

Main processes of body modification in gastropods: the lateralization

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Abstract

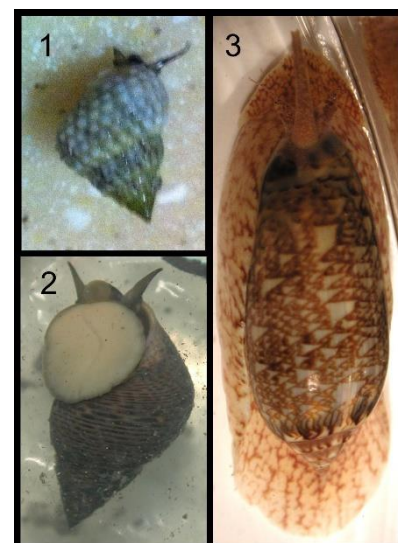
Lateralization is the evolutionary event that happened in some gastropod lineages, resulting in rather cylindrical shells with an anteroposteriorly elongated aperture situated in the lateral-right side of the shell (from which the name is derived). It can be didactically divided into 2 degrees; degree 1 shells have an exposed apex, while degree 2 shells have an entirely covered (or internalized) apex. An analysis of the reasons behind lateralization and its morpho-anatomical modifications are addressed, mainly regarding the pallial organs, head-foot and anterior end of the visceral mass. A brief discussion on the incidence of lateralization in the gastropod phylogeny is also presented, showing convergences in some higher taxa of both heterobranchs and caenogastropods. DOI: 10.13140/RG.2.2.28474.24005

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Introduction

Lateralization is the common name of an evolutionary event that happened in some gastropod lineages. It results in cylindrical shells, which have an elongated aperture that reaches the upper (and oldest) whorls, sometimes even covering them completely. The name was introduced elsewhere (Simone, 2011) and is derived from the lateral position of the aperture (Fig. 3), which is situated anteriorly in non-lateralized gastropods (Figs. 1-2). Lateralization also results in interesting inner anatomical modifications, which are concisely explained below.

1-3. Examples of crawling gastropods: **1-2**, littorinids, typically non-lateralized snails; **1**, *Cenchritis muricatus* from Barbados (MZSP; L~20 mm). **2**, *Littoraria angulifera* from Florida (MZSP, L~26 mm); **3**, *Americoliva circinata* from Ilhabela, SP, Brazil, a typical lateralized snail (MZSP, L~45 mm).



Ordinary gastropod shells usually have a rounded aperture situated anteriorly (Figs. 1-2). Most of the remaining shell structures are posterior to the aperture, and normally perform a conical spire, turned posteriorly and slightly to the right when the animal is crawling (Fig 1). A lateralized gastropod shell normally has a more cylindrical shape, with an elongated aperture situated along the lateral-left side of the shell; the apex, on the other hand, is situated practically directly aligned with the posterior region of the active animal (Fig. 3). Needless to say, it is assumed that lateralization only occurred in lineages that had coiled shells, to begin with. The many consequences of lateralization are explored herein, mainly concerning outer and inner somatic modifications, which occurred independently in several gastropod branches.

Why does one become lateralized? Consequences.

The possible evolutionary reasons behind lateralization are only speculative, as apparently this phenomenon has only been recently evidenced, and obviously, no experimental procedure has been carried out yet. Lateralized gastropods are mostly found digging into unconsolidated substrates, such as sandy and muddy bottoms. A more cylindrical shell looks better adapted to these environments, as it exerts less friction, which would reduce the drag during digging.

Another possible positive consequence of lateralization is the narrowing of the apertural space, which normally becomes anteroposteriorly elongated and narrower if compared to the rounded apertures of non-lateralized snails. A narrow aperture seems to be more difficult to be violated by a predator, and is thus a more efficient barrier. This could explain why lateralized snails rarely bear an operculum, as is the case for olivids, most volutids, etc., or have a reduced operculum, e.g., in conids, cassids, strombids, etc.

