

Main processes of body modification in gastropods: the limpetization

Luiz Ricardo L. Simone

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

Abstract

Limpetization is the gastropod evolutionary event that results in limpets. It has 3 degrees: degree 1 – ear-shells; degree 2 – almost limpets; and degree 3 – true limpets, which are regarded as possible evolutionary steps. The main morpho-anatomical modifications are explored, mainly in head-foot musculature, and displacement of the pallial structures and the visceral mass. The horse-shoe shaped shell muscle evolved from an ordinary columellar muscle, having separated bundles of muscles as an intermediary state. It is emphasized that the limpetization process only occurred in secondary limpets, which could be a reversion to the primary limpet condition found in the Recent patellogastropods and cocculiniforms. Details of the conformation of structures, main branches that suffered limpetization, the special case of the siphonariids, the pseudolimpets, and other issues are also addressed.

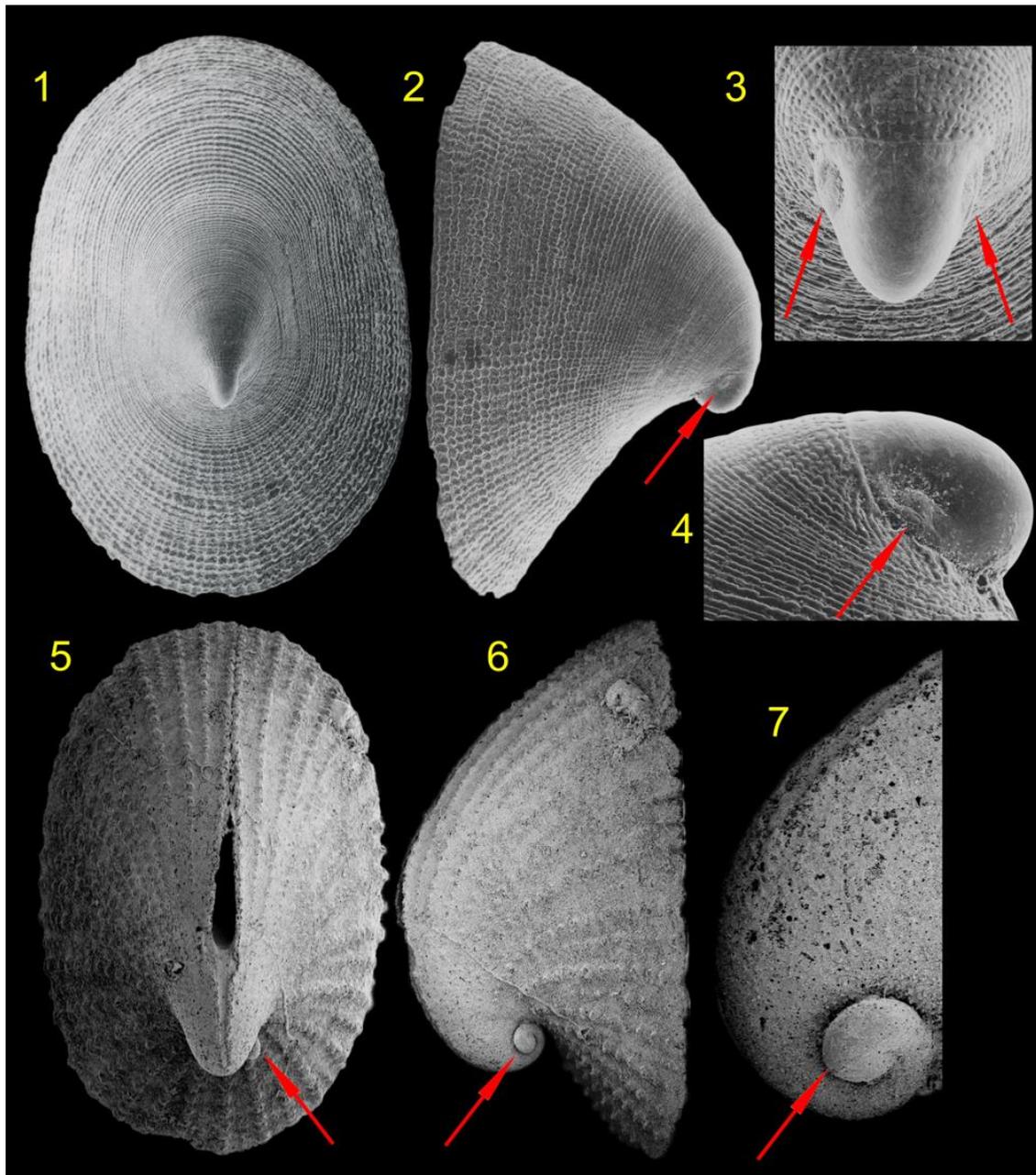
Keywords: limpet, gastropod evolution, morphological modifications.

Introduction

Limpetization is the common name of an evolutionary event that results in limpets, i.e., snails (gastropod mollusks) with a flattened, broadly conical, cap-shaped shell. It is also known as “patellization”, a term derived from the Latin word “patella”, meaning small plate or dish. The name “*Patella*” is also used for a gastropod genus that used to include virtually every gastropod species with a limpet-like shell in the 18th century (and is also curiously the anatomical term for our kneecap). The limpet shell is a simple cone that shelters the entire animal, including parts usually harbored inside the whorls of spiraled shells, i.e., the visceral mass, the pallial cavity, and even the head-foot when the animal is retracted. An unpretentious definition of the result of the limpetization event is the complete transference of structures of a snail from the earliest whorls of the shell into its aperture.

