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Main processes of body modification in gastropods: the limacization

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Abstract

Limacization is the evolutive process that transform a snail into a slug. The modifications and implications of this process are exposed and discussed herein, emphasizing the modification of the visceral mass that migrates to the head-foot haemocoel; the pallial structures also have similar modification or disappear. The limacization is divided in 2 levels: degree 1) with remains of visceral mass and pallial cavity in a dorsal hump; degree 2) lacking any vestige of them, being secondarily bilaterally symmetrical. Despite several gastropod branches suffered the limacization process, the degree 2 is only reached by the Systellommatophora and part of the Nudibranchia (doridaceans). Some related issues are also discussed, such as the position of the mantle in slugs, if the slugs have detorsion (they do not have), the absence of slugs in some main taxa, such as Caenogastropoda and the archaeogastropod grade, and the main branches that have representatives with limacization.

Introduction

The process called "limacization" is the transformation of a snail into a slug. The name is derived from the Latin *limax*, meaning slug.

The limacization consists of the evolutionary process of relocation of the visceral mass into a region inside the cephalo-pedal mass, as well as the reduction and even loss of the pallial cavity and its organs. In this course, the structures of those regions tend to be replaced within the head-foot, and the shell becomes from reduced to lost.

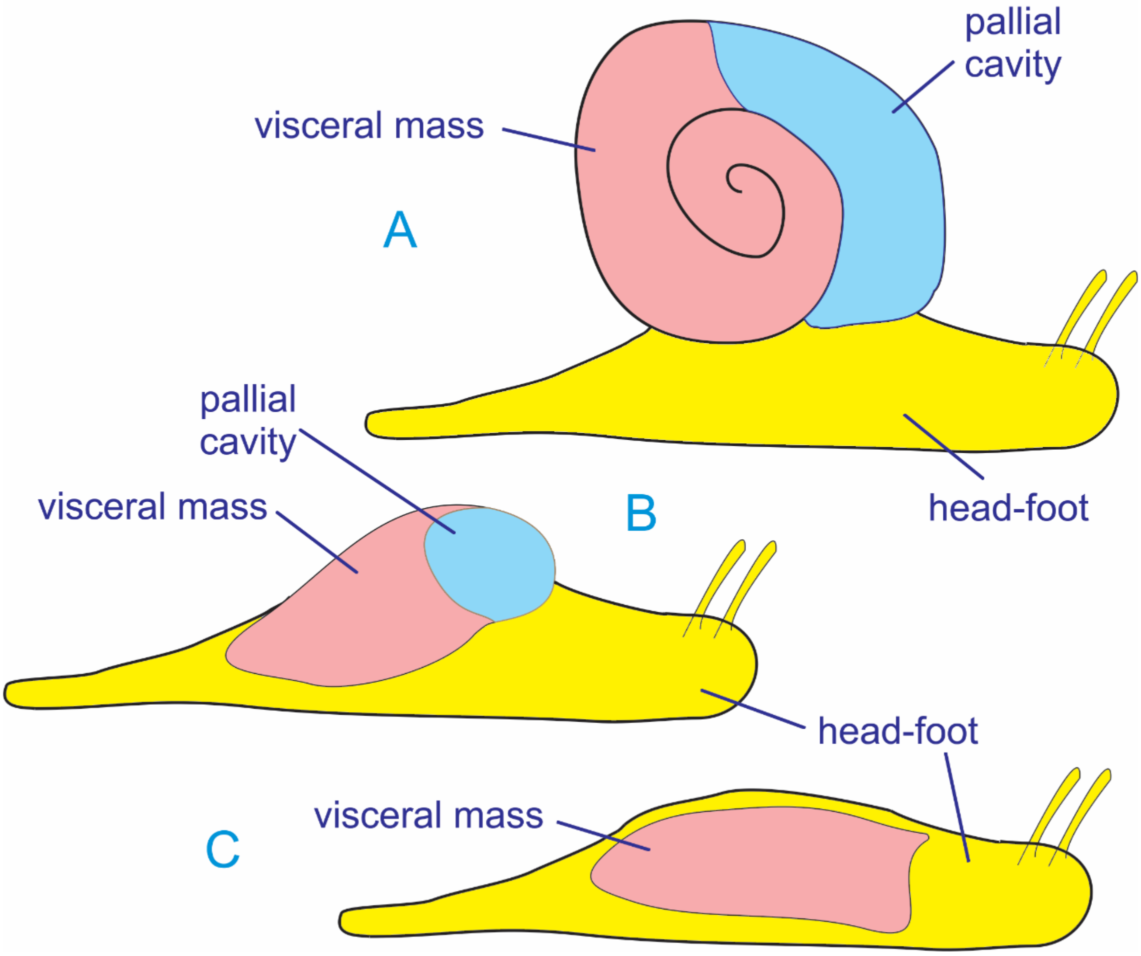
In an unpretentious definition, the limacization is the process of the snail becoming a crawling, isolated head-foot.

