Malacopedia

São Paulo, SP, Brazil | ISSN 2595-9913
Volume 3(7): 40-51 | November/2020

The gastropod operculum

Luiz Ricardo L. Simone

Museu de Zoologia da Universidade de São Paulo
lrsimone@usp.br; lrlsimone@gmail.com
ORCID: 0000-0002-1397-9823

Abstract

The operculum is a larval structure that covers the shell's aperture in gastropod larvae. It evolved to be maintained as an adult structure and has further modifications in several gastropod branches. In the present paper, the evolution, modification, and anatomy of the operculum are explored. The operculum can be standardized in categories such as high multispiral, low multispiral, paucispiral, unguiculate, and excentric, according to the position of its nucleus and outer sculpture. It also can be corneous or calcareous. Its edges can be flexiclaudent and rigiclaudent. And it can be large, reduced, or lost. All these main kinds of classifications are discussed from a phylogenetic and taxonomic standpoint.

DOI: 10.13140/RG.2.2.23455.18080

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

Introduction

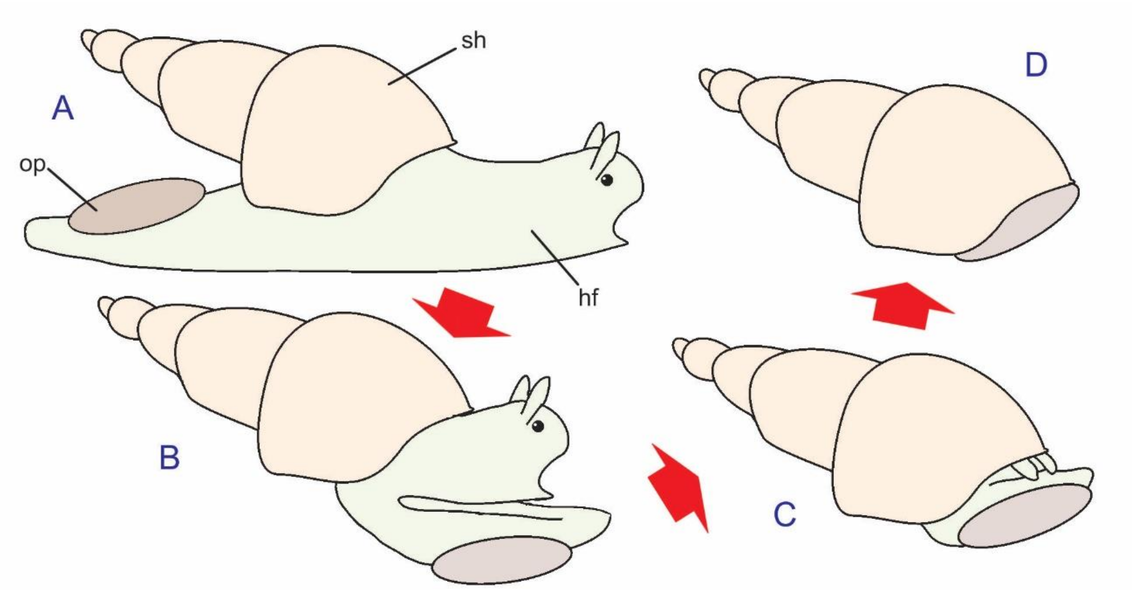
The **operculum** is a hard structure that works like a lid that closes the shell aperture in gastropods. It is located on the dorsal surface of the posterior region of the foot. Typically, this part of the foot is the last to be drawn in when the animal retracts into the shell. The operculum thus "corks" the shell, offering additional protection.

According to ontogenetic and phylogenetic studies, the operculum is a synapomorphy of Gastropoda (Ponder & Lindberg, 1997; Simone, 2011) and appeared as a structure of planktonic larvae, while it lives in the plankton. Virtually all gastropods have an operculum, at least during the larval phase. Basal groups such as the primary limpets, i.e., patellogastropods and cocculiniforms, have an operculum during the larval phase, which is later lost in metamorphosis into the adult stage. Few gastropod taxa lack an operculum at all in early ontogenetic phases, e.g., the systellommatophoran slugs.

Nevertheless, some gastropod branches evolved to maintain the operculum in the adult stage, and the structure serves as additional protection. By contrast, the adult operculum was further lost in several taxa, as discussed below.

The operculum is the second most studied gastropod structure after the shell itself. Since it presents an enormous assortment of modifications, the taxonomic application of this structure is quite straightforward. The putative primitive operculum and several modifications are explored below, including some phylogenetic and taxonomic implications.

