with vermetids, campanilids, triphorids, and epitoniids, the most notable features include a normally turritiform shell with determinate growth and an anterior siphonal canal. There is a reversion to a spiral-sculptured operculum and a mantle border with a series of papillae. Additionally, there is a reversion to a thick hypobranchial gland with sub-chambers and a reduction to an open condition of the pallial oviduct. A head-foot furrow is present, running along the right side from the female genital pore to the right side of the foot (Simone, 2001). The internal organization of cerithioidean families is depicted in Fig. 2 at the tip of the Cerithioidea branch, showing Vermetidae and Campanilidae as closely related to Turritellidae. The positions of what are currently considered Triphoroidea and Epitonioidae are still provisional, marked by a question mark.

Peogastropoda:

This taxon derives its name from the Greek word "peos," meaning penis, which is the primary synapomorphy of peogastropods. All members possess an exophalic penis, typically located behind and to the right of the right cephalic tentacle (Fig. 13). So far, no reversion (loss) of this feature has been detected, even in sessile forms such as *Hipponix* and *Magilus*. This does not imply that taxa preceding peogastropods lack internal fertilization; rather, they utilize other means (e.g., a spermatophore) or have developed different copulatory structures, such as a copulatory tentacle (e.g., cocculiniforms, viviparoideans) or a retractile penis (e.g., heterobranchs). Additionally, some non-peogastropods have independently acquired an exophalic penis through convergent evolution. Examples include certain branches of cyclophoroideans, neritimorphs, and even the vetigastropod *Neomphalus*. For more details, see Simone (2020a).

Other synapomorphies of peogastropods include the presence of a nephridial gland, the loss of the pair of auxiliary muscles (m12) in the odontophore, and the development of albumen and capsule glands in the pallial oviduct. Additionally, each statocyst contains a single statolith, with the loss of the statoconia.

The basal organization of peogastropods remains uncertain. Morphological phylogeny indicates that two penis-bearing taxa, Eulimidae and Zeratulidae, are at its base (Fig. 2). However, eulimids are parasitic organisms with several reduced or absent structures. For example, the adult form of *Entoconcha* is little more than a sac with a gonad, with no other discernible structures, which precludes any morphological comparative analysis. Despite being relatively diverse, few eulimid taxa are anatomically known (Warén, 1984; Simone & Martins, 1995; Simone, 2015). Zeratulids are a scanty group, mostly Antarctic, with very few species that are anatomically and incompletely known (Simone, 2017). Molecular studies on eulimids have produced incongruent results with each other and with morphological findings. For example, eulimids have been found to be a sister group to Vanikoridae (Takano & Kano, 2014), a family morphologically related to



13. Example of exophalic penis, a synapomorphy of Peogastropoda: *Siratus consuela* from Brazil, Shell (right) (L ~40 mm) and extracted head-foot, dorsal view. Arrow indicated penis.

Calyptraeoida (see below). This nebulous scenario does not currently permit a more precise allocation of eulimids and zerotulids beyond confirming that they are peogastropods. In Simone (2011: 214, 311), 19 synapomorphies support the node between cerithioideans and eulimids, 14 synapomorphies support the node between eulimids and zerotulids, and additional 9 synapomorphies support the node between zerotulids and littorinoideans.

Littorinoidea

This megadiverse superfamily, from a morphological perspective, includes Rissoida and Truncatelloidea, as they share important synapomorphies. However, in Simone's (2006a, 2011) papers, this taxon was named Rissoida. Littorinoidea is the correct senior name, established by Children in 1834, while Rissoida is a junior synonym (Gray, 1847). Species in this branch are usually minute in size. Large species, such as *Tectarius pagodus*, which reaches about 50 mm, are exceptions. Most littorinoideans sensu lato are typically 2-3 mm long, with some smaller than 1 mm (e.g., *Amphithalamus*, *Phreatodrobia*). They are predominantly aquatic, inhabiting both marine and freshwater environments, but some terrestrial forms also exist (e.g., annulariids, pomatiids).

As depicted in Fig. 2, the taxa currently classified as Littorinoidea are more basal, with Truncatelloidea and Rissoida considered more derived and closely related. It is likely that one or more of these three taxa could be paraphyletic. If the superfamily status is to be maintained for them, a rank indicating their closer relationship compared to other peogastropods should be created. However, the most appropriate approach may be to consider all of them within the same superfamily.