The limacization occurred several, independent times in Gastropoda, in all environments. Most of the main branches possess representatives in different degrees towards the slug form, as it is argued more detailed below. However, the apogee of the limacization occurred only in few gastropod taxa, in such the animals become a simple, crawling head-foot mass, lacking any clear visceral or pallial region in an external view, and an apparently bilaterally symmetrical animal. The mantle becomes internal or a small part of the integument, and the shell is totally, sometimes even embryologically, lost.

Why to become a slug? Consequences.

As the shell is an obvious protective structure, the evolution towards the loss of it must be accompanied by other kind of protections. Although camouflage is an important feature, mostly slugs develop chemical defenses ranging from bad taste to mortal poisons, which discourage any fortuitous predator or troublemaker.

A lot of biological effort is dispended for making a shell, so, there is some benefit if the animal can safe this expense. Without a shell, the animal become much more plastic and moldable, fitting in hiding places and exploring sites in such a shelled snail does not fit.



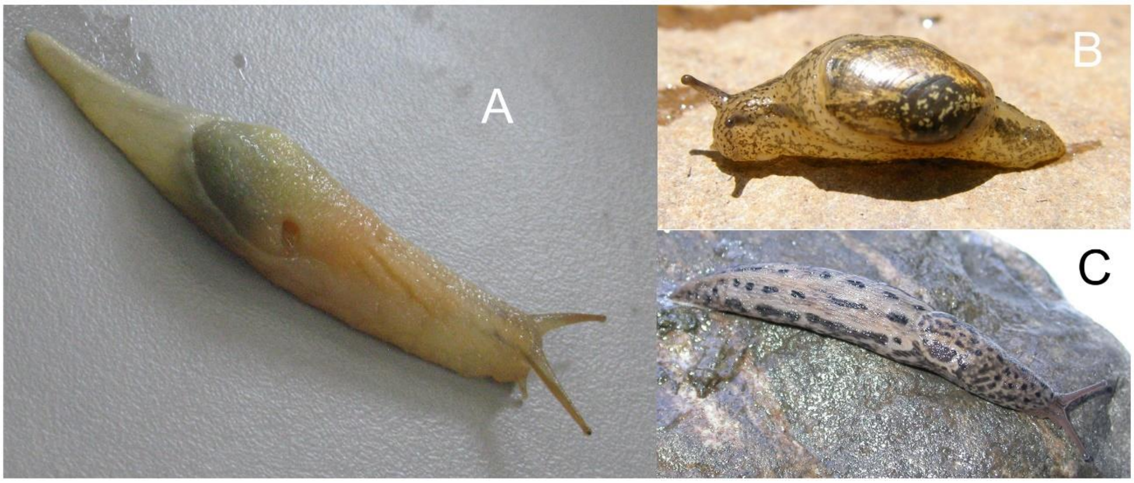
1. Schemes of gastropod organization, showing evolutive modifications from a current snail into a slug. A, current snail with visceral mass and pallial structures inside the shell, head-foot is showing protruded, in activity; B, slug with degree 1 of limacization, in such visceral mass and pallial structures are migrating inside head-foot; C, slug with degree 2 of limacization, with total gathering of visceral structures inside head-foot and loss of pallial cavity.

On the other hand, the limacization process demands a somatic modification to embed the visceral mass and pallial structures, normally delicate organs, inside the head-foot. However, possibly the worse problem is the reduction or loss of respiratory structures like gill and lung. Losing these structures, the respiration must be transferred to the integument and/or expansions that permit the gas exchange, as secondary gills. Gastropod gills and lungs demand a very delicate epithelium, which facilitates the blood contact with the environment (water or air respectively), then they must be placed in a protected cavity like the pallial one. The tegument has the additional function of avoiding injuries and must be hard and resistant. This obviously precludes the respiration, and the slug metabolism must be adequate to this restriction. Some slugs have secondary gills, pseudogills, expansions like cerata, etc., which increases the integumentary surface and its contact which the environment. But these also have the problem in being rustic enough to support the environmental stress. Additional problem is the necessity of humidity to facilitate the respiration, something difficult in a structure permanently exposed to the air in land slugs' integument.

Degrees of limacization

Starting from a current snail, the limacization process may obey intermediary steps as follows:

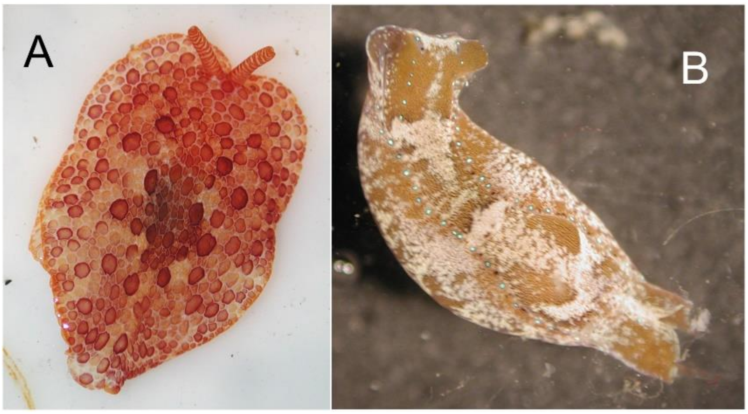
Limacization degree 1: the slug still has external remains of the pallial cavity and the visceral hump. The main somatic form is cylindric, but a dorsal humpback, large to small, is still clearly visible normally in its middle or anterior region.



