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The gastropods columellar folds, plicae and furculae

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Abstract

The columellar appendages of gastropod shells are discussed in this study. The presence of a fold, or plica (a series of folds), observed exclusively in Apogastropoda, is proposed as a strategy to enhance the attachment of the columellar muscle and, consequently, increase its strength. Additional potential advantages of columellar folds and plicae are also explored. The columellar furcula, an inferior (anterior) or superior groove, prevents the animal from being easily extracted from its shell. To date, it has been found in Pleurotomariidae (vetigastropods – superior), as well as in Muricidae and certain buccinoideans (neogastropods – inferior).

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Introduction

The coiling process of the shell is intrinsic to gastropod evolution. The biological factors, evolutionary background, and various types of gastropod shell coiling were previously explored in an earlier issue of *Malacopedia* (Simone, 2022). In that essay, three types of spiralization observed in Gastropoda are presented. Two of these are associated with paired columellar muscles—one in Vetigastropoda and another in Neritimorpha. The third type, exclusive to Apogastropoda, is linked to taxa possessing a single (left) columellar muscle.

Like any biological structure, the shell has undergone numerous modifications, ranging from reduction or complete loss (Simone, 2018a) to secondary uncoiling, transforming into a limpet form (Simone, 2018b). This essay focuses on another conchological modification related to the columella—the presence of folds, plicae, and furculae.

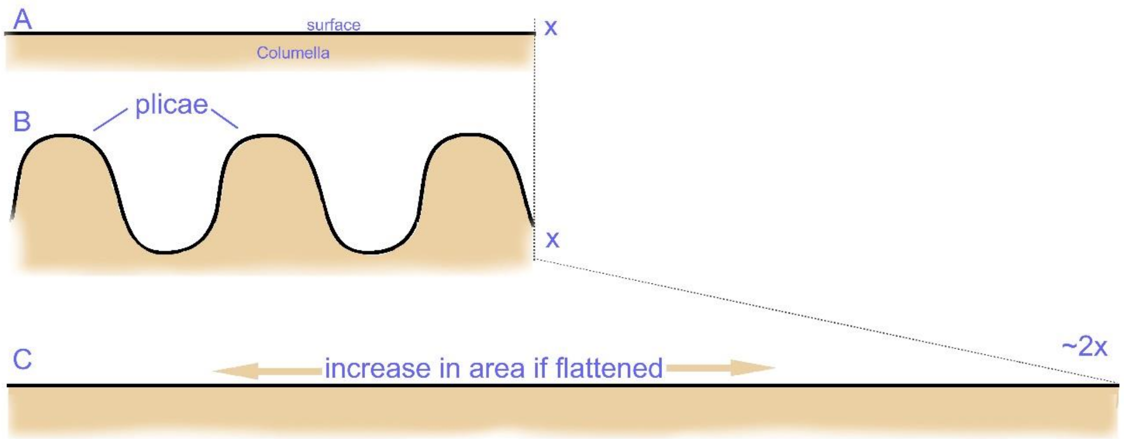
The columella is the axis around which the shell coils. It can form a straight line when the shell's whorls grow around an imaginary axis, resulting in an elongated, turriform shell.

Alternatively, the shell's growth can be broader, creating a more discoid shape. In this case, the columella forms a hollow cone, which produces a feature known as the umbilicus. The opposite pattern can also occur, where each successive whorl lies below the previous one, as seen in fusiform snails, resulting in a zigzagging columella. Some coiled gastropod shells lack a columella altogether, as in cases of extreme lateralization, leading to involute or planispiral shells (Simone, 2018c). The columella itself will be the subject of a future *Malacopedia* issue.

Columellar folds and plicae occur exclusively in apogastropods (Heterobranchia + Caenogastropoda) and are absent in the archaeogastropod grade. It is important to note that these structures differ from the teeth or folds found in the peristome. Peristome folds are present in several archaeogastropods, such as *Clanculus* and *Gibbula* within Vetigastropoda, and *Nerita* in Neritimorpha. However, these peristome structures do not extend continuously along the columella. Furculae, as explained below, have a broader taxonomic distribution.

These columellar structures are better explained below. As furcula is a different morphological phenomenon, it is explained separately.

