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Evolution of gills in gastropods

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Abstract

This study focuses on the evolutionary modifications of the gill structure in Gastropoda, particularly the transition from the basal condition of a paired bipectinate gill to a single gill, including the emergence of the monopectinate condition. The loss of gills is also discussed. These modifications are analyzed in the context of phylogenetic relationships and certain anatomical features.

Keywords: evolution, phylogeny, taxonomy, morphological modifications.

Introduction

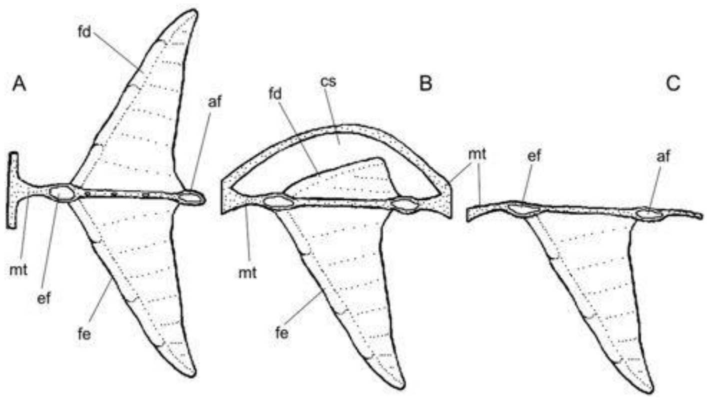
The basic bauplan of the phylum Mollusca includes a pair of bipectinate gills located within the pallial cavity. These structures, also known as branchiae or ctenidia, serve as the primary respiratory organs in aquatic species.

As previously discussed (Simone, 2021), the primary molluscan gills are housed within the pallial cavity. This protective arrangement allows the gills to develop thin, fragile walls that facilitate efficient gas exchange, although they also render the gills vulnerable to predation and other environmental hazards. In gastropods, in particularly, as megadiverse group, various modifications of the gills have occurred. The two main modifications, which are examined in this study, are: (1) the transition from a bipectinate to a monopectinate condition, and (2) the reduction or complete loss of gills—most commonly the right gill—resulting in species with a single gill or none at all.

This paper does not focus on the detailed structure of the gill itself, which will be addressed in future issues of *Malacopedia*. Instead, the main objective is to explore the gill as a whole, with emphasis on the evolutionary and anatomical aspects discussed above. Finally, the occurrence of each gill type is presented within a phylogenetic framework.

Bipectinate and monopectinate gills

A gill is termed bipectinate when it bears leaflets on both sides of its central axis, along which the afferent and efferent vessels run. The afferent vessel carries blood into the gill, while the efferent vessel—commonly referred to as the ctenidial vein—carries blood out. Between these vessels lie the leaflets, also known as filaments, through which blood flows. Because the filaments have thin walls, oxygen from the surrounding water diffuses into the blood, while carbon dioxide diffuses out into the environment. This mechanism represents the typical respiratory process in most aquatic metazoans.