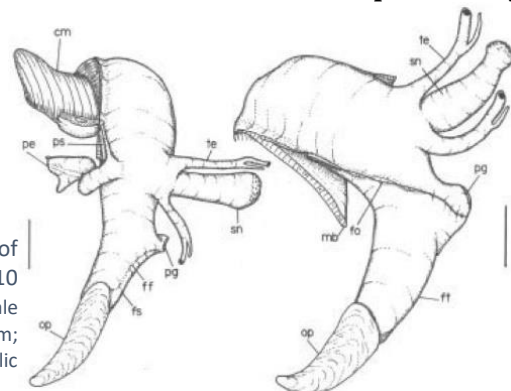
Among the synapomorphies supporting Littorinoidea sensu lato, the most noteworthy include a typically globose shell, a reversion to a paucispiral sculptured operculum, and a short pallial cavity. The osphradium is shortened to less than half the length of the gill. There is a complete loss of ventral tensor muscles (m11) and a very long radular sac with rachidian basal cusps. The stomach features a broad central pad, and in males there is a wide pallial prostate equivalent to the oviduct of females. The pallial vas deferens and penis duct are closed (tubular), with the penis insertion located relatively far posteriorly from the right tentacle.

Strombogastropoda

This caenogastropod branch is primarily distinguished by the elongation of the snout (Fig. 14: sn). The snout becomes long and capable of independent movement compared to the rest of the head-foot, with some shortening ability provided by longitudinal retractor muscles. It is classified as a snout, not a proboscis, because it cannot retract into the haemocoel and remains permanently exteriorized. Further details are elaborated elsewhere (Simone, 2019).

In addition to the elongation of the snout, other notable synapomorphies of Strombogastropoda (Simone, 2011) include an operculum that is

14. Head-foot of *Strombus pugilis* (Strombidae): example of elongated snout (sn), male (left) and female (right), Scales= 10 mm (from Simone, 2005). Lettering: cm, columellar muscle; fa, female furrow; ff, foot furrow; fs, foot sole; mb, mantle border; op, operculum; pe, penis; pg, pedal gland; ps, pallial vas deferens; sn, snout; te, cephalic tentacle.



ovoid or elliptical with an eccentric nucleus, smaller than the shell aperture. There is an enlargement of the mantle edge, which covers the head during activity, and the auricle is attached to the inner surface of the anterior wall of the pericardium. The odontophore muscle pair m7 inserts as a single bundle, and the radula features sharp, pointed apices on the marginal teeth. In total, 13 synapomorphies support this node in Simone (2011: 214, 311).

Stromboidea

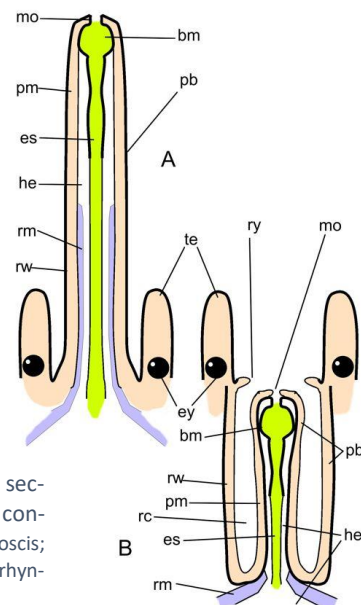
This group, while not highly diverse, includes charismatic taxa such as strombids and xenophorids. Xenophorids were previously classified in their own superfamily, Xenophoroidea, until recent morphological studies clearly indicated their close relationship with strombids, leading to their inclusion within Stromboidea (Simone, 2005, 2011). However, definitive confirmation came with molecular studies (e.g., Irwin et al., 2021). The phylogenetic arrangement of the families included is depicted at the tip of the Stromboidea branch in Fig. 2, where Aporrhaidae are paraphyletic, and xenophorids are shown to be closer to strombids than other studied stromboideans.

Among the more notable synapomorphies of Stromboidea are a fusiform shell with determinate growth and an incurrent shell canal. There is an enlargement of the distance between the base of the head and the furrow of the pedal gland, along with a muscular diaphragmatic septum. The operculum features a terminal nucleus, and there is a pallial tentacle located in front of the anus. Other characteristics include a thickened hypobranchial gland, the loss of a pair of longitudinal folds in the middle esophagus, and a bursa copulatrix of females situated anteriorly in the pallial oviduct, originating from the genital pore. Females also possess a furrow running along the right side of the head-foot, originating from the genital pore.