1. Functional operculum approach

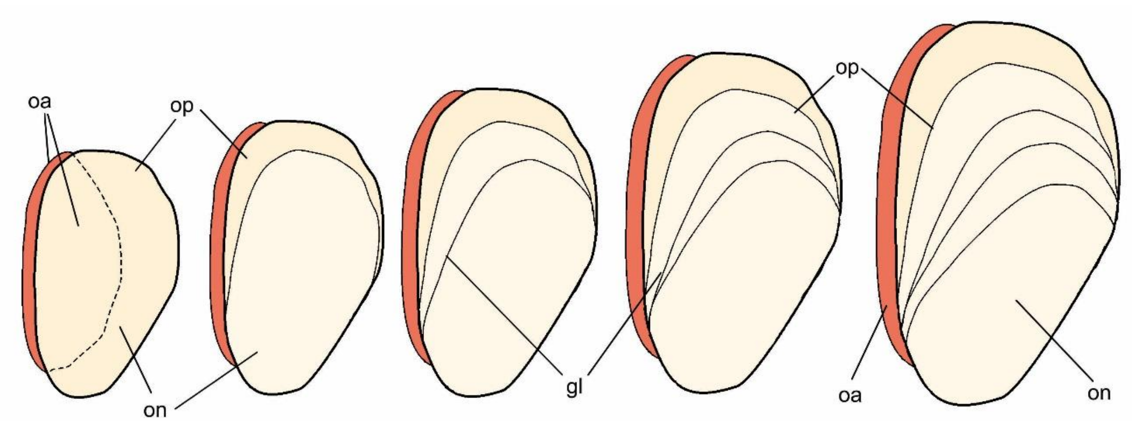


1. Schematic representation of a generic shelled gastropod in head-foot retraction movement, in which the operculum blocks the aperture: **A**, crawling active snail; **B**, middle movement foot bending ventrally; **C**, retraction of head and foot into the shell's last whorl; **D**, completely retracted snail, with the operculum blocking the aperture. Lettering: **hf**, head-foot; **op**, operculum; **sh**, shell.

Usually, a shelled snail will retract into its protective shell when disturbed (Fig. 1). Despite having a lot of variation, this movement is shown in the scheme above as it is commonly found in most gastropods. The posterior region of the foot, to which the operculum is dorsally attached (Fig. 1A), bends ventrally when the animal retracts (Fig. 1B). Using the contraction of the columellar muscle, the head-foot is gradually drawn inside the shell's last whorl (Fig. C). Strategically, the operculum is the last structure to be drawn, and its outer surface is left exposed. When the head-foot retraction movement ends, the operculum then seals the shell aperture, blocking the advance of any potential offender. This head-foot retraction movement is relatively quick, but it can be slower if the foot is larger.

2. Operculum formation

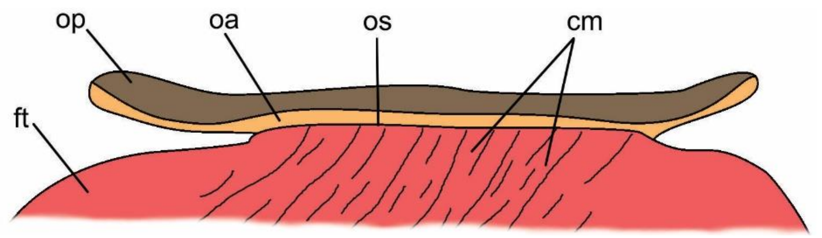
The operculum is generated by the opercular pad, a flat structure that deposits consecutive layers of material, much like the mantle edge does when producing the shell. The most accepted theory for the origin of the opercular pad is that it came to be a separated portion of the mantle itself. Interestingly, if proven true, this theory would make gastropods the true bivalve mollusks,



2. Schematic representation of a growing operculum, from left to right, outer view. The dotted line in first image shown the extension of the opercular pad in inner surface. In a usual dextral shell, the operculum grows by increment in inner (left in Figs.) and superior edges by opercular pad, forming growth lines. The first element is the nucleus. Lettering: **gl**, growth line; **oa**, opercular pad; **on**, opercular nucleus; **op**, operculum.

as its shell is truly divided into two separate parts, while the Bivalvia have a single, bilobed shell united by ligament (their mantle is a single, bilobed structure, with a wide medial connection).

To be efficient, the operculum must grow with the shell. In a usual dextral shell, the operculum grows by an increment of the inner (left) and superior edges. The previous operculum piece thus rotates clockwise during growth, forming consecutive growth lines (Fig. 3). The oldest portion of the operculum becomes the nucleus, and, as such, the growth lines are commarginal. Interestingly, distinct types of shell coiling coincide with different types of opercular growth. A true sinistral shell has a mirrored opercular growth. If the snail is hyperstrophic, i.e., the shell is sinistral, but the soft parts are not (e.g., *Lanistes*), the operculum has the same growth architecture as a dextral shell.

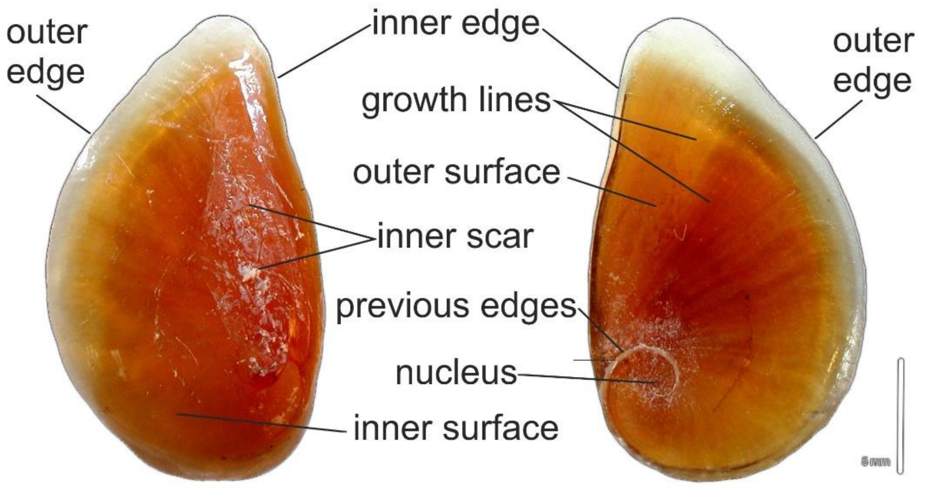


3. Schematic representation of a transverse middle section in a generic horny operculum, showing the different layers from it, integument and adjacent region of head-foot musculature, including proximal portion of a branch of the columellar muscle. Lettering: **cm**, columellar muscle; **ft**, foot; **oa**, opercular pad; **op**, operculum; **os**, opercular scar.