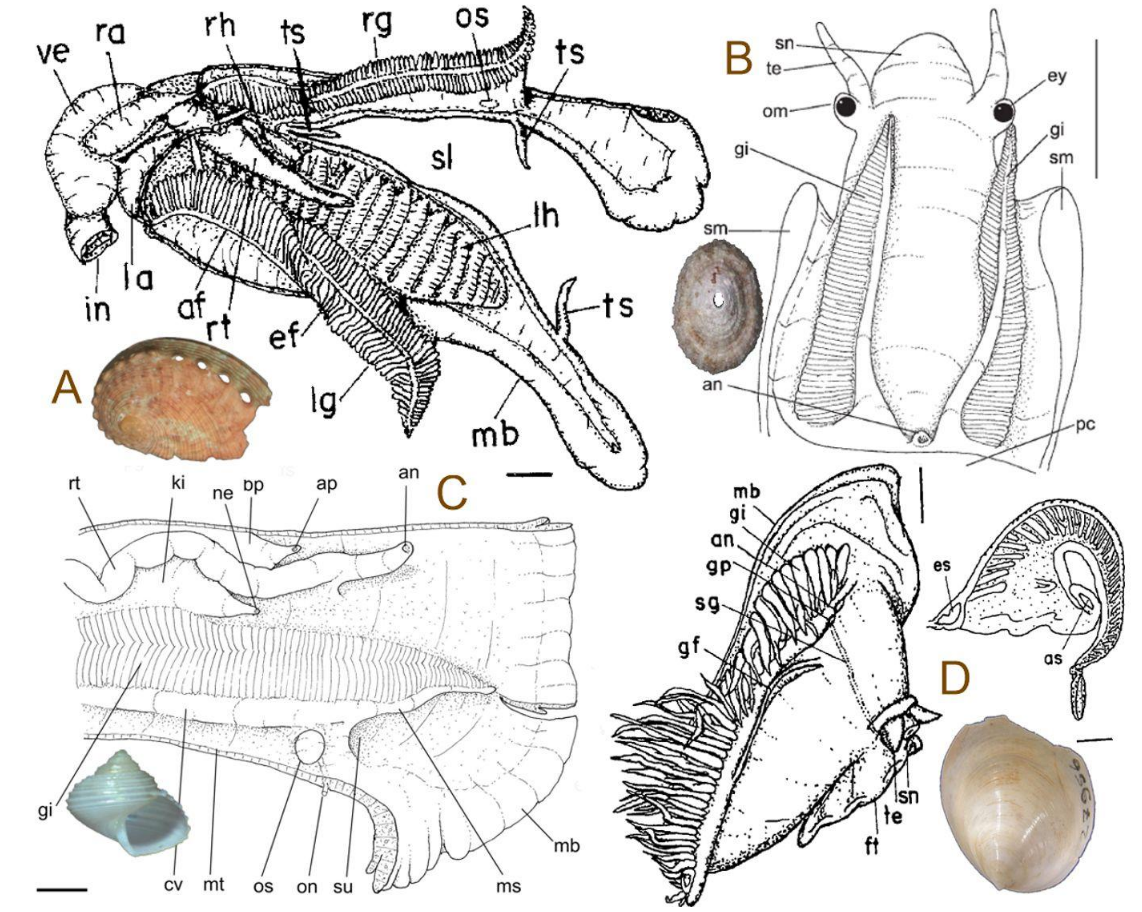
1. Transverse section of a gill of 3 gastropod lineages. **A**, a pleurotomariid (Vetigastropoda), with typical bipectinate gill; **B**, a trochoidean (Vetigastropoda, with bipectinate gill with dorsal leaflet reduced; **C**, a generic caenogastropod with monopectinate gill (from Simone, 2011). Lettering: af, afferent gill vessel; cs, suprabranchial chamber; ef, efferent gill vessel or ctenidial vein; fd, right or dorsal gill filament; fe, left or ventral gill filament; mt, mantle or connection to mantle.

As is typical in mollusks, the basal gill pattern in gastropods is the bipectinate model (Fig. 1A). In the most basal taxa, the filaments on both sides of the gill axis are similar in size. This gill configuration is clearly observed in gill-bearing patellogastropods (Fig. 4), as well as in slit-bearing vetigastropods such as pleurotomariids, haliotids (Fig. 2A), and fissurellids (Fig. 2B). In more derived bipectinate-bearing gastropods, the dorsal filaments are still present but are significantly smaller than the ventral ones (Fig. 1B). In these taxa, the posterior region of the gill is also enclosed within a specialized suprabranchial chamber (Fig. 1: cs). Most vetigastropods exhibit this type of gill structure, including trochoideans (Fig. 2C) and seguenzioideans, as well as aquatic neritimorphs (Fig. 3B).

The next evolutionary step involves the complete loss of the dorsal filaments, resulting in the monopectinate gill configuration (Fig. 1C). In this condition, the original gill axis becomes fused with the adjacent mantle tissue, and both the afferent gill vessel and the ctenidial vein are incorporated into the pallial vascular system (Fig. 1C: af, ef). The former suprabranchial chamber is also lost, possibly through fusion with the mantle itself.