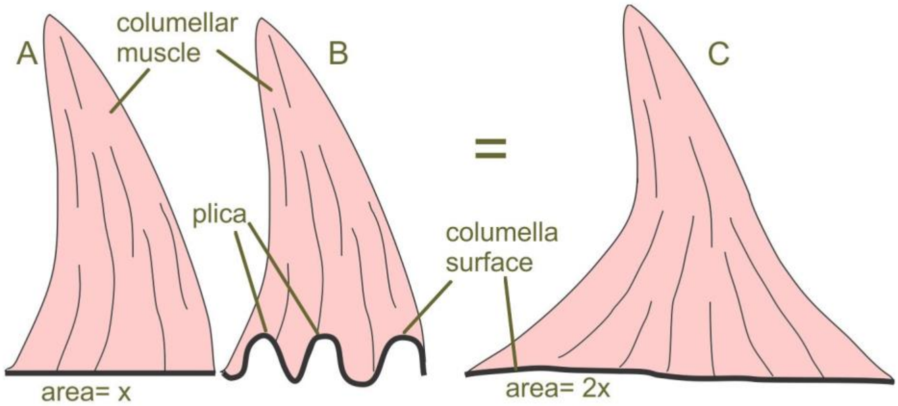
Columellar folds and plicae



1: Schematic representation of a portion of the columella in transverse section. A, a smooth columella, with plane surface; **B**, a plicate columella, possessing 3 folds; **C**, this same region if its folds were flattened, showing the increment of area ~2 times.

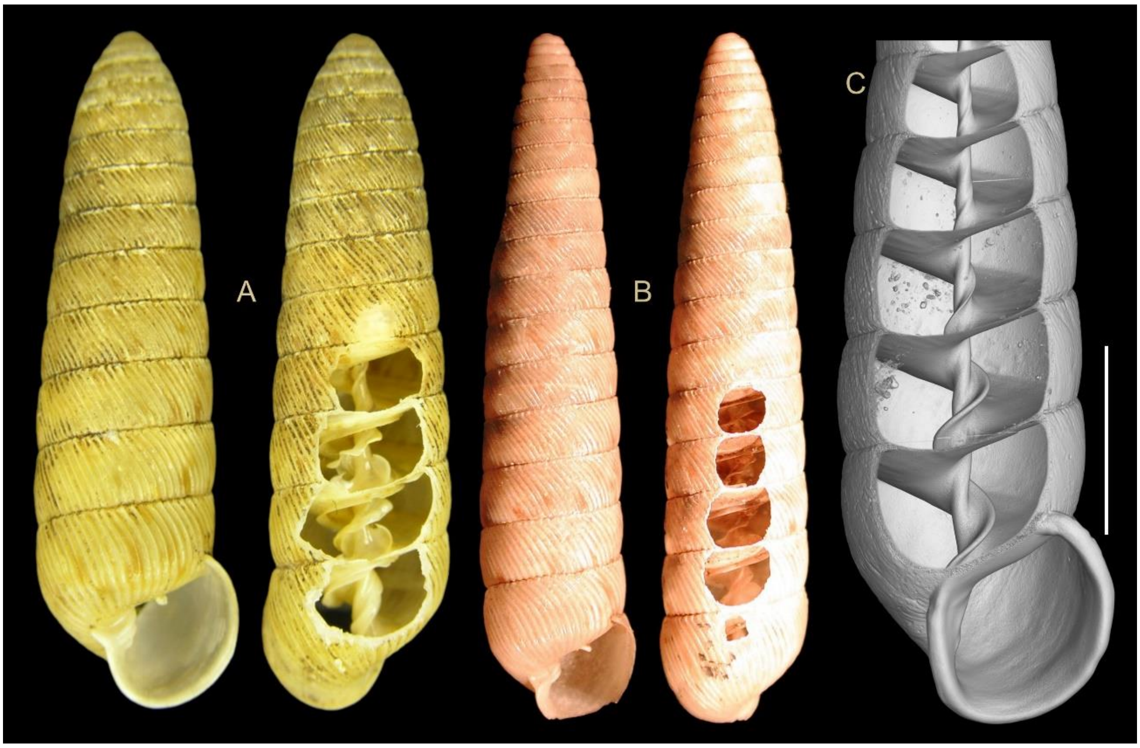
Plicae are understood here as a series of folds. When there is a single fold on the columella, it is considered unique, but when multiple folds are present, they are referred to as plicae. Columellar folds and plicae typically emerge early in ontogeny. If the shell is broken, the plicae can often be observed in the preceding whorls along the spire (Figs. 3, 4F). In some taxa, such as cysticids, the number of folds increases as the shell grows. In others, like marginellids and mitrids, the number of folds remains constant from the earliest whorls to the adult peristome (Fig. 4D).