In a cross-section (Fig. 3), the different layers of tissues adjacent to the operculum are schematically represented to the right. The operculum (op) is loosely attached to the opercular pad (oa), and more firmly attached to the integument at the base of a dorsal branch of the columellar muscle (cm). This firmer region is called opercular scar (os). The opercular pad is also present in the region of the scar, as the operculum must thicken there as well. Thus, the dorsal branch of the columellar muscle has the function of contracting the operculum inside the shell, and maintain it firmly occluding its aperture.

3. Anatomy

Despite the many opercular conformations, a basic anatomical terminology can be applied to most of them (Fig. 4). The usual operculum has an outer surface that is exposed when the animal is retracted inside the shell. During the crawling movement, the ventral region of the shell's last whorl is supported by its outer surface. The inner surface is on the other side, usually not visible and covered by the opercular pad, which generated the operculum. The inner surface usually is glossy, shiny, while the outer surface is opaque. The growth lines are clearer on the outer surface, and are parallel to the inner edge, marking previous inner edges from when the operculum was smaller. Previous outer edges are usually marked by a spiral line, beginning at the opercular nucleus. The inner edge is named like that because it is in contact with the inner lip of the shell in a contracted condition; while the outer edge contacts the outer lip of the shell aperture. It is possible, also, to designate superior and inferior edges when necessary; usually. the superior edge is angled; the interior edge is rounded and touchs the siphonal region of the aperture. The scar is present on the inner surface. Its format and size are variable, but the scar usually has a rather elliptic outline, occupies ~½ to 1/3 of the inner surface area, and is located closer to the inner edge. The nucleus is usually apparent, and it is the oldest portion of the operculum. The embryonic operculum, if preserved, is located at the nucleus.



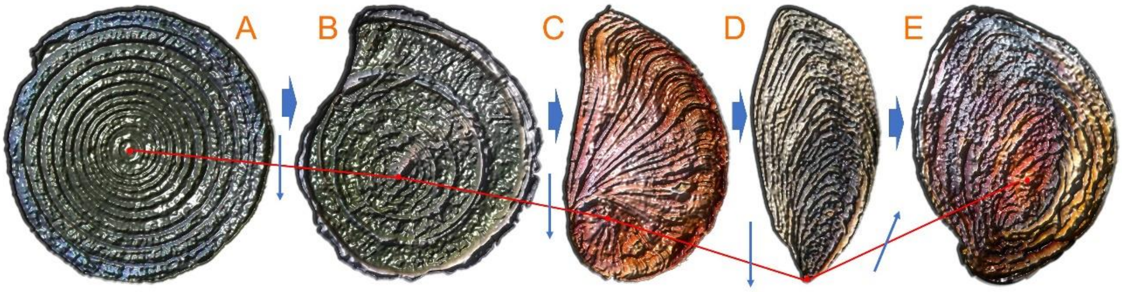
4. Main anatomical parts of an operculum in inner (left) and outer (right) views, of *Neverita duplicata* (MZSP 32268, Florida). The operculum is usually placed with the usual apex pointing upwards.

4. Types of opercula

Just like the shell itself, the operculum has a profusion of classifications. However, in this paper, the standardization of the opercula is focused on four criteria (some of which overlapping) that seem more important for taxonomy and phylogeny.

5. Photos of examples of the five main categories of opercula, including the respective shell (below). These are typical examples, as a total gradation exists, and suggests an evolutionary trend. **A**, high multispiral, *Calliostoma meliferum* (W ~2 mm) (from Cavallari & Simone, 2018; MZSP 55522, L ~5 mm); **B**, low multispiral, *Gaza compta* (W ~10 mm) (from Simone & Cunha, 2006; MZSP 40324, L ~26 mm). **C**, paucispiral, *Euspira heros* (W ~26 mm) (NJ Marine Ecol, Stud Fish collection 5255; ~60mm). **D**, unguiculate, *Pugilina tupiniquim* (L ~22 mm) (from Abbate & Simone, 2015; MZSP 116299, L ~80 mm). **E**, excentric, *Triplex brevifrons* (W ~25 mm) (MZSP 24120; L 120 mm).

4.1. Main sculpture. Most opercula can be classified into five main categories (Fig. 5). They are not separated from each other, since a complete gradation exists. However, most species that bear opercula in the adult stage can fall into one of these categories (Fig. 5). **A: high multispiral**, the operculum is usually circular or subcircular, the nucleus is central and from it, several coils of previous edges begins; this kind of operculum is common among the Vetigastropoda. **B: low mul-**



6. Schematic representation of opercula of Fig. 5 with suggestion that they represent an evolutionary pathway (indicated by broader blue arrows). The nucleus is indicated by red dots and its migration by red line, in such evolutionary migration obeyed the movement of the narrow blue arrows.