The monopectinate gill condition is a well-established synapomorphy of Apogastropoda, a clade that includes Heterobranchia and Caenogastropoda (Simone, 2011). Among aquatic caenogastropods, the presence of a monopectinate gill is consistent and well documented (Figs. 1C, 3A), reinforcing its status as a defining character (Simone, 2011). In heterobranchs, however, the situation is less clear, and the origin of their gills remains uncertain. Although several basal heterobranch lineages possess relatively typical monopectinate gills—such as certain Sacoglossa (e.g., *Ascobulla*, *Cylindrobulla*; pers. obs.), some Pyramidelloidea (e.g., Amathinidae; Simone & Bieler, 2025; Fig. 3C), and some Acteonimorpha (e.g., Rissoellidae; Simone, 1995)—the presence of gills in these groups, and in heterobranchs generally, has often been considered secondary, i.e., the result of gill loss followed by reacquisition (Ponder et al., 2019).

However, anatomical, topological, and structural analyses of the gills in these taxa reveal no clear evidence supporting a secondary origin. Their gills share similar features with those of



2. Examples of gastropod gills. **A**, *Haliotis aurantium* (Vetigastropoda) pallial cavity, ventral view, scale= 1 mm, shell of USNM 856447 (Gulf of Mexico) (19 mm) (from Simone, 1998); **B**, *Fissurella mesoatlantica* (Vetigastropoda) pallial cavity, dorsal view, scale= 2 mm, shell holotype MZSP 87462 (L 14 mm) (from Simone, 2008); **C**, *Margarites mirabilis* (Vetigastropoda) pallial cavity, ventral view, scale= 0.5 mm, shell MZSP 63018 (Brazil) (W 9 mm); **D**, *Addisonia enodis* (Cocculiniformia – Brazil), right view with pallial structures exposed, scale= 2 mm, an isolated gill filament, scale- 0.5 mm, shell of holotype MZSP 27956 (L 16.5 mm) (from Simone, 1996). Lettering: af, afferent gill vessel; an, anus; ap, genital aperture; as, afferent gill vessel; bp, brood pouch; cv, ctenidial vein; ef-es, efferent gill vessel; ey, eye; ft, foot; gf, gill fold; gi, gill; gp, gonopore, in, intestine; ki, kidney; la, left auricle; lf, left hypobranchial gland; lg, left gill mb, mantle border; ms, gill suspensory stalk; mt, mantle; ne, nephrostome; om, ommatophore; on, osphradium nerve; os, osphradium; pc, pericardium; ra, right auricle; rg, right gill; rh, right hypobranchial gland; rt, rectum; sg, spermgroove; sl, slit; sm, shell muscle; sn, snout; su, suprabranchial chamber; te, cephalic tentacle; ts, slit pallial tentacle; ve, ventricle.