Interestingly, stromboideans possess an enormous style sac and respective crystalline style. Particularly in strombids, it originates in the stomach, located in the last whorl of the visceral mass, and extends anteriorly, passing through the kidney, continuing along the roof of the pallial cavity, and ending close to the mantle edge. This development of the style sac is evident in the phylogenetic arrangement, with struthiolariids and aporrhaidae, the more basal branches, where it only touches the kidney; in xenophorids, it crosses the kidney; and it reaches its described peak in strombids (Simone, 2005).

Rhynchogastropoda

The suffix of this taxon means "snout," referring to the development of a true proboscis. Basal gastropods have a short snout that elongates and develops some shortening capacity in strombogastropods, one branch before. In rhynchogastropods (Fig. 15), the snout becomes a true proboscis capable of retraction. Therefore, all taxa included in this branch, to varying degrees of elongation, possess a proboscis. This is an important synapomorphy, and further details are explained elsewhere (Simone, 2019, 2021a).



15. Schematic representation of a usual pleurembolic proboscis in dorsal view, sectioned longitudinally (from Simone, 2021a): A. extended condition; B, retracted condition. Lettering: bm, buccal mass; es, esophagus; he, haemocoel; mo, mouth; pb, proboscis; pm, proboscis buccal mass; rc, rhynchodeal cavity; rm, proboscis retractor muscle; rw, rhynchodeal wall; ry, rhynchostome; te, cephalic tentacle.

Another distinctive synapomorphy is the bipectinate type of osphradium, where filaments are connected directly beside the osphradial ganglion, giving it an elliptical outline and a length shorter than half that of the gill. Additional features include a long oral tube, with both buccal ganglia situated closely together. A set of 19 synapomorphies supports this branch in Simone's phylogeny (2011: 214, 312).

As further explained by Simone (2019, 2021a), the rhynchogastropod type features a pleurembolic proboscis, characterized by a part that remains uninverted (Fig. 15B: pm). This proboscis type is exclusive to this taxon. While other gastropods, including other caenogastropods like triphoroideans, have also developed proboscises, they exhibit acrembolic types, where the proboscis inverts entirely.

Calyptraeoidea

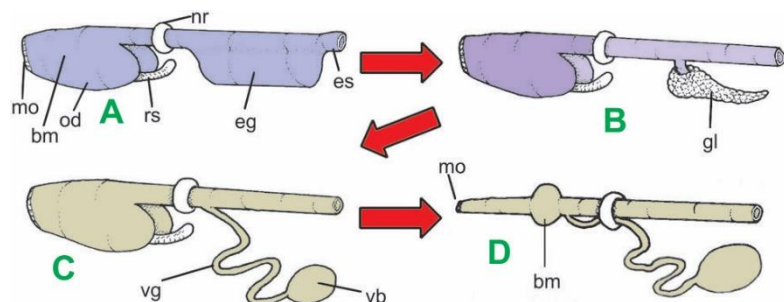
From a morphological perspective, this superfamily also encompasses taxa that some classifications segregate into monotypic superfamilies, such as Capuloidea, Vanikoroidea, and Hipponicoidea. The families included in these groups share interesting and significant synapomorphies, as depicted in the phylogenetic arrangement at the tip of the calyptraeoidean branch in Fig. 2. These characteristics are further detailed elsewhere (Simone, 2002, 2006b, 2011). Another intriguing feature of calyptraeoideans is the variation in shell morphology; only trichotropids and vanikorids typically have coiled shells, whereas the shells of other taxa are limpet-shaped or limpet-like.

Other notable synapomorphies include the presence of a hairy periostracum, well-developed nuchal flaps on both sides of the head, relatively long salivary ducts free from the nerve ring, the loss of a pair of longitudinal folds in the middle esophagus, and protandrous hermaphroditism. Simone (2011: 214, 312) identified a total of 21 synapomorphies for this superfamily.

Adenogastropoda

The prefix of this branch is derived from the Greek word "adenos," meaning gland, alluding to the esophageal gland, one of its main synapomorphies. This feature is detailed extensively in Simone (2022B) (Fig. 16). The primary synapomorphy of Adenogastropoda is the presence of a well-developed ventral mid-esophageal gland, characterized by glandular tissue reinforced by transverse septa (Fig. 16A). This type of gland is present in its first three branches (naticoideans, cypraeoideans, and tonnoideans), but it undergoes modification into the gland of Leiblein (Fig. 16B) in Rachiglossa (discussed below), or into a venom gland in certain rachiglossans and conoideans (Figs. 16C, D) (Simone, 2022B).