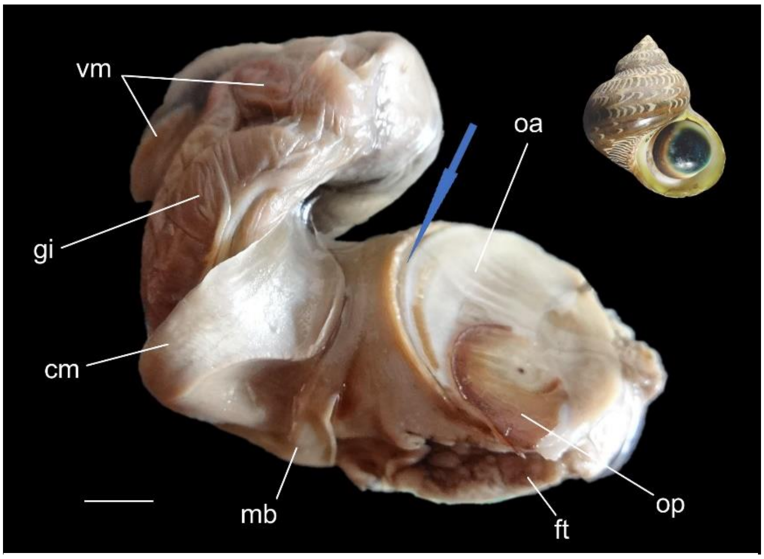
tispiral, similar to the preceding type, but there are few spiral coils, and the nucleus is slightly dislocated inferiorly; this kind of operculum is common in some Vetigastropoda, Neritimorpha, and basal Caenogastropoda. **C: paucispiral**, it is slightly more elongated and has few (2-3) coils only, the nucleus is located in the inferior third; it is common in Neritimorpha and mesogastropod Caenogastropoda. **D: unguiculate**, or “nail-like”, is further elongated and has a terminal, inferior nucleus, from which successive commarginal sculpture begins; it is usual in higher Caenogastropoda. **E: excentric**, it is slightly more rounded, the nucleus is in the inferior third or in the middle region, from which the commarginal sculpture begins; it occurs in several neogastropod branches.

Taking opercular development, embryogenesis, and the position of the respective taxa on the cladograms into account, the given classification represented from A to E (Fig. 5) is a single pathway that seems to have occurred independently in several gastropod branches. This is schematized in Fig. 6, with special concern to the migration of the opercular nucleus (red dots). In cladograms of Gastropoda as a whole, and within several of its branches (Simone, 2011), the more basal taxa have the opercula of the left side of the Figs. 5-6, while the more derived have those of the right side. The suggested evolutionary pathway is the migration of the nucleus towards the inferior region, with a consequent diminishment of the coils (Figs. 5-6A to C). This culminates in an inferior terminal nucleus (Figs. 5-6 D): the operculum lacks a spiral sculpture which in turn becomes a commarginal sculpture. An additional evolutionary step exists, with the further return of the nucleus to upper regions, but with the sculpture maintaining the commarginal conformation (Fig. 5-6E). In Fig. 6, the nucleus migration is represented by the red line and narrow blue arrows. The branches that usually have each type of operculum are schematized below.

4.2. Calcified operculum. Another way of classifying the opercula considering their degree of calcification. There are (1) non-calcified, corneous opercula, and (2) calcified opercula (Fig. 7). A few taxa have an intermediary operculum, mostly corneous but with some sparse points of calcification. They are found in some Neritimorpha and Naticidae.

7. Examples of calcified opercula. **A**, *Naticarius cayenensis* MZSP 28565 (W ~20 mm), outer and inner views; **B,** *Turbo canaliculatus* MZSP 35483 (W ~30 mm), outer and inner views.

The calcified operculum can be thin, flat (Fig. 7A) up to very thick (Fig. 7B), looking like an additional shell occluding the shell's aperture. The calcified operculum can be also categorized in the previous classification (4.1) as well, but the kind of spiralization (or not) is better shown in the inner surface (right images of each species of Fig. 7), as the calcification of the outer surface cloaks the sculpture. In the illustrated examples, *Naticarius* has a paucispiral calcified operculum (Fig. 7A), while *Turbo* has a low multispiral one (Fig. 7B). Calcification of other kinds of opercula also exists, despite being rare.



8. *Turbo petholatus* as example of species with calcified operculum and the modification of opercular pad for building the calcified layer on internal organic matrix (blue arrow). Specimens just removed from shell, mostly seen ventrally-slightly left (USNM 594207. Scale = 5 mm), and respective shell (L ~40 mm). Courtesy APS Dornellas (part from Dornellas & Simone, 2020). Lettering: cm, columellar muscle; ft, foot; gi, gill; mb, mantle border; oa, opercular pad; op, remains of inner layer of operculum; vm, visceral mass.

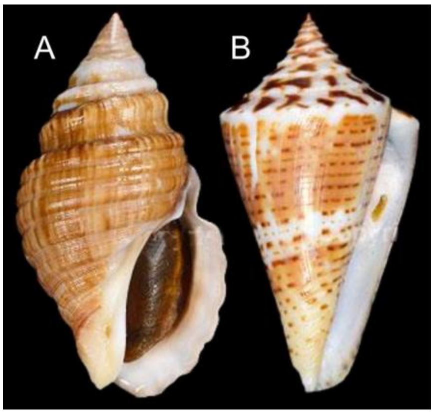
The calcification of the operculum is done on a corneous matrix, which is homologous to the non-calcified models of allied groups. The calcified layer is provided by the outer edge of the opercular pad, in its inner edge, which is particularly wide in taxa that have calcified opercula (Fig 8: arrow). This can be verified by a narrow portion of the calcified layer of the inner edge of the operculum (Fig. 7, the right images of each example, notice the white edges).