The lateralization event that results in the migration of the aperture towards the shell apex is followed by internal modifications such as the ones explored below. Beyond a narrow, flattened head-foot, the organs of the pallial cavity and the anterior portion of the visceral mass are the most affected by these modifications.

Degrees of lateralization

Starting from a current snail (Figs. 1-2, 4), the lateralization process may be didactically divided into different degrees, as follows.

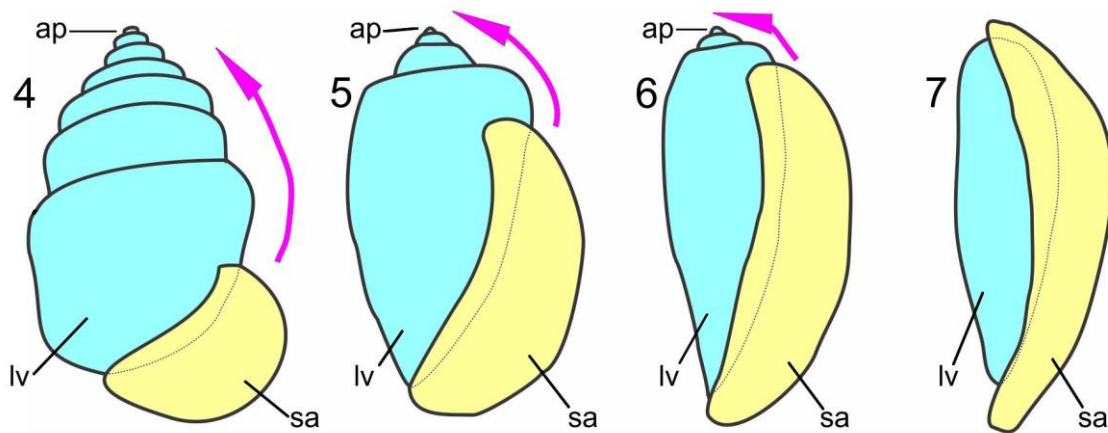
Lateralization degree 1 – superior region of peristome slightly separated from shell apex, keeping it still exposed (Figs. 5, 6):

In degree 1 lateralized shells, the shell apex is still exposed or visible. The peristome, particularly its superior region near the preceding suture, is sharply angulated and remains separated from the apex, not covering it or any part of the spire at all.

Lateralization degree 2 – involute shells (Fig. 7):

In degree 2 lateralized shells, the apex is not exposed or visible since the peristome migrated upwards, covering it completely. The shell is, then, called involute because the youngest

whorls successively cover the preceding ones and only the peristome and the last whorl are externally visible. The shell spire becomes internalized, embedded, replacing the columellar axis of the shell coiling.



4-7. Degree of lateralization. Shell 4, ordinary not lateralized shell; 5-6, degree 1 lateralized shell, apex and spire exposed; 7, degree 2 lateralized shell, a.k.a., an involute shell (apex internalized). legends: ap, apex; lv, last (body) whorl; sa, aperture.

Of course, this classification is not absolute, as several taxa can be intermediary or have a doubtful ranking. A notorious group are the cowries of the family Cypraeidae (Fig. 10), which are mostly in the borderline between the above-mentioned degrees.