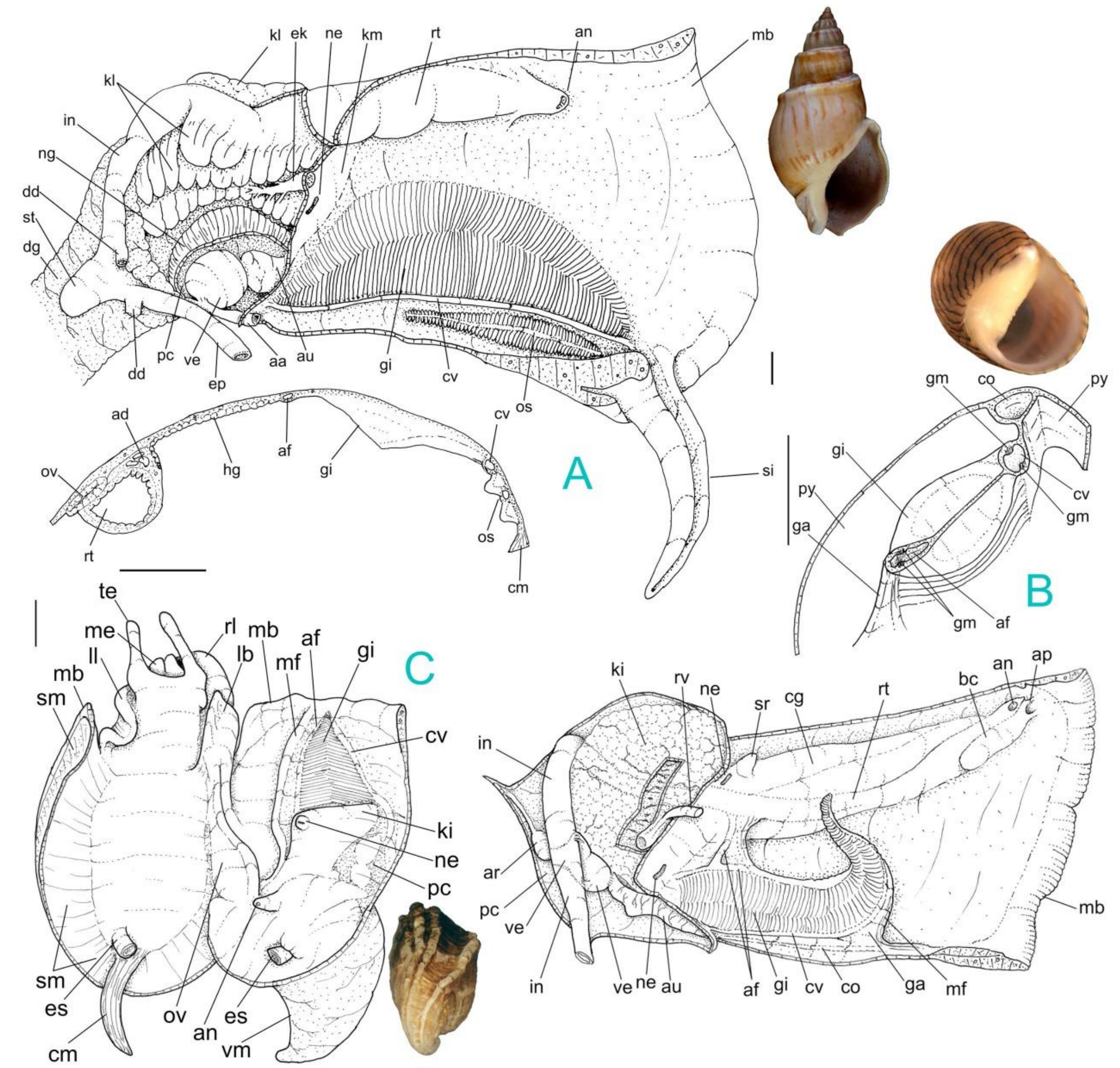
caenogastropods. Furthermore, to date, no developmental or embryological studies have been conducted to investigate the histology or cellular composition of these gills, which could provide evidence of a secondary or derived origin.

Based on the morphological similarities between the monopectinate gills of caenogastropods and those of some basal heterobranchs, these gills are considered homologous, supporting their status as a synapomorphy of Apogastropoda. This character is highly conserved in caenogastropods but rare among heterobranchs, with only a few basal lineages retaining it. As its name implies, Heterobranchia has lost the original gill, as discussed in detail below.

The transition from a bipectinate to a monopectinate gill has also occurred within Cocculiniformia, where some lineages retain the bipectinate gill, while others—such as the addisoniids (Fig. 2D)—exhibit a clearly monopectinate gill.

Loss of gills

This paper also explores a second aspect of gill evolution: the loss of gills. This phenomenon can be divided into two types: (1) loss of the right gill, and (2) complete loss of the primary gill.