4.3. Types of edges. A very interesting approach to operculum morphology and evolution was provided by Checa & Jiménez (1998). Among other characters that the authors analyzed, the standardization of two kinds of opercular edges is noteworthy: (1) **Flexiclaudent**, is the operculum in which the edges are flexible and mostly thinner than the remaining opercular regions. When contracted, the flexible opercular edges seal the shell aperture more efficiently, as they cover more closely the adjacent peristome's inner surface. An example is in Fig. 9, in which the opercular edges are thinner, and easily damaged. The opercula illustrated in the Figs. 4, 5A-C above are additional examples of flexiclaudent opercula. (2) **Rigiclaudent**, is an operculum with blunt edges, i.e., the opercular edges are rigid, almost as thick as the remaining areas. Rigiclaudent opercula seal the shell aperture with more difficulty, as they depend on matching the peristome's contour more precisely. To achieve that, the operculum outline must have the same profile as the aperture, e.g., as in turbinids (Fig. 8). Usually, the rigiclaudent operculum has not the function of sealing the aperture, but to be an additional protective armor. Examples of rigiclaudent opercula are in Figs 5D-E, 7, and 8.

9. Example of flexiclaudent operculum of *Pomacea crosseana* (W ~23 mm), outer and inner views, including its shell (L ~50 mm) (modified from Simone, 2004a).

4.4. Presence/absence/reduction. Another kind of opercular classification considers its size compared to the aperture's size in adult individual. The operculum can be (1) **large**, i.e., almost as large as the aperture, closing it completely or almost completely (Fig. 10A); (2) **reduced**, i.e., the operculum is much smaller than the aperture, and it is not able to close it (Fig. 10B); and (3), **absent**, i.e., no operculum is present.

The reduction or loss of the operculum usually occurs when the peristome has additional protective architecture. Examples are the very narrow aperture of conids (Fig. 10B) (reduction), and the narrow and toothed aperture of cowries (cypraeids) (loss). Additionally, reduction and loss of the operculum are detected in gastropods with a huge foot, usually adapted to unconsolidated substrates. In these cases, the large foot blocks the shell aperture efficiently when contracted. The loss of the operculum is also usual in groups with enlarged apertures, such as those that underwent the limpetization process (Simone, 2018a); and also obviously occurs in the limacization process (Simone, 2018b).



10. Examples of relative size of operculum. **A**, *Burnupena cincta*, South Africa (L 55 mm), large operculum; **B**, *Dauciconus anabathrum* Florida (L 38 mm), reduced operculum. Courtesy Femorale.

The evolutionary pathway of large » reduced » loss of the operculum is intuitive. Considering that all gastropods have an operculum at some point during their ontogeny, its absence in the post-larval phase is usual in the more basal, primary limpet branches – the Patellogastropoda and Cocculiniformia. In the remaining gastropod branches, the presence of a large adult operculum is the rule, and all internal branches that have reduced or lost the operculum present a secondary evolution, i.e., the reduction and the loss are apomorphic. This will be explored below.

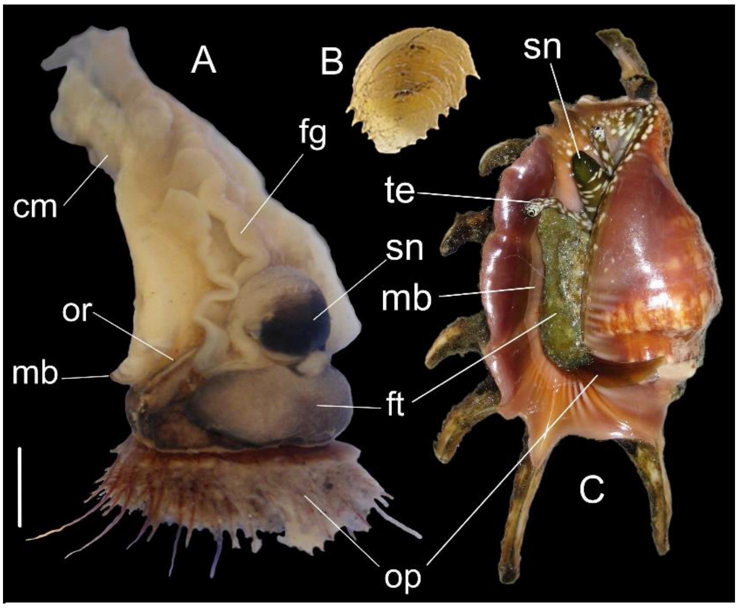
Some gastropod branches have species with a large adult operculum, a reduced one and species lacking it at all. At least in this regard, the taxa with larger opercula are expected to be more basal, while those lacking it are more derived this attribute. Those with vestigial/partial opercula are intermediary. This is noteworthy in the Heterobranchia, but is also found in some caenogastropod families such as, e.g., Volutidae and Olividae.

The case of the Naticoidea is particularly intriguing. According to a phylogenetic approach considering several naticoideans representatives based on morphology (Simone, 2011), the more basal branches have corneous opercula, the middle branches have calcareous opercula; the corneous operculum appears as a novelty in the final branches, preceding a terminal branch including species with reduced opercula (the Sininae). This is particularly important, as the kind of operculum rules the present subfamiliar classification (corneous: Polinicinae; calcareous: Naticinae: reduced: Sininae). According to the same phylogeny, only Sininae is monophyletic. The remaining branches show an interesting naticid evolutionary trend for calcifying the operculum, a reduction to the corneous condition, culminating with its reduction.