2. Examples of land slugs with degree 1 of limacization. A, *Peltella palliolum* (L ~50 mm); B, *Omalonyx* cf. *unguis*, semi-aquatic, with shell slightly protruding (L ~30 mm); C, *Limax maximus* (from Simone, 2011, courtesy Gerber) (L ~70 mm).

The Fig. 2 has some examples of land slugs with the degree 1 of limacization, with *Omalonyx* (Fig. 2B) with remains of the shell still visible and partially exposed; while *Limax* has not shell anymore (Fig. 2C), its place is still visible by a small hump in anterior third of the animal. *Peltella* (Fig. 2A) is intermediary.

Similar analogy can be evoked to sea slugs (Fig. 3), in such a small shell is present in *Berthella* (Fig. 3A, dark central region), and only a visceral hump in *Navanax* (Fig. 3B).

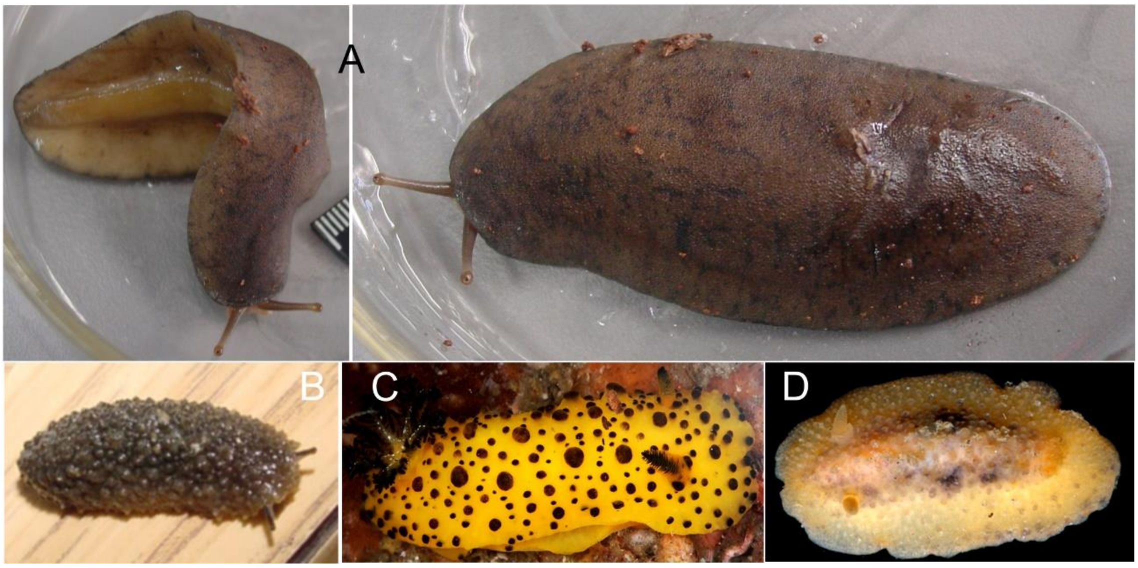


3. Examples of sea slugs with degree 1 of limacization. A, *Berthella agassizii* (L ~30 mm); B, *Navanax gemmatus* (L ~15 mm); both from Ilhabela.

Of course, a total gradation of a complete, ordinary snail to a complete slug can be found amongst gastropod taxa. Then, the limacization degree 1 has a wide range of scopes. But the main point for the degree 1 is to recognize the animal as a slug (not a clear snail), with remains of the visceral or pallial structures still visible on external surface.

Limacization degree 2: the slug totally lacks any vestige of visceral mass or pallial structures in the outer surface. These structures are totally embedded inside haemocoel of head-foot or are lost. The slug lacks any hump and its integument is uniformly smooth.

Only few branches of heterobranchs reached the degree 2 of limacization, notoriously the marine doridacean nudibranchs and the terrestrial systellommatophorans.