It is well known that various factors significantly influence the efficiency and strength of muscles. One such factor is the attachment area—the larger the area where a muscle originates or inserts, the stronger and more efficient its contraction. The columellar muscle, as its name suggests, attaches to the columella of the shell. Its primary function is to retract the head-foot into the shell, and the stronger and more efficient the columellar muscle, the better equipped the snail is to defend itself. A stronger muscle enables quicker contractions and enhances the snail's ability to resist attempts by predators (or biologists) to remove it from its protective shell.



2: Schematic representation of columellar muscle attached to a portion of the columella. A, muscle attached to a smooth columella, with plane surface, with area X; **B**, muscle attached to a plicate columella, possessing 3 folds; **C**, this same region if its folds were flattened, showing the increment of muscle attachment area ~2 times.

Given the limited space inside the shell, there is little room to increase the base area of the columellar muscle to strengthen it. One solution to this limitation is the formation of folds on the attachment surface. As illustrated in Figs. 1-2, a flat surface (Figs. 1A, 2A), used by several gastropods for columellar muscle attachment, can develop folds (Figs. 1B, 2B). When there is more than one fold, they are referred to as plicae. In this example (Figs. 1B, 2B), three folds are present. The columellar muscle attaches to these folds at its origin (Fig. 4G) and runs toward the head-foot structures that will be retracted during contraction. The muscle grips the folds tightly, fitting snugly between them (Fig. 4G). If the folds were flattened, it would reveal that the attachment area had nearly doubled (Figs. 1C, 2C). Despite some evidence to the contrary (Price, 2003), it is intuitive to deduce that this increase in attachment area results in a stronger and more secure muscle compared to a flat surface without folds.