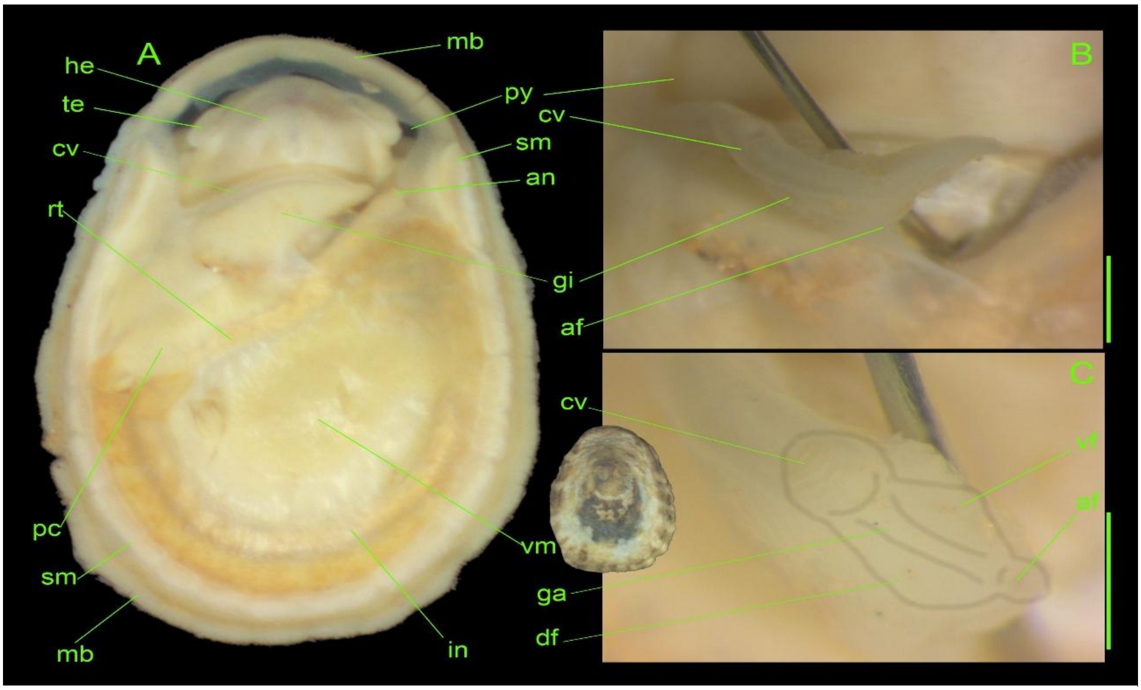
3. Examples of gastropod gills. **A**, *Buccinanops cochlidium* (Caenogastropoda – Argentina), pallial cavity and anterior region of visceral mass, ventral view, below transverse section in middle level of osphradium, scales= 5 mm, shell MACN 20099 (80 mm) (from Pastorino & Simone, 2021); **B**, *Vitta zebra* (Neritimorpha – Brazil), pallial cavity and anterior region of visceral mass, ventral view, below transverse section in middle level of osphradium, scales= 2 mm, shell CMPHRM 2673 (W 18 mm) (form Barroso et al., 2012); **C**, *Cyclothyca pacei* (Heterobranchia – Florida) whole specimen, dorsal view, pallial cavity sectioned along left side and deflected to right, scale 5 mm, shell FMNH 301979 (L 14 mm) (from Simone & Birman, 2025). Lettering: aa: anterior aorta; ad: adrectal sinus; af: afferent gill vessel; an: anus; ap, female aperture; ar, right auricle; au: auricle; bc: bursa copulatrix; cg: capsule gland; cm: columellar muscle; co, collar vessel; cv: ctenidial vein; dd: duct to digestive gland; dg: digestive gland; ek: efferent renal vessel; ep: posterior esophagus; es: esophagus; ga, gill's anterior projection or suspensory membrane; gi: gill; gm: gill muscle; hg: hypobranchial gland; in: intestine; ki: kidney; kl: kidney lobe; km: kidney membrane with pallial cavity; lb, genital pallial lobe; ll, left lobe of neck sole; mb: mantle border; me, mentum; mf, muscle fibers or dorsal fold of pallial cavity; ne: nephrostome; ng: nephridial gland; os: osphradium; ov: pallial oviduct; pc: pericardium; py: pallial cavity; rl, right lobe of neck sole; rt: rectum; rv: afferent renal vessel; sm, shell muscle; si: siphon; sr, seminal receptacle; st: stomach; te: tentacle; ve: ventricle; vm, visceral mass.

The loss of the right gill, which often coincides with the loss of other right-sided pallial structures such as the osphradium and hypobranchial gland, is an evolutionary consequence associated with shell coiling, as detailed elsewhere (Simone, 2022a).

As explained in that paper (Simone, 2022a), there are three types of shell coiling in gastropods, each reflected in their internal somatic organization: the vetigastropod type, the neritimorph type, and the apogastropod type. In all three, the shell spire causes compression of the right pallial structures. Among vetigastropods, some basal taxa still retain paired pallial structures (Figs. 2A, B), but even within this group, more derived branches have evolved to suppress the right pallial organs (Fig. 2C). The single-branch condition is a synapomorphy of the Adenogonogastropoda, a clade that includes Neritimorpha (Fig. 3B) and Apogastropoda (Figs. 3A, C).