4. Examples of sea slugs with degree 2 of limacization. A, *Sarasinula sp* (L ~50 mm), a terrestrial systellommatophoran; B, *Onchidella indolens* (L ~15 mm), a supratidal systellomatophoran; C, *Doris ananas* (L ~20 mm) (from Lima et al, 2016); D, *Doris bovena* (L ~30 mm) (courtesy A. Migotto), both doridacean marine nudibranchs

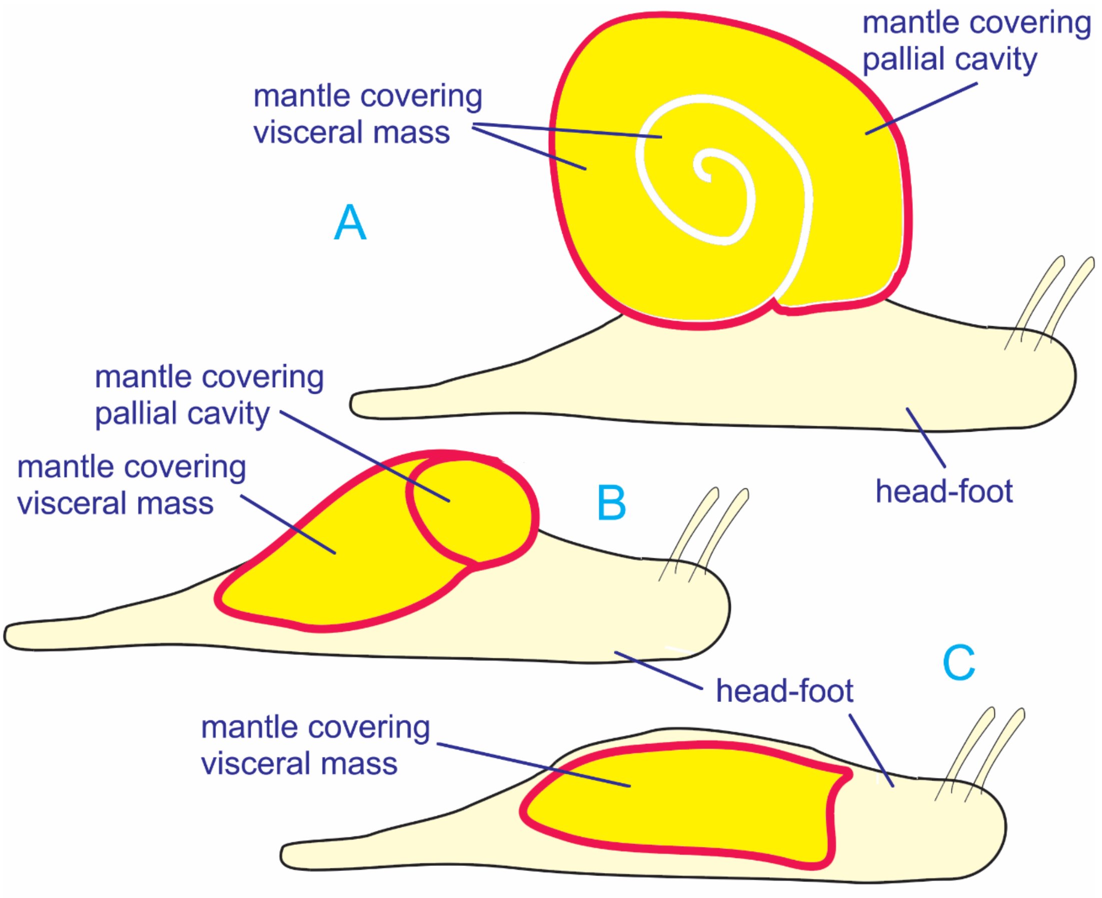
The Fig. 4 shows some examples of groups that reached the degree 2 of limacization, showing no vestige of hump. The Figs. 4A and 4B are Systellommatophora, an example of terrestrial veronicellid *Sarasinula* (4A) and the marine, supratidal onchidiid *Onchidella indolens*. The Figs. 4D and 4D are marine doridacean nudibranchs, showing only a pair of anterior rhinophores, and a posterior tuft of gill surrounding the anus.

As any systematization in Biology, there are lots of exceptions and doubtful cases. Of course, there are taxa that are of difficult categorization. Examples are the aeolidacean nudibranchs (Fig. 5), which in fact belong to the degree 1, but have their body almost totally symmetrical. A minute hump, with the anus placed at right (red arrow in Fig. 5), is normally found in them, denouncing its category.

5. Example of an aeolidacean nudibranch *Spurilla* cf. *neapolitana* (L ~25 mm), red arrow shown small hump with anus at right (bellow in figure).

Another example is the philomycid *Meghimatium pictum*, and allies, a land slug. They look like, but are not close related to the systelommatophorans. They can be considered intermediary between the degree 1 and 2. They have no hump, but in fact still have a small aperture in the right side of the anterior third of their body, working as pneumostome and tailings exit (Gomes et al., 2011: fig. 3C).