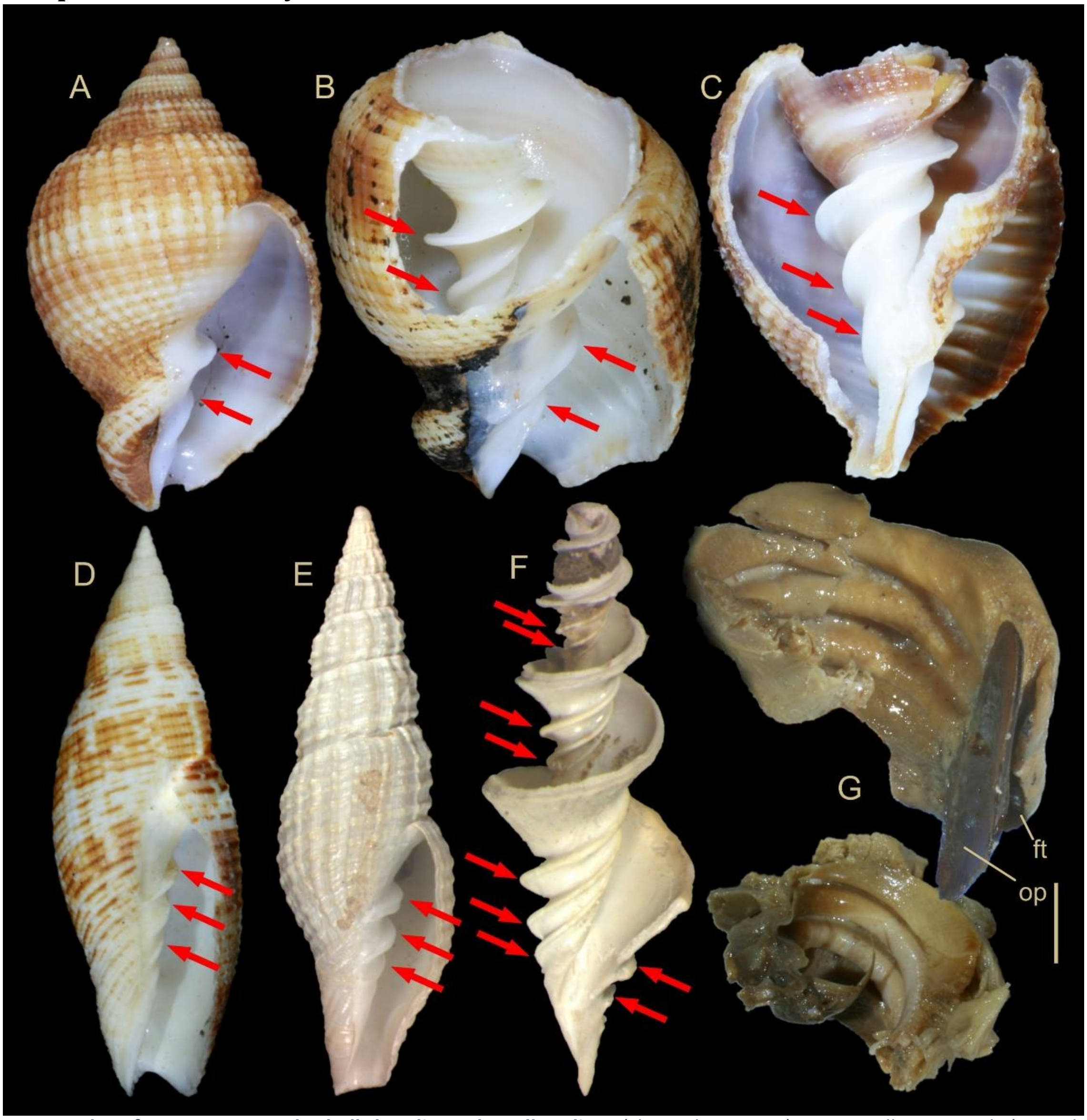


3: Examples of heterobranch shells beading columellar folds and plicae (Eupulmonata, Megaspiridae, Brazil)**. A**, *Megaspira iheringi* (holotype ANSP 100532, 28 mm) (From Simone, 2006); **B**, *Megaspira elata* (holotype USNM 5503, 38 mm); **C**, *Megaspira* sp (MZSP, scale= 10 mm, tomography, courtesy Daniel Cavallari, FFCLRP-USP).

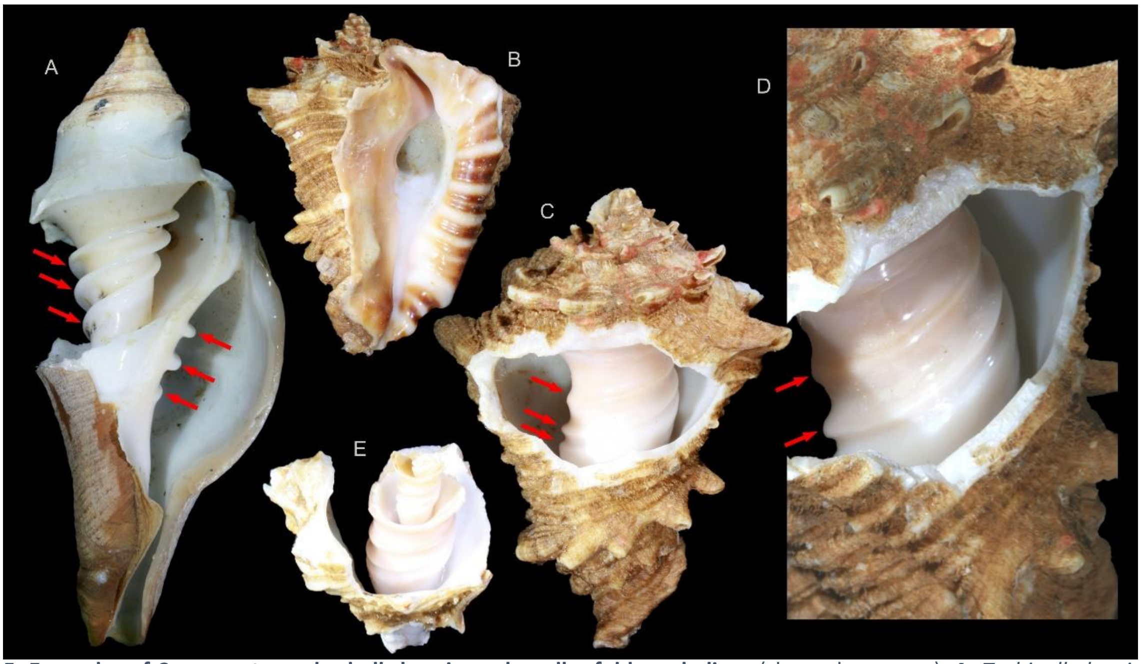
Anyone who has attempted to remove a snail with a plicate columella (e.g., a mitriform snail) from its shell knows how difficult it can be, even if the shell is broken. The columellar muscle is so firmly anchored that it is nearly impossible to extract the snail without causing damage. In most cases, the portions of the muscle that are lodged between the folds remain attached to the shell. The columellar folds remain marked in the muscle surface (Fig. 4G).