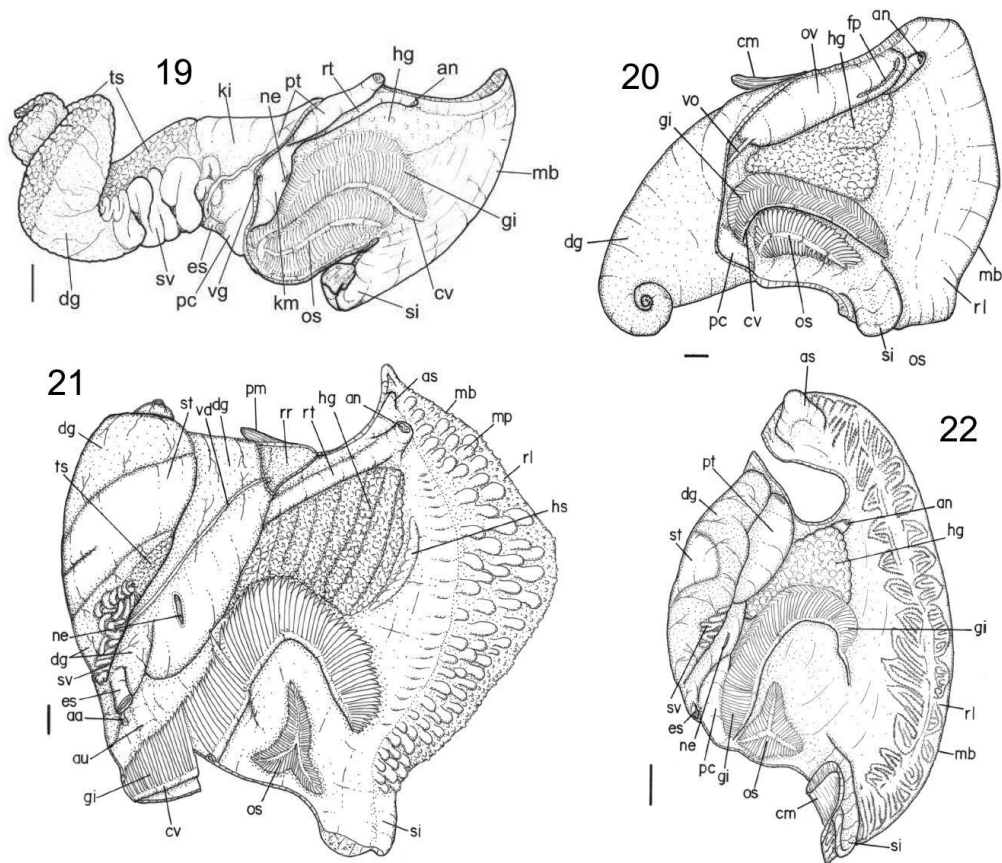
8-18. Examples of shells of species with different degrees of lateralization, above cypraeoideans, below heterobranchs. Figs. 8, 12, 13: no lateralization; 9, 10, 14, 15, 16: degree 1 of lateralization; 11, 17, 18: degree 2 of lateralization. 8, *Velutina velutina* (France, 17 mm); 9, *Erato panamensis* (W Panama, 6 mm); 10, *Erosaria acicularis* (Brazil, 26 mm); 11, *Pseudocyphoma intermedium* (Brazil, 20 mm); 12, *Otopleura nitida* (Philippines, 10 mm); 13, *Crenilabium birmani* (Brazil, 8 mm); 14, *Mysouffa cumingii* (Brazil, 20 mm); 15, *Acteocina* sp (Brazil, MZSP, 5 mm); 16, *A. candei* (Brazil, BMNH, 4 mm); 17, *Cylichnella bidentata* (Cuba, BMNH, 2 mm); 18, *Bulla occidentalis* (Brazil, 27 mm). most courtesy Femorale (except if collection acronym indicated).

The Figures above (Figs 8-18) show examples of shells of species belonging to groups in which the lateralization took place, notoriously the Cypraeoidea (upper row) and the Heterobranchia (bottom row). There is no intention of predicting any phylogenetic inference in this sequence,

but at least in cypraeoideans this tendency was really detected. A phylogenetic analysis of a cypraeoideans sample was performed by Simone (2004, 2011), and, there, a tendency toward lateralization was detected along the cladogram. The basal taxa are not lateralized (Fig. 8), one of the top taxa – ovulids – have degree 2 lateralization (Fig. 11), and taxa with the intermediary degree 1 (Figs. 9, 10) are located between them in the resulting topology.