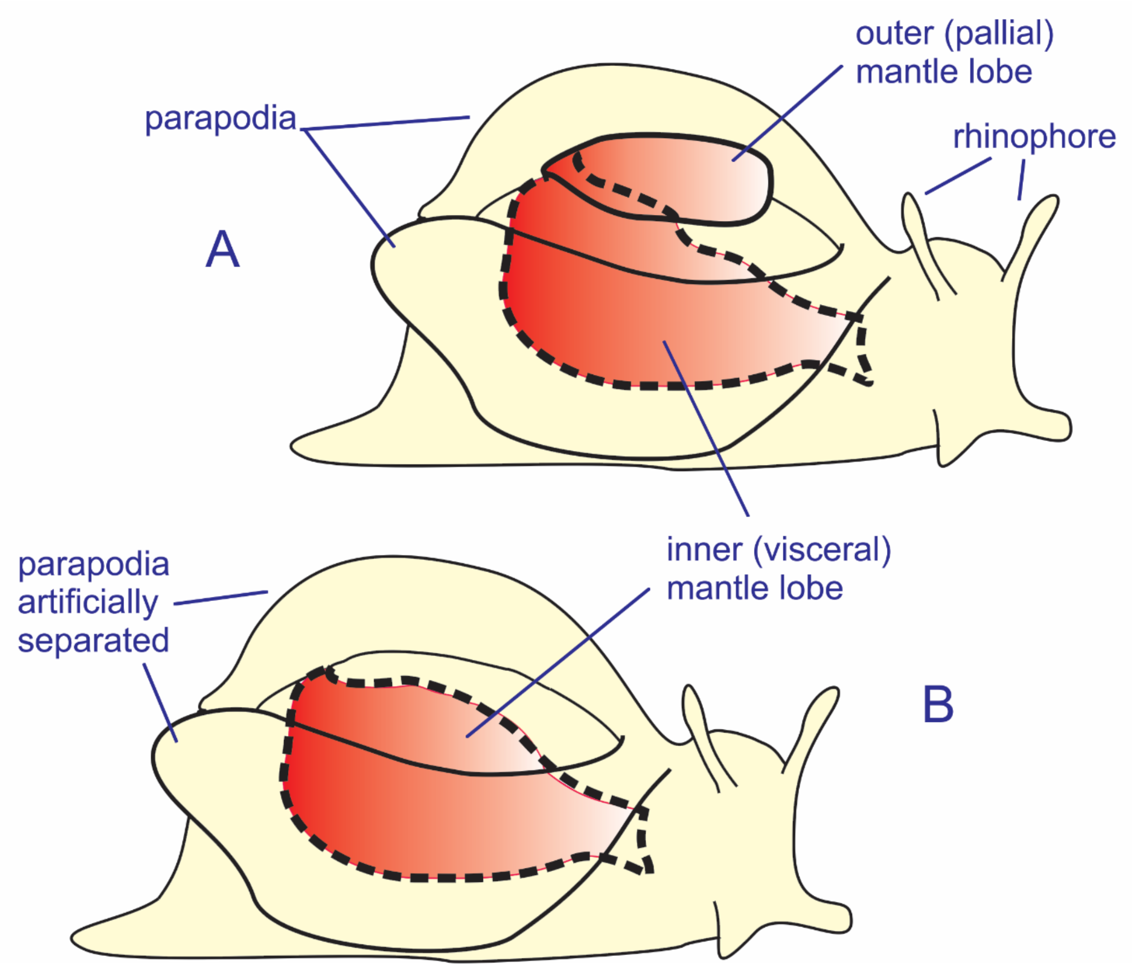
Where is the mantle in slugs?



6. Schemes of gastropod organization, showing evolutive modifications from a current snail into a slug, with special concern to the **mantle** (pink and yellow). A, current snail with mantle covering inner surface of shell, including both, the pallial cavity and the visceral mass; B, slug with degree 1 of limacization, with mantle also covering both regions, partially immersed in head-foot; C, slug with degree 2 of limacization, with remains of the mantle only surrounding the visceral mass totally immersed in head-foot, working as mesentery, not visible outside.

There are some mentions to the mantle in slugs, mainly in doridacean nudibranchs, as the animal's dorsal region, the notum. This is particularly not accurate. The following scheme explains the mantle evolution in limacization:

In some point of view, the first impression is that the mantle is the region surrounding the peristome of the gastropod shells. However, the mantle edge region is only that in such the mantle is thicker. The mantle extends further, entirely covering the inner surface of the shell, surrounding both, the pallial cavity and the entire visceral mass (Fig. 6A). In the limacization process, as told above, both regions migrate into the head-foot, and the mantle surrounding them goes together. In the limacization degree 1, remains of the mantle are visible externally, particularly the region correspondent to the pallial cavity. The region covering the visceral mass migrates deeper inside the head-foot (Fig. 6B). In the limacization degree 2, in such the visceral mass becomes totally immersed into the head-foot, and the pallial cavity disappears, the mantle remains only as a thin membranous layer surrounding the visceral structures, looking like a mesentery (Fig. 6C). In this way, no mantle is visible externally in systelommatophorans and in doridacean nudibranchs. Of course, a portion of the internal mantle of these taxa remain attached to the dorsal region of the integument, marking the point in such the mantle was interiorized in the evolution or in the embryogenesis.