5. Opercular extra adaptations

Much like the shell itself, the operculum is an important adaptative structure for adult gastropods. Sometimes, it even has functions beyond the simple occlusion of the aperture.

There are several examples, but three of them are good choices of opercular oddities: (1) The **hairy operculum** of some siliquariid cerithioideans like the genus *Stephomoma* (Fig. 11A). The operculum is flat, but it has an outer multispiral surface covered by chitinous hair. Each hair filament is built by a long and stubby projection of the right edge of the opercular pad (Fig. 11A: or). This projection has a longitudinal ventral furrow that secretes the filaments (Bieler & Simone, 2005). The hair function is debatable, but may help in food



11. Examples of extra modifications of operculum. **A**, *Stephopoma nucleogranosum*, extracted head-foot, anterior-slightly right view (scale= 5 mm), hairy operculum (from Bieler & Simone, 2005); **B**, *Nassarius arcularia*, isolated spiny operculum, outer view (L ~3 mm) (from Abbate et al., 2018); **C**, *Lambis* sp., Philippines, living specimen, ventral view, operculum for leaping movement (courtesy Gijs Kronenberg). Lettering: cm, columellar muscle; fg, food groove; ft, foot; mt, mantel border; op, operculum; or, opercular pad projection; sn, snout; te, tentacle.

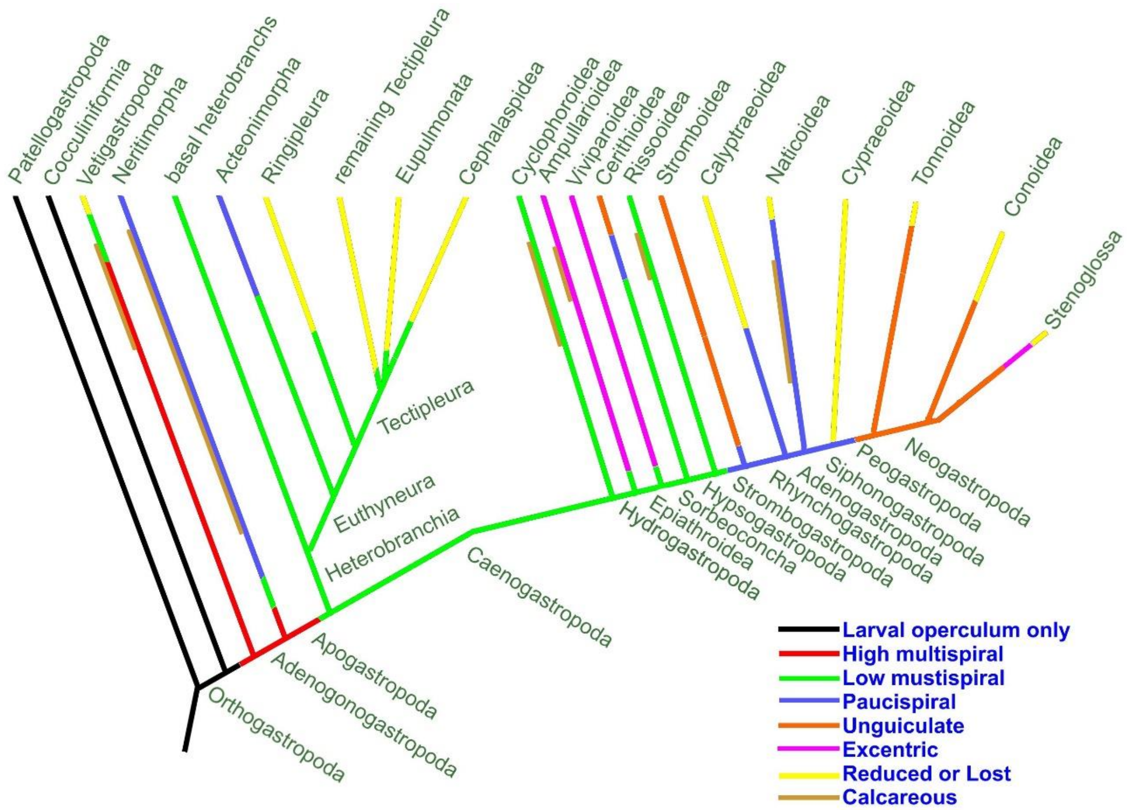
capture. (2) The **spiny operculum** of some nassariids, such as *Nassarius arcularia* shown above (Fig. 11B), in which the opercular edges bear a series of protective spines. (3) The **sickle-shaped operculum of leapers**, such as the strombids (Fig. 11C: op). A typical strombid lacks a foot bearing a crawling sole. The foot works as a muscular stalk with an elongated, strong, and pointy operculum at the tip (Simone, 2005). The animal initially anchors the posterior end of the foot by thrusting the point of its operculum into the substrate. In a quick movement, the foot contracts, lifting the shell and throwing it forwards (Parker, 1922). This so-called leaping movement is the strombid alternative for crawling on the unconsolidated sediment and can be used as a defense mechanism. If a strombid is disturbed and its shell is turned upside down, the animal may use quick movements of the foot-operculum to strike the attacker. They have good eyes and can even aim their strikes. The strombid leaping motion is useless in hard substrates.