In heterobranchs, the basal taxa are not lateralized (Figs. 12, 13), and two main processes appear to be present in this clade: the reduction/loss of the shell (see Simone, 2018), and the lateralization, culminating in the bullomorph cephalaspideans and allies. In that branch, some taxa are clearly lateralized, but with shell apex still exposed (Figs. 14, 15, 16), while in others the shell apex is embedded by part of the body whorl and peristome (Figs. 17, 18).

Anatomical modifications of lateralization



19-22. Pallial cavity roof (ventral-inner view) and visceral mass in species with different degrees of lateralization. **19**, non-lateralized *Zemira australis*, male, scale= 1 mm (from Simone, 2007); **20**, lateralized degree 1 *Hesperato maugeriae*, female, scale= 0.25 mm; **21**, lateralized degree 1 *Macrocypraea zebra*, scale 5 mm; **22**, lateralized degree 2 *Cyphoma signatum*, male, scale= 2 mm (all 3 from Simone, 2004). Legends: aa, anterior aorta; an, anus; as, anal siphon; au, auricle; cm, columellar muscle; cv, ctenidial vein; dg, digestive gland; es, esophagus; fp, female pore; gi, gill; hg, hypobranchial gland; hs, pallial septum; ki, kidney; km, membrane between kidney and pallial cavity; mb, mantle border; mp, mantle papillae; ne, nephropore; os, osphradium; ov, pallial oviduct; pc, pericardium; pm, branch of columellar muscle; pt, prostate; rl, right lobe of mantle border; rr, anterior caelomatic area of visceral mass; rt, rectum; si, siphon; st, stomach; sv, seminal vesicle; ts, testicle; vd, vas deferens; vg, visceral ganglion; vo, visceral oviduct.

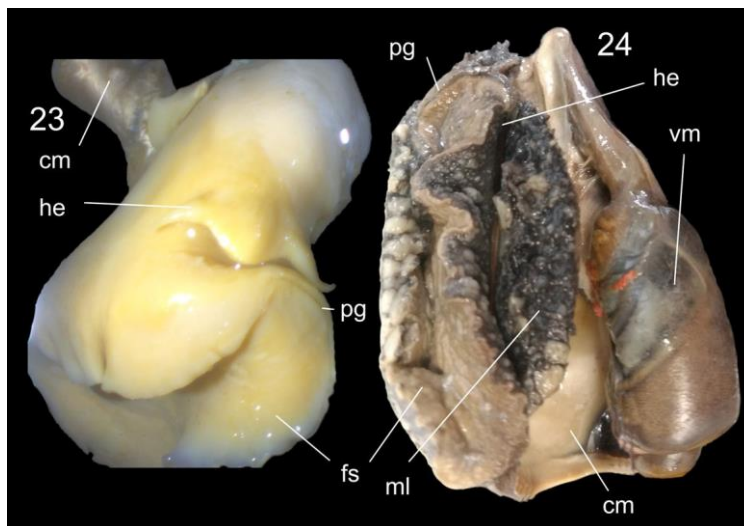
One of the main modifications in the lateralization process is shown in the Figures above (Figs. 20-22). It refers to the displacement of the pallial and anterior visceral mass structures. If

compared to a non-lateralized taxon (Fig. 19), the organs of the pallial cavity are situated closer to each other and more anteroposteriorly. Particularly the osphradium (os), the gill (gi) and the rectum (rt) are closer to each other and slightly aligned horizontally (in that view). In taxa with different degrees of lateralization, these organs become spread (Figs. 20-21), culminating with those of the degree 2 (Fig. 22), in which these structures are separated by wide spaces, mainly in the anterior region. These modifications resemble what happens with stems of a hand fan when it is opened. The analysis of the evolution of these characters is precluded in the heterobranchs, since their pallial organs are greatly modified, and are too distinct among lineages to be compared. An example is the gill, which is mostly absent in heterobranchs (from which the name is derived). The gill, at least in lateralized caenogastropods (Figs. 19-22: gi), becomes more and more curved the more the lateralization process progresses.