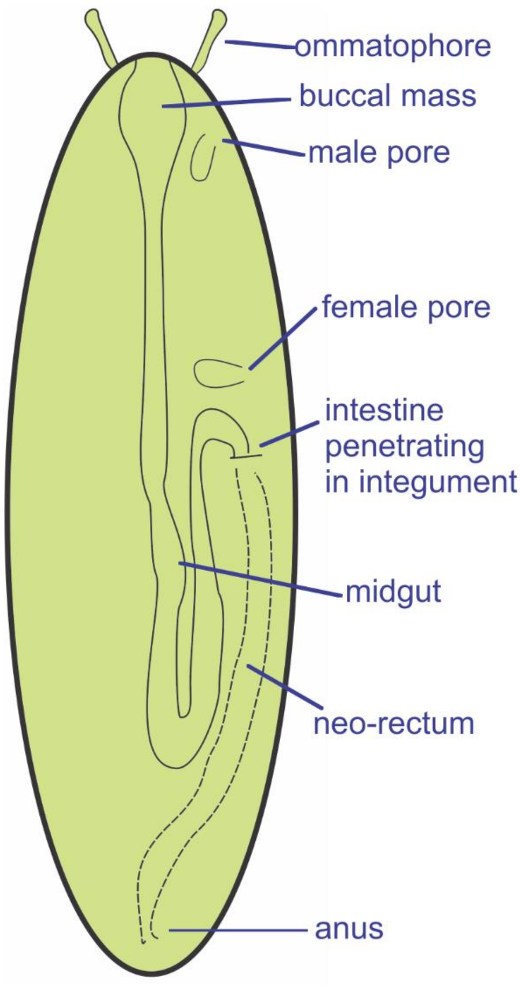
7. Schemes of Aplysiidae species, with special concern to the mantle (red). A, species in such there is an external visceral hump and pallial cavity protected by vestigial shell; B, species in such the visceral hump is embedded into head-foot, lacking shell and pallial cavity, the parapodia is fused dorsally, and are artificially sectioned.

The above scheme of evolution of the mantle in limacization process is also clear in Aplysiidae. This family has genera in such a small shell protecting an external visceral hump, and a pallial cavity, is present (Fig. 7A), as, e.g., *Dolabella*, with calcified shell, and *Aplysia*, with scanty-calcified shell. But it also has genera in such the shell was lost and the visceral hump is totally embedded inside head-foot, as, e.g., *Bursatella* and *Stylocheillus* (Fig. 7B).

The aplysiids that lost their shells clearly have the mantle surrounding the visceral mass located inside the head-foot's haemocoel, visible only in dissection. The mantle is attached to the body wall in same region in such the shell-bearing aplysiids have the shell, showing a correspondence of the region of pallial interiorization (Fig. 7B, small superior beak in red part). The parapodia of these aplysiids are normally fused with each other dorsally, keeping an anterior and a posterior aperture in such the water flows, ventilating the gill. The presence of external pallial structures precludes the inclusion of these aplysiids in the degree 2 of limacization, remaining in the limit of the degree 1.

Have slugs a detorsion?

No, they have not.



8. Scheme of a current Systellommatophora with special concern in digestive tubes, showing penetration of intestine in integument, originating a neo-rectum.

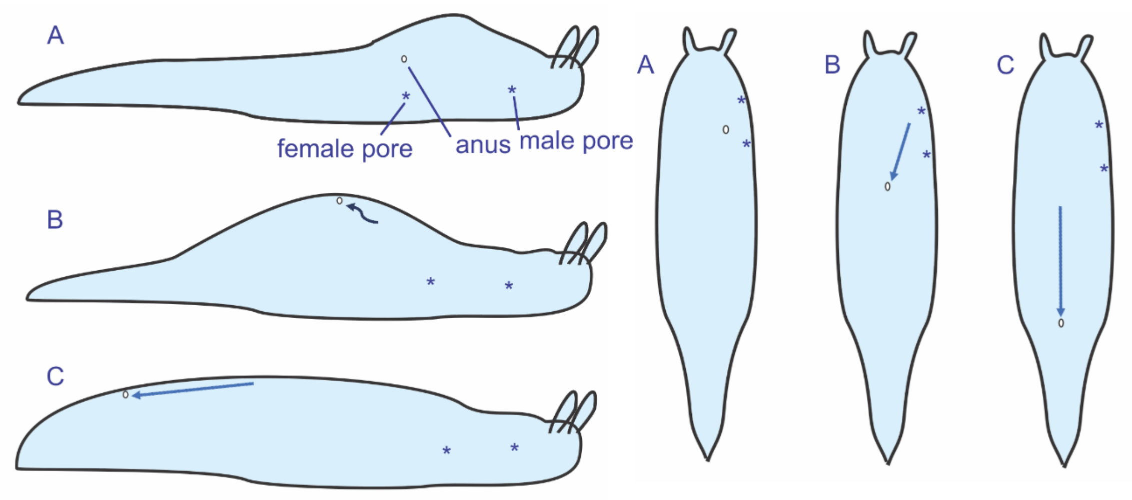
The torsion is regarded as one of the more important synapomorphy of the Gastropoda (Simone, 2011, and references therein), and it was not reverted in any group. There is a belief in which some heterobranchs are distorted, possibly because of their bilateral appearance, and anus placed in posterior region of the animal's body (Wägele & Willian, 2000).