Other additional synapomorphies of this taxon include a shell with a spire normally shorter than half the length of the aperture, an enlargement of the



16. Schematic representation of an uncoiled esophagus of Adenogastropoda (modified from Simone, 2022b). A, form with wide ventral esophageal gland, basing Adenogastropoda; B, Form with gland of Leiblein, of Rachiglossa; C, form with venom gland inserted posteriorly to nerve ring, found in basal Conoidea and some Marginellidae; D, same, with venom gland passing through nerve ring, and loss of odontophore, state found in most Conoidea, some Marginellidae and Volutidae. Lettering: bm, buccal mass; eg, esophageal gland; es, esophagus; gl, gland of Leiblein; mo, mouth; nr, nerve ring; od, odontophore; rs, radular sac; vb, venom muscular bulb; vg, venom gland.

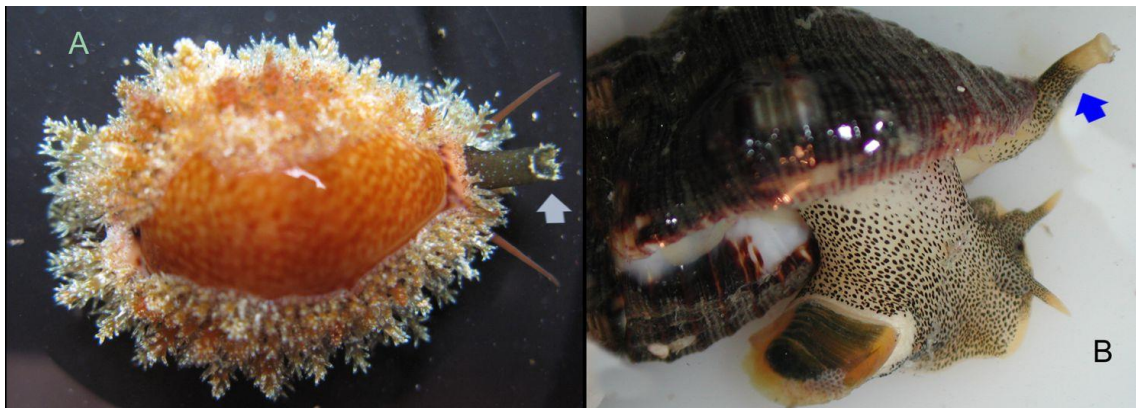
mucosa-like hypobranchial gland, a pair of retractor muscles of the buccal mass inserting close to the radular sac, and an accessory pair of ventral protractor muscles of the buccal mass (m14). There is a reversion to a posteriorly inserted esophagus in the stomach, the loss of a crystalline style sac, and a narrow stomach resembling a simple curve of digestive tubes. Females have a bursa copulatrix positioned in the anterior region of the pallial oviduct. In total, 17 synapomorphies support this branch according to Simone (2011: 215, 313).

Naticoidea

Also known as "moon-snails," this superfamily includes a single extant family, Naticidae. Naticids are active predators, typically preying on other mollusks, using their main synapomorphy, the Accessory Boring Organ (ABO), to perforate the shells of their prey. The ABO is located at the ventral tip of the proboscis, and its acid secretion aids in shell perforation.

A more detailed monographic study on naticoideans is currently in preparation. Currently, data on the taxon can be found in Simone (2011), further updated by Simone (2014). In addition to the ABO, naticoideans share synapomorphies such as a globose shell without a canal, and the reversion of the operculum to a paucispiral form with a subterminal nucleus. Simone (2011: 313) identifies a total of 46 synapomorphies for this group.

Siphonogastropoda



17. Examples of species with pallial siphon (arrows). Living crawling specimens (from Simone 2020b). **13**, cypraeid *Naria acicularis* from Fernando de Noronha (L ~ 25 mm); **16**, pisaniid *Gemophos auritulus* from Ilhabela, Brazil (L ~ 30 mm).

As the suffix suggests, siphonogastropods are characterized by the presence of a pallial incurrent siphon (Fig. 17: arrows). This feature is distinct from the siphonal canal present in the shell, which may or may not be associated with the pallial siphon. Further details on this distinction are provided elsewhere (Simone, 2020b). However, all members of this taxon possess both a siphonal canal in the shell and a pallial incurrent siphon.