The total loss of the gill is almost universal within Heterobranchia. Apart from a few basal lineages that retain gills with primary characteristics, the vast majority of heterobranchs have lost the original gill. In many cases, they replace the gill with alternative structures, such as cerata or secondary gills found in nudibranchs. However, the Eupulmonata represent a distinct group that has evolved to breathe air, with their pallial cavity transformed into a lung, completely lacking any gill structures. For further information on lung evolution, see Simone (2022b).

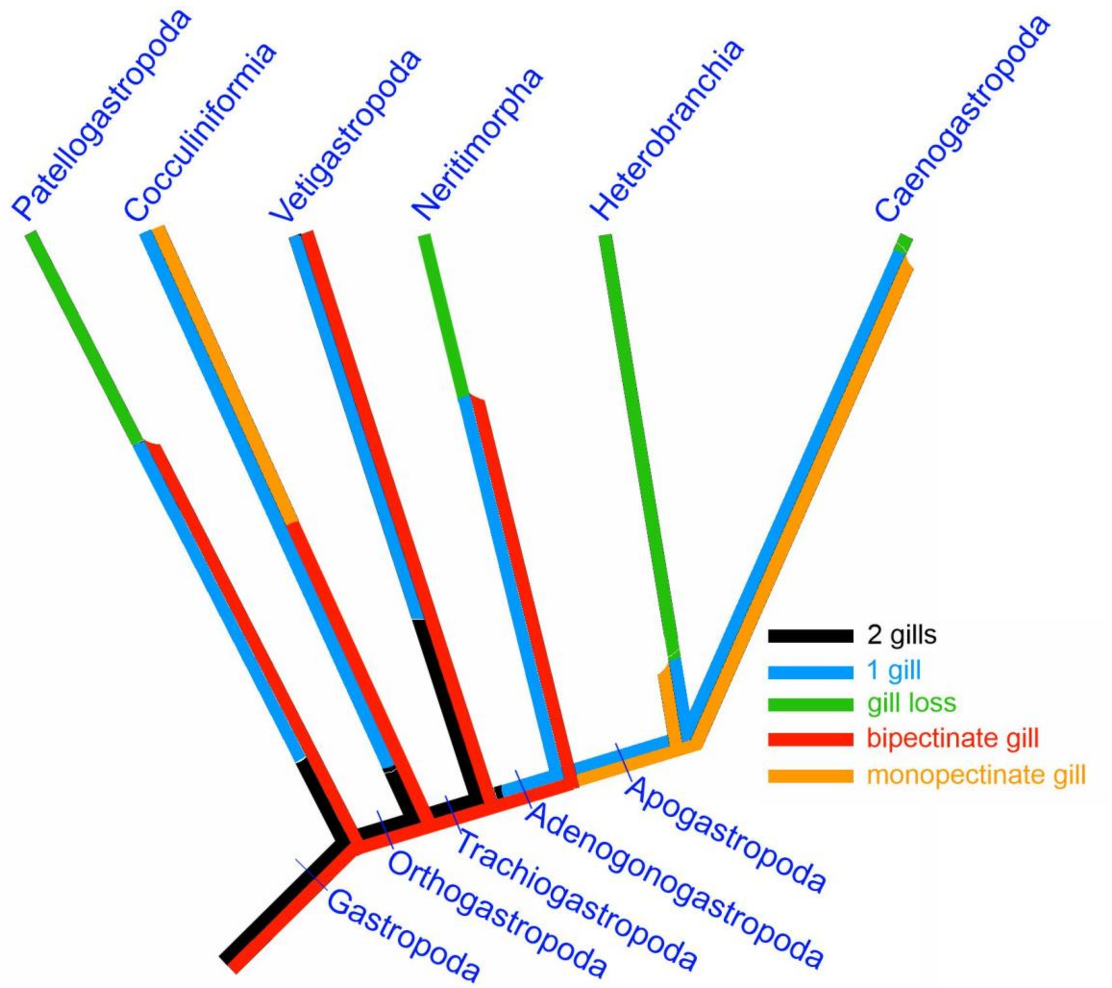
Total loss of gills has also occurred in some caenogastropods and neritimorphs, particularly in lineages that have adapted to terrestrial environments (Simone, 2011, 2022b). Additionally, extreme miniaturization has been linked to gill loss, as observed in certain littorinimorphs—for example, some species of *Phreatodrobia* (Hershler & Longley, 1986).