6. Phylogenetic implications

The text above presenting the main kinds of opercula is already provided in a comparative scenario, in which the evolutionary treads are suggested. Thus, any particular way of evolution of opercular features must be checked above. The present item concerns the occurrence of these types of opercula along the cladogram (Simone, 2011). Most different kinds of opercula are represented on the cladogram using different colors (Fig. 12). Each terminal branch represents a complex particular tree, which would be impracticable to represent. Nevertheless, most of them are present in the indicated literature, which brings a detailed description and discussion of the characters.

In the analysis of the cladogram below (Fig. 12), it is possible to realize that the two basal branches (Patellogastropoda and Cocculiniformia) have opercula only during the larval phase. It is, then, lost after metamorphosis. The operculum becomes an adult structure in the Orthogastropoda after the cocculiniform branch. The high multispiral operculum appears to be the most basal one. In the following branch, Vetigastropoda, the high multispiral operculum is almost a rule; it evolved to a low multispiral conformation in some taxa (e.g., *Gaza*), while some few ones lost it at all (e.g., haliotids and stomatellines). The Neritimorpha have a low multispiral or paucispiral operculum, with reductions in few taxa (e.g., *Septaria*). The neritimorph operculum is characteristically calcareous and complex, however, a preliminary analysis of the neritimorph branches suggests that the terrestrial forms, such as the helicinids, tend to reduce opercular complexity, with some branches having a pure corneous, paucispiral operculum (Simone, 2018).

The Apogastropoda have the low multispiral operculum as a basal form, which was further modified in its all branches. Among the Heterobranchia, the operculum is present only in the basal taxa, and the main modification is its loss, which occurred throughout in its internal branches. In the acteonimorphs, the operculum is more persistent and varies from low multispiral to paucispiral. In eupulmonates, which has a neotenic origin (Simone, 1995, 2011), the operculum is only present in the basal Amphibolidae. Within the Caenogastropoda, the basal Ampullarioidea and Viviparoidea have an enigmatic excentric operculum. No other kind of operculum is known in these superfamilies, and its evolutionary pathway is a mystery (Simone, 2004a). Some Cerithioidea acquired paucispiral and even unguiculate opercula, such as, e.g., the cerithiids (Simone, 2001). The paucispiral operculum is a synapomorphy of the Strombogastropoda, which was modified to an unguiculate type in most Stromboidea, its first branch (Simone, 2005). In the following branch, the



12. Morphology-based gastropod phylogeny, mostly based on Simone (2011), showing different types of opercula as indicated by the colors (see text for details). The survey is not exhaustive.

Calyptraeoidea, several lineages lost the operculum, as they evolved to limpet, or limpet-like forms (Simone, 2002, 2018a). The Naticoidea have characteristically a paucispiral operculum, being reduced in the Sininae (Simone, 2011). The Cypraeoidea, in contrast, have the loss of the operculum as synapomorphy (Simone, 2004b). The Peogastropoda have a characteristic unguiculate operculum. Some internal branches have reduced or lost the operculum, such as, e.g., Ficidae and several Tonnidae within Tonnoidea; Conidae and some Terebridae in Conoidea; and several stenoglossans like Marginellidae, Cancellariidae, Mitridae, Costellariidae, and several Volutidae. Another interesting stenoglossan modification is the excentric operculum, found in several Muricidae, Buccinidae, etc.

As the evolution of the calcareous operculum is independent of its type, the presence of the calcareous layer is represented in another (gold) color in Fig. 12, placed alongside the represented branch. However, the calcareous form is much more common in multispiral and paucispiral opercula, being rare elsewhere. For example, *Pila*, an ampullariid, has a calcareous excentric operculum, while *Fasciolaria*, a fasciolariid stenoglossan, has an unguiculate calcareous operculum. The Vetigastropoda have calcareous opercula in, e.g., turbinids and phasianellids. The Neritimorpha have most of its marine (e.g., *Nerita, Neritina*) and part of the terrestrial forms with a calcareous operculum, which was lost in some terrestrial lineages as discussed above. The Cyclophoroidea also have some branches with a calcareous operculum, such as *Cyclophorus, Cyclotus, Neocyclotus*, etc. The Rissoidea, which includes the littorinoideans (Simone, 2006, 2011), have calcareous opercula in some terrestrial forms only, like the pomatiids. The evolution of the operculum in Naticoidea is interesting as reported above, with the calcareous operculated taxa located in the middle of the tree (Simone, 2011); its basal taxa have a corneous operculum, which evolved into a calcareous one, and returned to the corneous state, culminating in a reduction in terminal branches like the sinines.

Of course, the presented opercular survey is not thorough, as several exceptions exist in all branches. The intention is to present the typical opercula conformations of each main branch and the opercular evolution as a whole.

7. Discussion

The operculum is, thus, an important structure in several aspects, from the animal's survival to its interpretation for comparative studies. As referred to above, the operculum is only surpassed by the shell in taxonomic importance, and has been usually described and presented even in dry samples.

The present survey describes the most important issues regarding the operculum, but several additional patterns can be evoked, mainly when differentiating gastropods at the species level. The many references cited above are rich in examples in which the operculum was useful to differentiate gastropod species, genera, and families.

Acknowledgements

Thanks to Daniel C. Cavallari, FFCLRP-USP, for several suggestions. I am also grateful to Ana Paula S. Dornellas for Fig. 8; and Gijs Kronenberg for Fig. 11C.