There are additional potential functions for columellar folds and plicae beyond increasing the attachment area of the columellar muscle and enhancing its strength. In some taxa, these folds extend to the peristome, helping to protect the shell's aperture, as seen in certain turbinellids and vasids (Fig. 5) and in cancellariids (Figs. 4A-C). Another possible function is to provide extra reinforcement to the shell, as the folds undoubtedly strengthen and harden the internal shell axis, making it more resistant to crushing.

Columellar folds have previously been considered a synapomorphy of Heterobranchia (e.g., Haszprunar, 1985), as they are found in several basal branches, such as fossil Nerineidae. However,



4: Examples of Caenogastropoda shells beading columellar plicae (shown by arrows)**. A**, *Cancellaria petuchi* (Cancellariidae) whole shell (Brazil, MZSP 30734, 31 mm); **B**, same lot, broken shell showing plica in aperture and penultimate whorl; **C**, same, another specimen showing plica in last whorl; **D**, *Domiporta granatina* (Mitridae), whole shell (Vanuatu, MZSP 131500, 50 mm); **E**, *Nodicostellaria crassa* (Costellariidae) holotype whole shell (Brazil, MZSP 27919, 25 mm); **F**, Same species, paratype MZSP 27925, isolated columella (L 18 mm); **G**, *Turbinella laevigata* (Turbinellidae), 2 pieces of the foot and columellar muscle, ventral view, showing grooves left by columellar plica (Brazil, MZSP 103868, scale= 10 mm). Lettering: ft, foot; op, operculum.