4. *Lottia subrugosa* (Patellogastropoda, Lottiidae – Brazil): **A**, shell (MZSP 121650 – L 15 mm) and specimen extracted from shell, dorsal view, dorsal mantle in region of pallial cavity removed; **B**, detail of pallial cavity, dorsal view, with gill deflected by a pin; **C**, same, gill sectioned transversely, contour artificially highlighted, scales = 1 mm. Lettering: af, afferent gill vessel; an, anus; cv, ctenidial (efferent) vein; dorsal gill filament; ga, gill axis; gi, gill; he, head; in, intestine; mb, mantle border; pc, pericardium; py, pallial cavity; rt, rectum; sm, shell muscle; te, cephalic tentacle; vf, ventral gill filament; vm, visceral mass.

Phylogenetic inferences

Based on the phenotypic phylogenetic framework of Gastropoda (Simone, 2011, 2024), it is evident that both the loss of gills and the transition from a bipectinate to a monopectinate condition have occurred multiple times throughout the evolutionary history of the class (Fig. 5).



5. Phylogenetic arrangement of main branches of Gastropoda based on phenotypic characters (Simone, 2011, 2024), with color of branches indicating in the branch the presence of 2 gills or 1 gill, gill loss, and if there are bipectinate and monopectinate gills. For color see as indicated.

As explained above, the basal condition in gastropods is the presence of a pair of gills (Fig. 5, black branches). Unfortunately, this condition is no longer found in any living species of the earliest branch, Patellogastropoda, except in fossil taxa. Within Patellogastropoda, there are two main divisions: one includes the lottiids, acmaeids, and their allies, which possess a single bipectinate gill (Fig. 5, blue) positioned transversely in the anterior pallial cavity (Fig. 4: gi). The other division comprises the patellids and their allies, which have completely lost the primary gill (Fig. 5, green); most of these have developed secondary gills located flanking the mantle edge.

Within Orthogastropoda, the earliest branch is the Cocculiniformia, where a few basal species still retain a pair of gills, but most possess a single gill. This gill is displaced to the right side, with its pericardial connection positioned anteriorly (Fig. 2D), which appears to result from hypertorsion (Simone, 1996, 2011)—a possible synapomorphy of this taxon.

The next branch, Trachiogastropoda (Simone, 2024), includes the vetigastropods, among which several superfamilies of the order Pleurotomariida retain paired gills (Figs. 2A, B). However, as explained above and in previous studies (Simone, 2011, 2022a, 2024), more derived vetigastropods have lost the shell slit and the right pallial organs—including the gill—resulting in a unibranchiate condition. This is observed in the orders Seguenziida and Trochida.

Within Adenogonogastropoda, the loss of the right gill is a synapomorphy (Simone, 2011, 2024), meaning that all neritimorphs, heterobranchs, and caenogastropods are unibranchiate. The only exceptions, of course, are those lineages within these groups that have completely lost the gill, as described above.

Regarding the bipectinate and monopectinate conditions, as explained above, the basal state for Gastropoda is the bipectinate gill (Fig. 5: red branches). The monopectinate condition (Fig. 5: orange branches) evolved independently in two lineages: some taxa within Cocculiniformia (Fig. 2D) and as a significant synapomorphy of Apogastropoda. Although the question of heterobranchs having secondary gills remains controversial, analysis of the character matrix and resulting cladogram (Simone, 2011) suggests that the basal heterobranch branches possess a typical monopectinate gill, while the remaining heterobranchs have lost it (Fig. 5: green branch). As noted above, gill loss in caenogastropods has occurred in a few lineages that have adapted to terrestrial environments (e.g., cyclophoroideans, annulariids) and some rare, highly miniaturized forms.

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