The depth and form of the pallial cavity also change in lateralized snails. It becomes shallower in more lateralized forms (Figs. 21-22). However, the shown examples (Figs. 20-22) are cypraeoideans, which possess the mantle border modified in lobes (rl) that expand over the aperture, reaching the dorsal region of outer shell surface, and producing a shining, porcelaneous outer surface. Letting aside the wide flap of the mantle lobe, it is possible to verify that the pallial cavity as a whole is shallower and more curved in the lateralized taxa.

The anterior region of the visceral mass is also slightly displaced in lateralized forms. The more lateralized the snail is, the more anteriorly dislocated its right side becomes. A triangular region of the anterior end of the visceral mass encroaches the right side of the pallial cavity (Figs. 20-22) in lateralized forms. Consequently, the pericardium (pc) and the kidney (ki, ne) are dislocated closer to the mantle border. The rectum (rt), for instance, becomes short; and the anus (an) is normally siphoned. The superior (in Figs) pallial structures are situated on the right side in non-lateralized forms (Fig. 19), but they are more posteriorly located in lateralized taxa (Figs 20-22).

The displacement of the anterior region of the visceral mass is particularly noticeable in

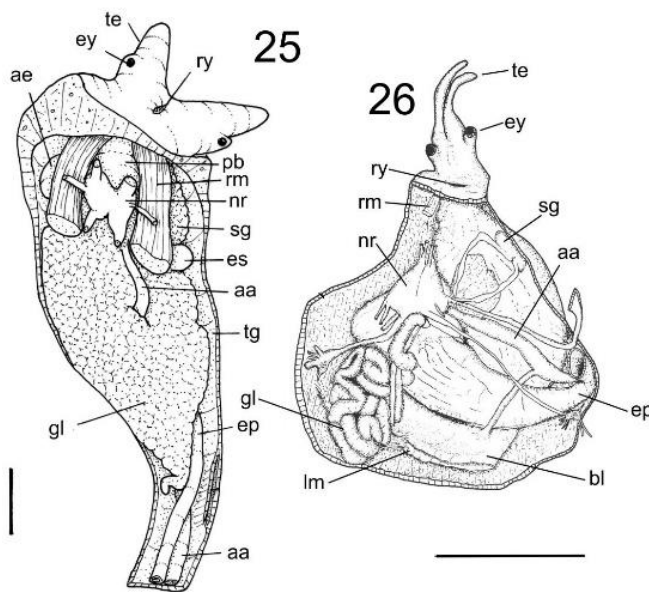


23-24. Modifications of head-foot in lateralization process. 23, isolated head-foot of *Buccinanops gradatus*, frontal view, showing transverse bowed way of foot retraction of non-lateralized forms (MZSP 53201; L ~30 mm); 24, whole specimen of *Macrocypraea* sp just extracted from shell, ventral view, showing longitudinal groove way of foot retraction (fs) (MZSP 137546; L ~100 mm). Lettering: cm, columellar muscle; fs, foot sole; he, head; ml, mantle lobe; pg, pedal gland anterior furrow; vm, visceral mass.

the reno-pericardial structures. The kidney is normally very long and flattened in lateralized forms, functioning as a right-posterior wall of the pallial cavity. The pericardium (pc), on the other hand, is also usually dislocated anteriorly and to the right, becoming dorsal to the posterior region of the gill. In some taxa such as some cypraeoideans (Figs. 21-22) and marginellids, the connection of the auricle (Fig. 21: au) and the ctenidial vein becomes subterminal, and the posterior-terminal portion of the ctenidial veins have an opposite, anteroposterior blood flow.

The whorls of the visceral mass obviously follow the modifications of the shell's spire in the lateralization process. The first coils of the visceral mass become more and more embedded in more lateralized taxa (Fig. 24: vm). The pinnacle of this state is found in degree 2 forms, in which each successive coil covers the preceding ones completely, and the first whorl is not exteriorized (Fig. 22: dg).