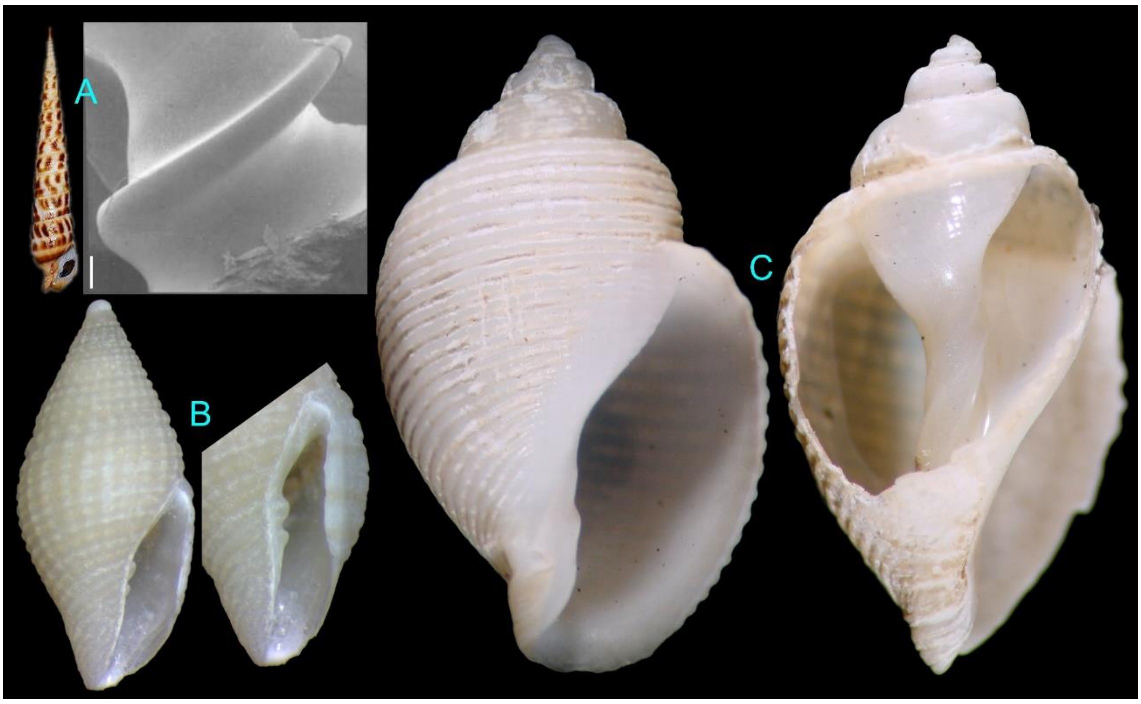


5: Examples of Caenogastropoda shells bearing columellar folds and plicae (shown by arrows)**. A**, *Turbinella laevigata* (Turbinellidae), shell partially broken showing plica in penultimate whorl (Brazil, MZSP 103868, 150 mm). **B-D**, *Aristovasum cassiforme* (Vasidae; Brazil, MZSP 39459); B, whole shell (L 96 mm); C, same, dorsal wall of last whorl extracted to show columella; D, same detail of columella; E, same lot, another specimen, detail of columella in penultimate whorl.

some living heterobranchs also exhibit columellar folds, including the eupulmonate family Megaspiridae (Fig. 3) and certain members of Acteonoidea. Megaspirids have wide folds in the last whorls (Figs. 3A, B), but they appear gradually in the middle level of the spire (Figs. 3A, C).

Columellar folds and plicae are much more prevalent in caenogastropods, particularly within Neogastropoda. Several neogastropod taxa, such as Vasidae (Figs. 5B-E), Turbinellidae (Fig. 5A), and Cancellariidae (Figs 4A-C, 6C), are defined by the presence of plicae in their conchological characteristics. One group, informally referred to as "mitriforms," considers plicae a significant trait (Figs. 4D-F). This group is named for its historical classification as a single family—Mitridae—which has since been gradually dismembered. The initial division separated Mitridae s.s. (Fig. 4D) from Costellariidae (Fig. 4E-F) (Ponder, 1972). Over time, additional families emerged, including Volutomitridae, Pyramimitridae, and Charitodoronidae, despite some conflicting molecular evidence (Fedosov et al., 2018, 2024), the mitriforms appear to form a morphologically cohesive group, which could be recognized as a distinct taxon. This issue remains under investigation and will be explored in the future.

Less developed columellar folds and plicae are also observed in Volutoidea and Olivoidea neogastropods. However, like all biological features, columellar folds and plicae can appear in groups that are generally thought to lack them and can disappear in representatives of groups that are expected to possess them. For instance, terebrids (Conoidea) typically do not have columellar appendages, yet *Terebra taunina*, from the Western Atlantic, does exhibit a columellar fold (Fig. 6A) (Simone, 1999). Among conoideans, which usually lack columellar appendages, the family *Mitromorphidae* (formerly classified as mitrids) possesses small plicae (Fig. 6B) (Simone & Cunha, 2012). Conversely, the genus *Iphinopsis* within Cancellariidae, a group known for its well-developed columellar plicae (Fig. 4A-C), exhibits a notable absence of these structures (Simone & Birman, 2006). While a faint columellar plica may be discernible upon close examination (Fig. 6C-right), it is far from the prominent plicae typical of ordinary cancellariids (Fig. 4A-C).



6: Cases of exceptions in columellar appendages. A, *Terebra taurina* (Terebridae) shell (L 100 mm), and SEM of columella of a broken shell, scale= 5 mm (shell courtesy Femorale) (from Simone, 1999); B, *Mitromorpha sama* (Mitromorphidae) whole shell of paratype MZSP 102973 (L 6.6 mm), and detail of aperture in slightly right view (from Simone & Cunha, 2012); C, *Iphinopsis splendens* (Cancellariidae), whole shell of holotype MZSP 45670 (L 10 mm) and broken paratype MZSP 45669 (L 10 mm) showing only vestiges of columellar plica (from Simone & Birman, 2006).