Beyond the siphon, other synapomorphies of Siphonogastropoda include a shell with determinate growth and an anterior siphonal canal. The pair of proboscis retractor muscles insert approximately at the middle level of the proboscis. The stomach is approximately cylindrical, with widths nearly equal to adjacent regions of the esophagus and intestine, and it has a U-shaped structure. Simone (2011: 313) identifies a total of 16 synapomorphies supporting this taxon.

Cypraeoidea

From a phenotypic perspective, this taxon includes Velutinoidea/Lamellarioidea, slug-like taxa with internal shells that are classified into different superfamilies in some classifications. However, they share several interesting attributes, detailed elsewhere (Simone, 2004b, 2011). The internal arrangement of the six families is depicted in Fig. 2 at the tip of the cypraeoidean branch. Their main synapomorphies include an involute shell, total loss of the adult operculum, mantle lobes covering most of the outer surface of the shell, part of the pericardium lying dorsal to the gill, and an auricle connecting subterminally to the ctenidial vein. Additionally, there is duplication of the horizontal muscle (m6) of the odontophore. Simone (2011: 313) identifies a total of 36 synapomorphies supporting this taxon. The well-known trifold bipectinate osphradium is found supporting an internal branch uniting ovulids and cypraeids, rather than at the base of the entire superfamily.

Hypsogastropoda:

Hypsogastropods are typically active predators that utilize their siphon and large osphradium to locate prey, and their proboscis along with a complex foregut glandular apparatus to attack and consume it. This taxon includes the tonnoideans and neogastropods (Fig. 2) (Simone, 2011), both of which have elongated their siphons and proboscis to accommodate their hunting habits. The siphon now functions as a structure that enables the animal to detect prey odors, aided by the increased size of the osphradium. The elongated proboscis is primarily used for attacking prey and occasionally for subduing it.

Beyond these modifications for hunting and predatory behavior, additional synapomorphies of Hypsogastropoda include a fusiform shell, an operculum with a terminal nucleus, and salivary glands consisting of two separate masses. Simone (2011: 314) identifies a total of 18 synapomorphies supporting this taxon.

Tonnoidea:

This superfamily includes Ficoidea from a morphological perspective. While a monograph on its phylogeny is still in preparation, the internal arrangement of families can be observed at the tip of the branch in Fig. 2. Simone (2011: 314) identifies no fewer than 41 synapomorphies supporting this branch. Among these, the most notable are the elongated distance between the head base and the furrow of the pedal gland, a muscular diaphragmatic septum, the insertion of odontophore muscle m4 in the tissue preceding its exposed portion in the buccal cavity, and significant enlargement of the salivary glands, divided into proboscis gland.

Neogastropoda

Also known as Stenoglossa, Neogastropoda is one of the oldest recognized monophyletic taxa. From a phenotypic viewpoint, neogastropods are divided into two basal branches: Toxoglossa and Rachiglossa (Simone, 2011, 2021c). Key synapomorphies include a tall spire in the shell, the loss of an accessory pair of protractor muscles of the odontophore (m14), lateral radular teeth that differ in shape from the rachidian, and salivary glands that are free from the nerve ring, with their duct passing outside it. The gland of the middle esophagus, which in earlier branches was a broad ventral diverticulum filled with septa, has evolved into a solid-acinar structure connected to the esophagus via a duct. This gland is known as the gland of Leiblein in rachiglossans (Fig. 16B) and as a venom gland in toxoglossans (Fig. 16C, D). A vestige of the septate primitive esophageal gland, known as the "gland framboise," is found at least in some muricids, basal neogastropods, and is located anteriorly as a continuation of the duct of the gland of Leiblein (Simone, 2011). Simone (2011: 315) identifies a total of 28 synapomorphies supporting this branch.

Toxoglossa

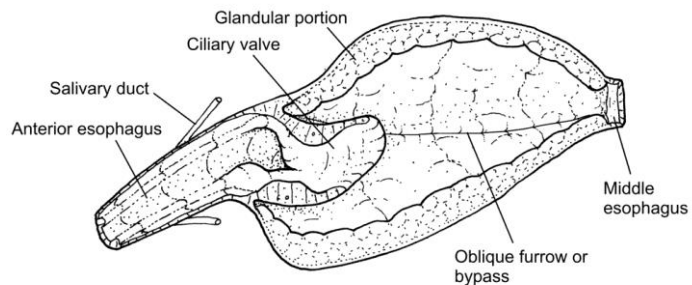
This taxon comprises a single Recent superfamily: Conoidea. It is supported by no fewer than 59 synapomorphies (Simone, 2011: 315, 2021c). Among these, the most significant include a thick-walled shell, reduction of the odontophore and mid-esophagus, and the elongated esophageal gland, which forms the venom gland. This gland features a muscular bulb at its distal end and is inserted into the esophagus near the nerve ring. The rhynchodeal wall is weakly muscular and does not protrude externally during proboscis protrusion (2021a).