Another modification detected in lateralized forms is the way the foot bends during withdrawal (Figs 23-24). In non-lateralized taxa, the foot usually bends transversally during withdrawal (Fig. 23: fs). In lateralized form, the way the foot retracts changes to a longitudinal bending, forming a wide longitudinal groove (Fig. 24: fs). The way the foot retracts in lateralized taxa keeps the foot sole exposed, and the posterodorsal region of the foot seldom bends itself (Fig. 24). That region usually bears the operculum, which requires the posterior foot bending to work as an apertural lid. This may be the reason why most lateralized forms lack an operculum.



25-26. Modifications of head-foot in lateralization process – the haemocoel connection to visceral mass. **25**, non-lateralized *Trophon geversianus*, haemocoel, ventral view, foot and columellar muscle removed, scale= 2 mm, connection with visceral mass posterior (ep); **26**, same for *Leptegouana guttata*, a lateralized marginellid, connection left (right in Fig.: ep), scale= 5 mm (Both from Souza & Simone in press). Lettering: aa, anterior aorta; ae, accessory salivary gland; bl, bulb of gland of Leiblein; es, esophagus; ep, posterior esophagus; ey, eye; gl, gland of Leiblein; lm, muscle of gland of Leiblein; nr, nerve ring; pb, proboscis; rm, proboscis retractor muscle; ry, rhynchostome; sg, salivary gland; te, cephalic tentacle; tg, integument.

tively easily done by means of longitudinal cut along the lateral borders of the hemocoel.

Main branches that suffered lateralization.

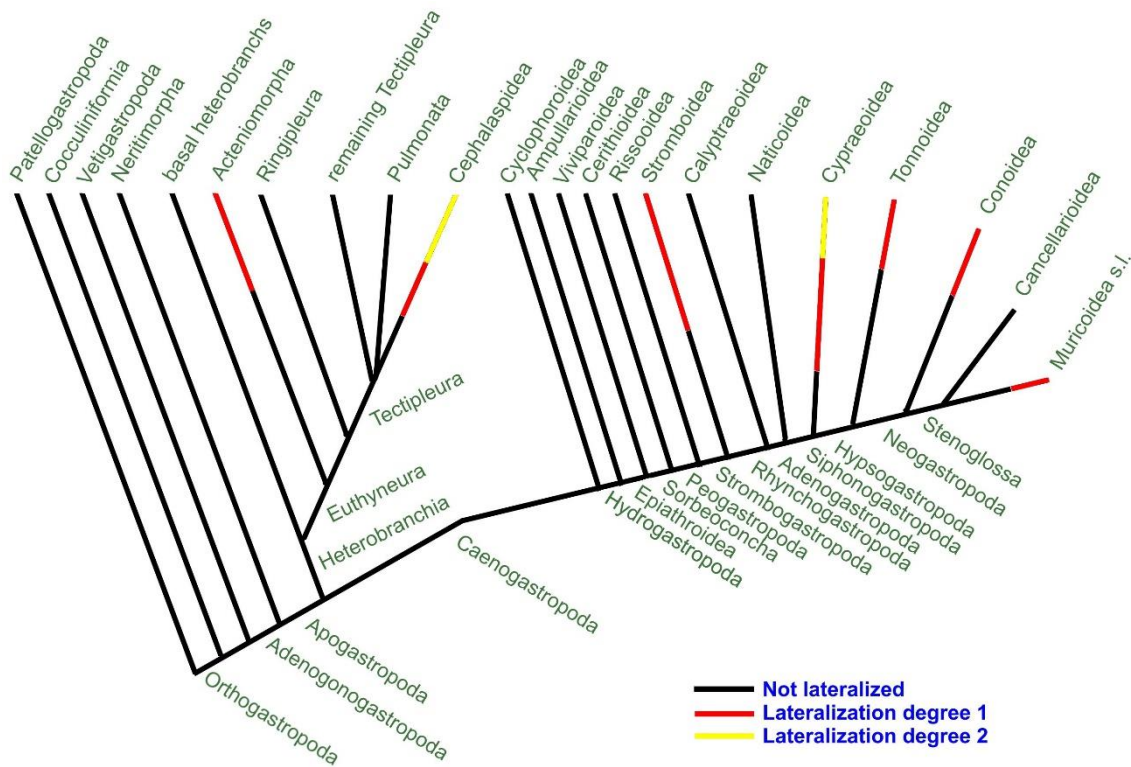
Figure 27 shows an unpretentious cladogram representing the main branches of the gastropod phylogeny in which the lateralization process occurred to any degree. The cladogram is mostly based on Simone (2011), with some information from WoRMS.