Columellar furculae

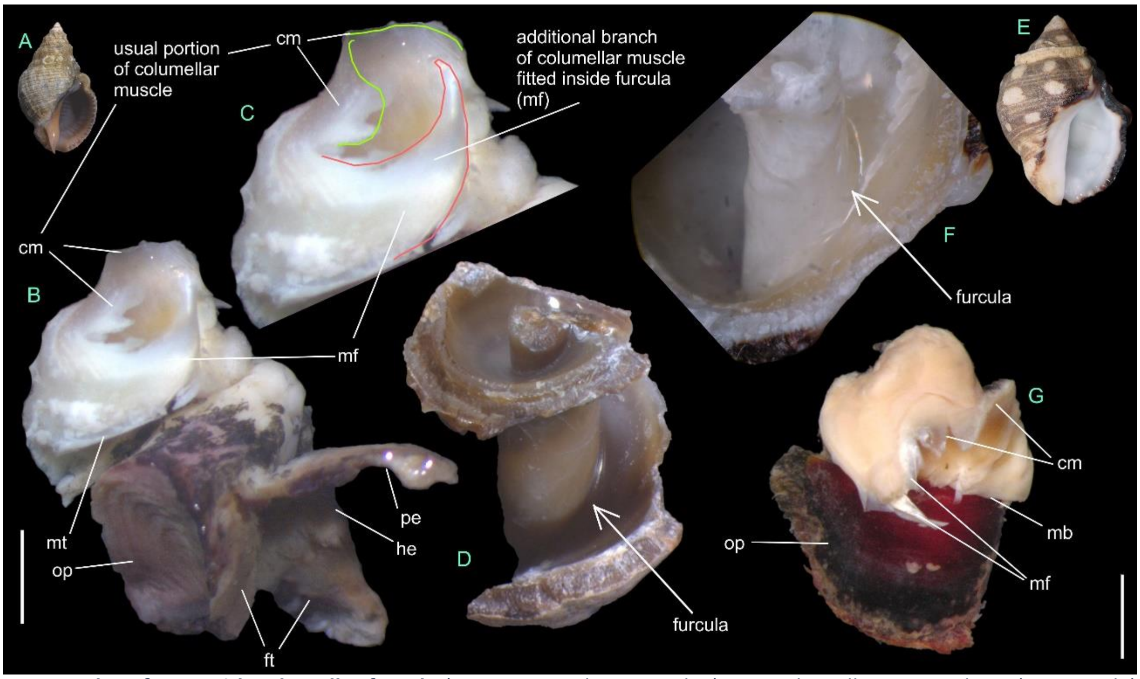
The columellar furcula is a broad groove located in the inferior (anterior, adapical) or superior (posterior, abapical) inner region of each whorl. It is distinct from the otherwise flat surface of each whorl, inserting into the columella at a near-perpendicular angle. In taxa that possess a furcula, this insertion is preceded by a deep groove.

The columellar furcula has largely gone unnoticed in the malacological literature thus far, but it plays a significant role in snail physiology. Taxa that possess a columellar furcula are virtually impossible to extract from their shells without breaking the shell itself.

Clear columellar furculae have so far been identified in the vetigastropod family Pleurotomariidae (Fig. 8) and in some neogastropods, particularly within Muricidae (Fig. 7) and certain Buccinoidea. In these cases, when the animal is pulled from the shell, its tissues—especially the columellar muscle—fit into the groove, effectively blocking any forward movement. This adaptation prevents the animal from being extracted from the shell, often resulting in the soft parts' breakage.

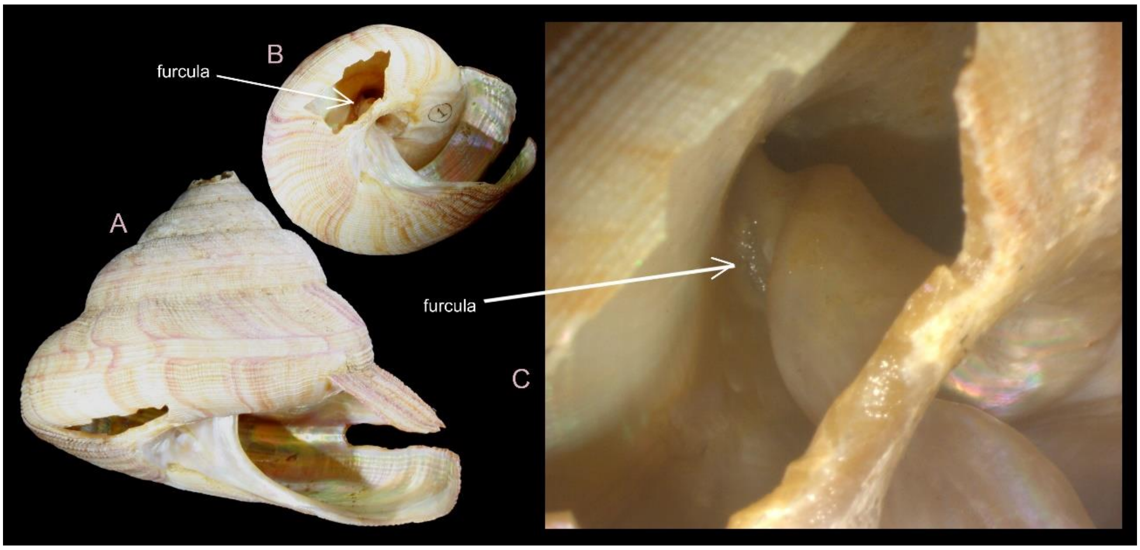
As the neogastropods mentioned above have no relationship with the pleurotomariid vetigastropods, it is reasonable to deduce that columellar furculae evolved independently more than once in gastropod evolution, representing instances of convergent evolution. Another clue of this independence is the furcula position, as it is superior in pleurotomariids (Fig. 8), and inferior in mentioned neogastropods (Fig. 7).