The apparent detorsion is found in those taxa that suffered a limacization degree 2. In the case of the Systellommatophora (Fig. 8), the slugs have a total bilateral shape, with the anus placed in the ventral region of posterior end. However, investigating their internal anatomy, it is possible to realize that the genital pores are located in the right-anterior region, as far as the remaining gastropods. The hindgut, on the other hand, also goes to the right side, being notorious the penetration of the intestine into the integument, normally at middle level of the right side (Fig. 8). From this region the rectum gradually runs towards median and posterior totally immersed in the integument, ending in the median-posterior anus. This passage of the rectum in the integument can be called as neo-rectum, as its histological constitution is different from the current digestive tubes (Thomé & Lopes, 1973).

In this point of view, the body plan of the systellommatophorans has as torsion as the remaining gastropods, mainly shown by the genital apertures, but also by the hindgut. The postero-median position of the anus is a secondary modification.

Another group with degree 2 of limacization that also bears an apparent detorsion are the doridacean nudibranchs. But, different from the systellommatophorans, the doridaceans suffered a displacement of the anus (Fig. 9).

Considering an ordinary aeolidian nudibranch (Figs. 5, 9A), in such the anus and genital pores are located anterior-right of the body, a possible evolution to Phanerobranchia doridaceans, in such the peri-anal gill is not retractable, and the anus is located at tip of a more central visceral elevation (Fig. 9B). In this path, the anus is displaced towards median and more central position of the animal's body. On the other hand, in the cryptobranch doridaceans (Cryptobranchia) (Fig. 9C), the gill, which in this group is retractile, and the anus migrated further towards posterior. In this last conformation, the outer appearance is of a bilateral animal, with a posterior anus (but different from that of the systellomatophorans, the anus is dorsal). However, the clue of a normal torsion is in the genital pores, maintained in the same region as the other gastropods, in the right-anterior region (asterisks in Fig. 9).



9. Scheme of a comparative conformation in right (3 left images) and dorsal (3 right images) views of nudibranchs. A, an aeolidian nudibranch; B; a phanerobranch doridacean; C, a cryptobranch doridacean. Anus (white circle) has displaced in directions shown by arrows. Asterisks indicate normal region of genital pores. Cerata and gill are omitted.

The Fig. 9 schematically shows a suggestion of evolution of the apparent bilateral doridaceans. Starting with an animal with right-anterior placed anus (Fig. 9A), similar to the present cladobranch aeolidian nudibranchs, the anus become in the center of a circular gill and migrated to the dorsal-central region of the dorsum (Fig. 9B). The position of the anus in the center of a circular gill filaments is convenient, as the water flow promoted by them helps in the fecal ejection. This condition is found in the phanerobranch doridaceans, considered a basal taxon as lack a retractile gill. The anus and surrounding gill migrated further towards posterior in the cryptobranch doridaceans (Fig. 9C), which also developed a retractile gill.

Concluding, the apparent detorsion of the opisthobranchs are restricted to those taxa that reached the degree 2 of limacization, and it is only apparent, as the internal constitution of the organs still show the current twisted model of the gastropods.

The absence of slugs in Caenogastropoda

The Caenogastropoda, a taxon considered from subclass to order, are a very widespread, high-biodiverse group that may constitute about half of all mollusk species. It has representatives in almost all habitats suitable for a mollusk. Even so, there is no true caenogastropod slug, which is intriguing. In a wide study on representatives of all caenogastropod main branches (Simone, 2011), one of the more interesting synapomorphy of them is the **diaphragmatic septum**, a character never reverted in any internal group.

10. *Lamellaria mopsicolor* dorsal view of a crawling specimen, anterior region at right, showing tentacles and siphon (L ~25 mm), an ordinary snail with enlargement of mantle. Courtesy Alvaro Migotto, Cebimar-USP.