It is interesting to notice that the lateralization process is convergent in several gastropod lineages (Fig. 27, yellow and red lines). It is, however, absent in more basal taxa in Gastropoda as

Another common modification of lateralized taxa is the connection between the head-foot and the visceral mass (Figs. 25-26). In non-lateralized forms, the connection is posterior (Fig. 25), the head-foot hemocoel is, then, anteroposteriorly elongate and slightly fusiform. On the other hand, in lateralized forms (Fig. 26), the head-foot hemocoel has a barely triangular form, and its connection with visceral mass is strongly bent to left. In Figs. 25-26, the connection to the visceral mass is indicated by “ep”, posterior esophagus, which runs directly toward the stomach in the visceral mass.

The best way to check this head-foot modification is by removing the foot and adjacent columellar muscle from the dorsal integument that covers the hemocoel (Figs. 25-26, as ventral views). This is rela-

a whole and within both main derived branches, the Heterobranchia and Caenogastropoda. This may indirectly indicate that lateralization is a derived specialization.



27. An unpretentious cladogram of Gastropoda, mostly based on Simone (2011) and WoRMS, showing important taxa that suffered lateralization during evolution. Black lines represent non-lateralized taxa; remaining color as indicated in bottom-right of the figure. The survey is not exhaustive.

In the Heterobranchia, the Acteniomorpha, some branches have lateralized groups, mainly in the family Acteonidae (degree 1). However, the peak of lateralization occurred along the Cephalaspidea grade. The cephalaspidean phylogeny is still obscure, so, any internal analysis is precluded, but it seems quite possible that lateralization evolved more than once in this taxon, and reached degree 2 several times independently. The bulloid shell, giving the name Bullomorpha, which is sometimes used for the group, is the rule in cephalaspideans. This kind of shell is greatly involute and easily classifiable as degree 1 and even degree 2. Some examples are the Bullidae (Fig. 18), and the Retusidae (Fig. 17), but several other examples can be suggested, e.g., haminoeids, aplustrids (considered sometimes Acteniomorpha) and philinids.

Caenogastropoda is another branch rich in lateralized taxa. A remarkable example is the strombids amongst the Stromboidea. However, in highly derived Siphonogastropoda, the lateralization process becomes common. Particularly in Cypraeoidea, the lateralization is almost a rule, absent only in more basal branch, the velutinids (Fig. 8). The family reaches the apothotic degree 2 in the ovulids (Fig 11), with genera possessing extreme involute shells, such as *Calcarovolva*, *Phenacovolva*, and *Volva*. Within the Tonnoidea, lateralization is found in cassids and tonnids, the more derived groups, as well as in ficids, the most basal branch. In Conoidea, lateralization is almost exclusive of the conids. In the Stenoglossa, several branches have an intermediary to high level of lateralization, but always in degree 1. Some notorious examples are the olivids, volutids, vasids, columbellids, mitrids, and costellariids. But the marginellids generally have the highest degree of lateralization, with some genera in the border between degree 1 and 2, such as *Bullata*, *Cryptospira*, and even some *Prunum*.

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