Within Neogastropoda, the furculae of *Muricidae* (Fig. 7) and some *Buccinoidea* may also be examples of convergence. However, since the phylogenetic relationships within Neogastropoda are not yet fully understood, the furcula itself is often overlooked in many branches, and given that



7: Examples of taxa with columellar furcula (Neogastropoda, Muricidae)**. A-D**, *Thaisella guatemalteca* (Guatemala) (from Simone, 2017); **A**, holotype shell MZSP 121000 (29 mm); **B**, head foot extracted just from shell, male, mantle and visceral mass removed, scale= 2 mm; **C**, detail of posterior region, showing both components of columellar muscle in different colors, being left one (orange, inferior in Fig.) that fitted inside furcula; **D**, middle level of columella of a broken shell showing furcula by arrow; **E-G**, *Acanthais brevidentata* (W Panama, MZSP 64193); **E**, shell (L 26 mm); **F**, middle level of columella of a broken shell showing furcula by arrow; **G**, head foot extracted just from shell. Ventral view, mantle and visceral mass removed, scale= 2 mm. Lettering: cm, columellar muscle (usual branch); ft, foot; he, head; mb, mantle border; mf, columellar muscle branch fitted inside furcula; mt, mantle; op, operculum or opercular pad; pe, penis.

Muricidae appears to be a basal lineage within neogastropods (Simone, 2021), there is a possibility that the neogastropod furcula could represent a basal character that has since reverted in several of its internal branches.



8: Examples of taxa with columellar furcula *Perotrochus atlanticus* (Vetigastropoda, Pleurotomariidae) (Brazil, MZSP 35059)**. A**, whole shell (W 85 mm); **B**, same slightly inferior view showing hole artificially done to show columella; **C**, same, detail of columella.

The neogastropod furcula is associated with the siphonal canal in the peristome, suggesting it may be a remnant from the canal's development during shell growth. However, some canal-bearing shells lack a furcula, and conversely, some furcula-bearing shells, such as those of the Pleurotomariidae, do not possess a siphonal canal. Thus, while the two structures are connected, they are distinct and independent phenomena. In neogastropod taxa that do possess a furcula, the columellar muscle is bifid, consisting of two parts: a broad right component that closely resembles the typical columellar muscle (Figs. 7B, C, G: cm) and a narrower, longer, pointed left component that is encased within the furcula (Figs. 7B, C, G: mf). As with the plicae (Fig. 4G), the furcula influences the shape of the columellar muscle, molding the left columellar muscle component.

The superiorly located furcula in pleurotomariids is particularly distinct (Figs. 8B, C) and has been observed in all living species of the family examined so far. However, it has not been detected in other vetigastropods. This feature may have been overlooked, as noted earlier, in previous studies, and it is possible that furcula could appear in other vetigastropods with coiled shells.

Final comments

The columella of the gastropod shell, like any biological structure, plays a significant role in the evolution of gastropods and exhibits a variety of adaptations and modifications. As noted earlier, the columella itself will be addressed in a future issue of *Malacopedia*, but its most important appendages are discussed here. Of course, further experimental confirmation is needed, as much of the information provided is based on empirical observations and deductions. Additionally, it is worth noting that the columellar furcula (Figs. 7, 8) has not been previously recognized in malacological literature.

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