References

Abbate, D & Simone, LRL, 2015. Review of *Pugilina* from the Atlantic, with description of a new species from Brazil (Neogastropods, Melongenidae). African Invertebrates 56(3): 559-577.

Abbate, D; Simone, LRL & Cavallari, DC, 2018. Anatomy of *Engoniophos unicinctus* from Isla Margarita, Venezuela (Gastropoda: Caenogastropoda: Nassariidae), with a discussion on the buccinid-nassariid relationship. Nautilus 132(3-4): 101-112.

Bieler, R & Simone, LRL, 2005. Anatomy and morphology of *Stephopoma nucleogranosum* Verco, 1904 (Caenogastropoda: Siliquariidae) from Esperança Bay, Western Australia. IN Well, FE; Kalker, DI & Kendrick, GA [eds] The marine flora and fauna of Esperance, Western Australia. Western Australian Museum. Perth, pp 159-175.

Cavallari, DC & Simone, LRL, 2018. A new species of *Calliostoma* (Vetigastropoda: Calliostomatidae) from Canopus Bank, off northeastern Brazil. Zootaxa 4457(1): 156-166.

Checa, AG & Jiménez J, AP, 1998. Constitutional morphology, origin, and evolution of the gastropod operculum. Paleobiology 24(1): 109-132.

Dornellas, APS & Simone LRL, 2020. Detailed anatomy of *turbo petholatus* (Vetigastropoda: Trochoidea: Turbinidae) and its implications for turbinid systematics. Vita Malacologica 19: 20-29.

Parker, GH, 1922. The leaping of the stromb (*Strombus gigas* Linn.). Journal of Experimental Zoology 36(2): 205–209.

Ponder, WF & Lindberg, DR, 1997. Towards a phylogeny of gastropod molluscs: an analysis using morphological characters. Zoological Journal of the Linnean Society 119: 83-265.

Simone, LRL, 1995. *Rissoella ornata*, a new species of Rissoellidae (Mollusca: Gastropoda: Rissoelloidea) from the southeastern coast of Brazil. Proceedings of the Biological Society of Washington 108(4): 560-567. http://www.moluscos.org/trabalhos/1995/Simone%201995-Rissoella.pdf

Simone, LRL, 2001. Phylogenetic analyses of Cerithioidea (Mollusca, Caenogastropoda) based on comparative morphology. Arquivos de Zoologia 36(2): 147-263. http://www.moluscos.org/trabalhos/2001/Simone%202001%20Cerithioidea.pdf

Simone, LRL, 2002. Comparative morphological study and phylogeny of representatives of the superfamily Calyptraeoidea (including Hipponicoidea) (Mollusca, Caenogastropoda. Biota Neotropica 2(2): 1-137.

Simone, LRL, 2004a. Comparative morphology and phylogeny of representatives of the superfamilies of architaenioglossans and the Annulariidae (Mollusca, Caenogastropoda). Arquivos do Museu Nacional 62(4): 387-504. http://www.moluscos.org/trabalhos/2004/Simone%202004%20-%20Architaenio%20phyl.pdf

Simone, LRL, 2004b. Morphology and phylogeny of the Cypraeoidea (Mollusca, Caenogastropoda. Papel Virtual. Fapesp. São Paulo, 186 pp. http://www.moluscos.org/trabalhos/2004/Simone%202004%20-%20Cypraeoidea.pdf

Simone, LRL, 2005. Comparative morphological study of representatives of the three families of Stromboidea and the Xenophoroidea (Mollusca, Caenogastropoda), with an assessment of their phylogeny. Arquivos de Zoologia 37(2): 141-267. http://www.moluscos.org/trabalhos/2005/Simone%202005-Stromboidea.pdf

Simone, LRL, 2006. Accounts on the phylogeny of the Rissooidea (=Hydrobioidea) and Littorinoidea, based on some American representatives, as base for a future taxonomic revaluation (Mollusca, Caenogastropoda). Strombus 13(2): 18-26. http://www.moluscos.org/trabalhos/2006/Simone%202006%20Rissooidea%20Phylogeny.pdf

Simone, LRL, 2011. Phylogeny of the Caenogastropoda (Mollusca), based on comparative morphology. Arquivos de Zoologia 42(4): 161-323. http://www.moluscos.org/trabalhos/Caenogastro/Simone%202011%20Caenogastropoda%20Phylogeny.pdf

Simone, LRL, 2018a. Main processes of body modification in gastropods: the limpetization. Malacopedia 1(4): 23-36. http://www.moluscos.org/trabalhos/Malacopedia/01-04%20Simone%202018%20Malacopedia%20Limpetization.pdf

Simone, LRL, 2018b. Main processes of body modification in gastropods: the limacization. Malacopedia 1(3): 12-22. http://www.moluscos.org/trabalhos/Malacopedia/01-03%20Simone%202018%20Malacopedia%20limacization.pdf

Simone, LRL, 2018. Phenotypic features of *Helicina variabilis* (Gastropoda: Neritimorpha) from Minas Gerais, Brazil. Papéis Avulsos de Zoologia 58: e20185832. DOI 10.11606/1807-0205/2018.58.32.

Simone, LRL & Cunha, CM, 2006. Revision of genera *Gaza* and *Callogaza* (Vetigastropoda, Trochidae), with description of a new Brazilian species. Zootaxa 1318: 1-40.