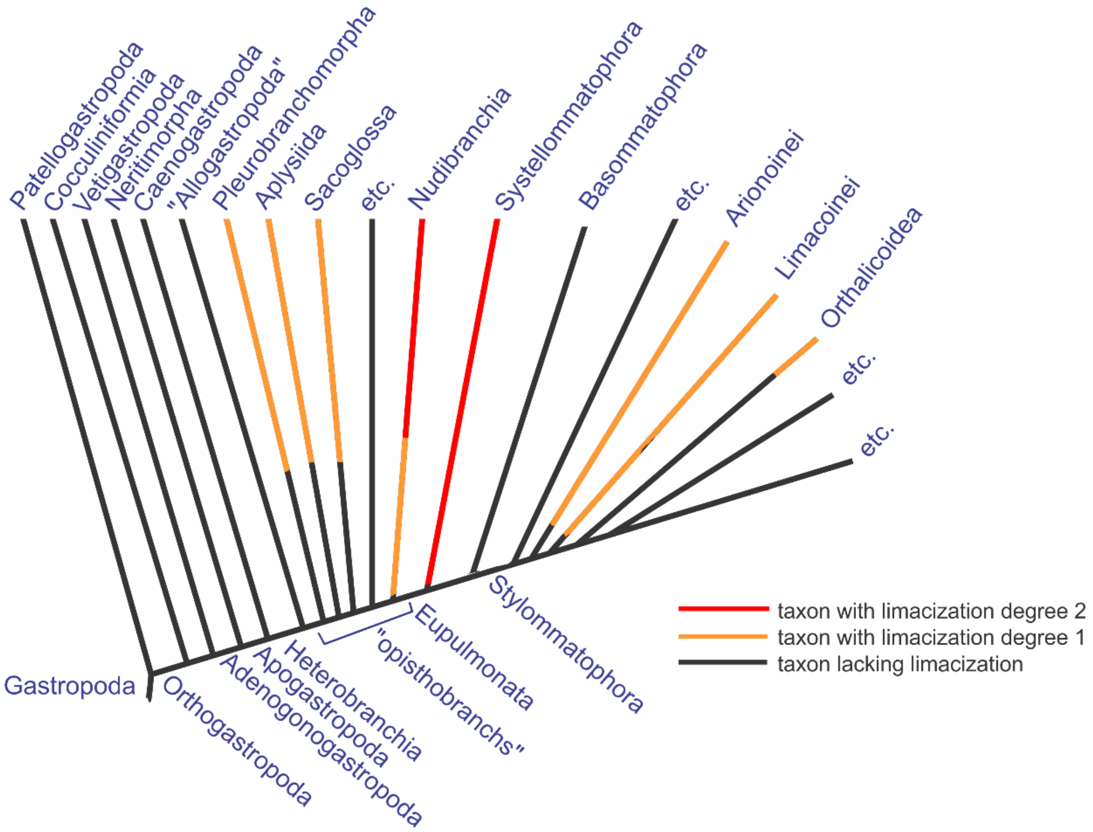
The diaphragmatic septum is located at posterior end of haemocoel, physically separating the haemocoelic structures from the visceral ones. As argued by Simone (2011), that septum improves the hydrostatic pressure inside the haemocoel, permitting the development of a strong proboscis, and more robust foot, so usual in that taxon. However, the structure impedes visceral structures, such as genital and mid digestive tubes, to reach haemocoel. Visceral structures inside haemocoel are usually found in archaeogastropod groups and in heterobranchs, coming from posterior, visceral region. As visceral structures cannot migrate to haemocoel, the evolutive limacization process becomes precluded.

A slug-like group is found in Caenogastropoda – the Velutinidae. Some of them still have an apparent shell, such as *Velutina*, exposed in disturbance; however, some genera have no external shell, such as *Lamellaria* (Fig. 10). The study of the morphology and anatomy of these cypraeoidean taxa (Simone, 2004) shows that the internal conformation is of an ordinary snail. The shell is internal, despite in having thin walls, and houses an ordinary visceral mass and part of a normal pallial cavity. The slug appearance of the velutinids is consequence of the enlargement of the mantle lobes, synapomorphic characteristic of the Cypraeoidea (Simone, 2004, 2011). In the velutinids, particularly in the lamellariines, the mantle lobes tend to fuse with each other dorsally. The *Lamellaria*'s (Fig. 10), in particular, have the mantle lobes totally fused with each other, and the shell becomes totally internal.

The archaeogastropod taxa also do not have any true slug, despite in having some genera with reduced, exposed shell, e.g., *Fissurellidea*. However, there is no good morphological explanation for this absence in Patellogastropoda, Cocculiniformia, Vetigastropoda and Neritimorpha.

Main branches that suffered limacization.

The Fig. 11 shows an unpretentious cladogram of the Gastropoda with its main branches organized according to the phylogeny by Simone (2011) with addition of Worms in heterobranchs. The branches in such no true slug is present are black, while those with representatives presenting limacization process are orange – degree 1, or red – degree 2. Note that only the heterobranchs has true slugs, and only the Systellommatophora and the Nudibranchia have reached the degree 2 of



11. Unpretentious cladogram of the Gastropoda, mostly based on Simone (2011) and Worms, showing important taxa that suffered limacization process in evolution. Black lines represent taxa lacking true slugs; orange lines representing taxa with representatives having degree 1 of limacization; red lines representing taxa with representatives having degree 2 of limacization. The survey is not exhaustive.

limacization as explained above. The remaining slug-bearing taxa have representatives that reached the degree 1 of limacization. It the branch has more than one color, it included representatives in different degrees of limacization. Of course, the survey that bases this cladogram is not exhaustive, and some minor taxa cannot be included.

Anyway, it is possible to infer that the limacization process is not uniform, and neither occurred once amongst gastropods. The limacization occurred at least in 8 taxa (Fig. 8), reaching the apogee of degree 2 in two of them.

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