Conoideans are renowned for their venomous nature. They possess a modified radula, ranging from sharp-pointed to harpoon-like, adapted for injecting venom into prey via the proboscis. Conoideans typically prey on polychaetes, fishes, and other mollusks. Their prey quickly succumbs, becoming paralyzed or sedated, and is then directed into a permanent rhynchodeal cavity—a modification of the pleurembolic proboscis (Simone, 2021a)—where it is chemically consumed. In more basal taxa, consumption may involve the assistance of the radula.

Presently, conoideans are classified into 18 families (MolluscaBase, 2024), primarily based on molecular approaches, although internal organization remains incongruent across databases. A preliminary morphological arrangement places chochlespirids at the base, characterized by retaining a typical pleurembolic proboscis, with the venom gland connected to the esophagus at the level of the nerve ring (Simone, 1999, 2011). Conidae and Terebridae are recognized as monophyletic. However, a more comprehensive morphological study of conoideans is currently underway.

Rachiglossa

The second branch of Neogastropoda, is more extensively detailed elsewhere (Simone, 2021c). It encompasses all non-conoidean neogastropods, traditionally grouped as Muricoidea + Cancellarioidea by Ponder (1973) and Simone (2011). According to the latest classification (MolluscaBase, 2024), it comprises 7 superfamilies, incorporating Muricoidea, while Cancellarioidea has been synonymized with Volutoidea.



18. Valve of Leiblein. *Trophon geversianus* (Muricidae, Argentina), isolated and opened longitudinally (L~ 2 mm).

A set of 26 synapomorphies supports the Rachiglossa branch according to Simone (2011: 316), with one of the most intriguing being the presence of the valve of Leiblein (Fig. 18), exclusive to rachiglossans (Simone, 2011, 2021c). This structure separates the anterior esophagus from the mid-esophagus, forming a bulbed portion. Internally, it features a valve composed of long cilia and highly glandular walls. Typically, it includes an oblique furrow or bypass connected to the duct of the gland of Leiblein, facilitating the secretion flow. The precise functions of both the valve and the gland of Leiblein vary among taxa and are not fully understood. Some rachiglossans, such as *Buccinanops*, have reduced versions, while others like *Cancellaria* and *Colubraria* have completely lost it, considered as secondary reversions.

Another intriguing synapomorphy of rachiglossans is the further simplification of the radula. The taenioglossan type, found in branches preceding the neogastropods, typically has 7 teeth per row, including 2 pairs of marginals. In rachiglossans, this pattern is reduced to 3 teeth per row:

a rachidian tooth and 2 lateral teeth, known as stenoglossan or rachiglossan radula. This naming convention derives from this characteristic. Many rachiglossans have further modified this radular pattern. The most common modification is reduction to a single tooth per row, typically retaining only the rachidian tooth (e.g., volutids, marginellids, cancellariids), while some taxa have completely lost their radula (e.g., coralliophilines).

Conclusion

As explained before, the above synthesis of classification has been proven to be more stable. It is clear that maintaining and refining the classification based on morphological approaches has been a longstanding challenge, yet it remains a robust framework even as new taxa are studied. This stability over three decades indicates its reliability, though ongoing refinement and inclusion of under-sampled taxa are necessary. Is there, anyway a difficulty in publishing comparative studies based on morphology and the challenges in gaining recognition for such work even after publication, as noted in Simone (2024).

The evolutionary history of mollusks, especially gastropods, has been a singular pursuit for biologists who strive to interpret it using available tools. The ideal approach is holistic, although it is impractical to comprehensively survey every aspect of all species, necessitating a focus on specific databases. However, dismissing morphology or phenotype as exhausted or useless could lead to a narrow scientific perspective, potentially forcing researchers to accept classifications that are less congruent and less refined.

If a more stable and well-resolved scenario (Fig. 2) is offered parsimoniously, why would another, less stable scenario (Fig. 1) be preferred? It's important to emphasize and taking into consideration that all the information reported above is duly published in international scientific, peer-reviewed journals, with all data, methods, vouchers, etc., properly documented.

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