Gastropod lineages in which limpetization took place have ancestors (now extinct) with coiled shells similar to our everyday snails (Figs. 27-29), from which the limpets (extant or extinct) descend (Figs. 36-38). Some extant groups seem to be somewhere in between a typically coiled and a limpet-like state (Figs. 30-35), which look intermediary steps to a full-fledged limpet.

Limpetization occurred independently in several, unrelated branches of Gastropoda (Fig. 26). However, prior to any explanation, it is important to emphasize that there are two kinds of limpets: 1) primary limpets; and 2) secondary limpets. **Primary limpets** include taxa or lineages that did not evolve from coiled snails, and, as such, in which limpetization did not take place. **Secondary limpets** belong to lineages that evolved from coiled ancestors.



1-7. Limpet shells showing the differences between primary (above) and secondary (below) limpets. 1-4, *Propilidium curumim* (L 1.5 mm) (from Leal & Simone 1998; courtesy José Leal), Patellogastropoda; 1, dorsal view; 2, left view; 3, detail of protoconch, dorsal view; 4, same, left view; 5-7, *Cranopsis apostrema* (L 4.4 mm) (from Simone & Cunha 2014), Vetigastropoda; 5, dorsal view; 6, right view; 7, detail of protoconch, right view. Red arrows showing protoconch's spire as symmetrical (above) and asymmetrical (below).

Primary limpets

Primary limpets belong to lineages in which the ancestors did not have coiled shells. Hence, knowing whether or not a given taxon is a primary limpet strictly depends on phylogeny. Since the Patellogastropoda and Cocculiniformia are placed at the base of Gastropoda, and, if a theoretical gastropod ancestor with a similar shell is considered, the ancestral condition of the limpet-like shell would be therefore inferred. However, morphologically, it is very hard to distinguish primary limpets from secondary ones, since their shell and the anatomical features (see below) are similar. The only morphological clue in the shell, capable of indicating a primary or secondary condition, is the protoconch symmetry. Primary limpets have a symmetrical, planispiral protoconch (Figs. 1-4) (Sasaki, 1998, fig.21); their protoconch is coiled in a single vertical plane, with diameter increasing away from the axis of coiling, producing a symmetrical profile (Fig. 3, arrows). On the other hand, secondary limpets have an asymmetrical protoconch, in contrast to their symmetrical teleoconch (Figs. 5-7). Their protoconch is not coiled in a vertical plane, and this slight inclination produces a taller spire on one side, and a resulting dextrally coiled shell (Fig. 7) that may have been inherited from a coiled ancestor.

Beyond this difference in protoconch morphology, primary and secondary limpets are quite similar in most features, indicating that limpetization may be a reversion in the Gastropoda. As told above, the Patellogastropoda and the Cocculiniformia, the two first branches in Gastropoda, are considered primary limpets (Fig 26). As such, a coiled shell would be one of the synapomorphies of the following branch (Simone, 2011).

Secondary limpets

Since a coiled, spired shell is one of the synapomorphies of the branch after the two basal ones (Patellogastropoda and Cocculiniformia) in Gastropoda, every limpet belonging to taxa phylogenetically allocated thereafter are secondary limpets evolved from a coiled ancestor. Hence, the morphological characteristics of limpetization explored below are only applicable to those secondary limpets. As discussed above, practically the single morphological clue for considering a limpet as secondary is the asymmetrical protoconch (Figs. 5-7) (Sasaki, 1998, fig. 38).

Why does one become a limpet? Consequences.

The limpet shape may be an adaptation to environments with high hydrodynamism, i.e., in ambiances impacted by waves, with strong water currents, etc. The low conical shape of the shell offers less drag to the water flow if compared to a coiled shell, and as such, limpets are well-adapted to these environments. However, limpets more rarely also occur in calmer environments, such as deep waters.

A remarkable example of the influence of the environment on shell morphology is that limpet specimens of a single species usually have flatter shells in higher energy areas. Those living in more sheltered spaces usually have taller shells (Vermeij, 1974, 2004; Simone 2008). Beyond the low drag factor, the large ventral area permits a wide adherence to the substrate (usually rocks). This, associated with the contraction of the shell muscle, transforms the specimen in a potent sucker that is nearly impossible to remove. Adherent mucus is also commonly produced and further

improves the attachment, since the surface is rarely even. All this strong machine of attachment is completely, or almost completely protected by an armor – the shell itself.

All these adaptations work well with the specimen in a normal position. However, if by misfortune the specimen is capsized, the shell shape becomes a problem: a cap-like shell is much harder to untwist if compared to coiled, more cylindrical shells. Moreover, the wide, unprotected shell aperture of the limpets is a problem for a displaced specimen since the operculum is usually absent, leaving the animal exposed to predators and dehydration. In some groups, e.g., the intertidal lottiids, an irregular shell border completely encases the animal in a specific place of the hard substrate. The specimen is only active during low or high tides, returning to its exact place when the waves turn back (Beckett, 1968).

Diverse anatomical modifications occur in the limpetization process, mainly in the pedal-columellar musculature, and in the visceral hump. These modifications are better explained below, according to the degree of limpetization.

Degrees of limpetization

Starting from a current snail (Figs. 27-29), the secondary limpetization process may obey intermediary steps, as follows.

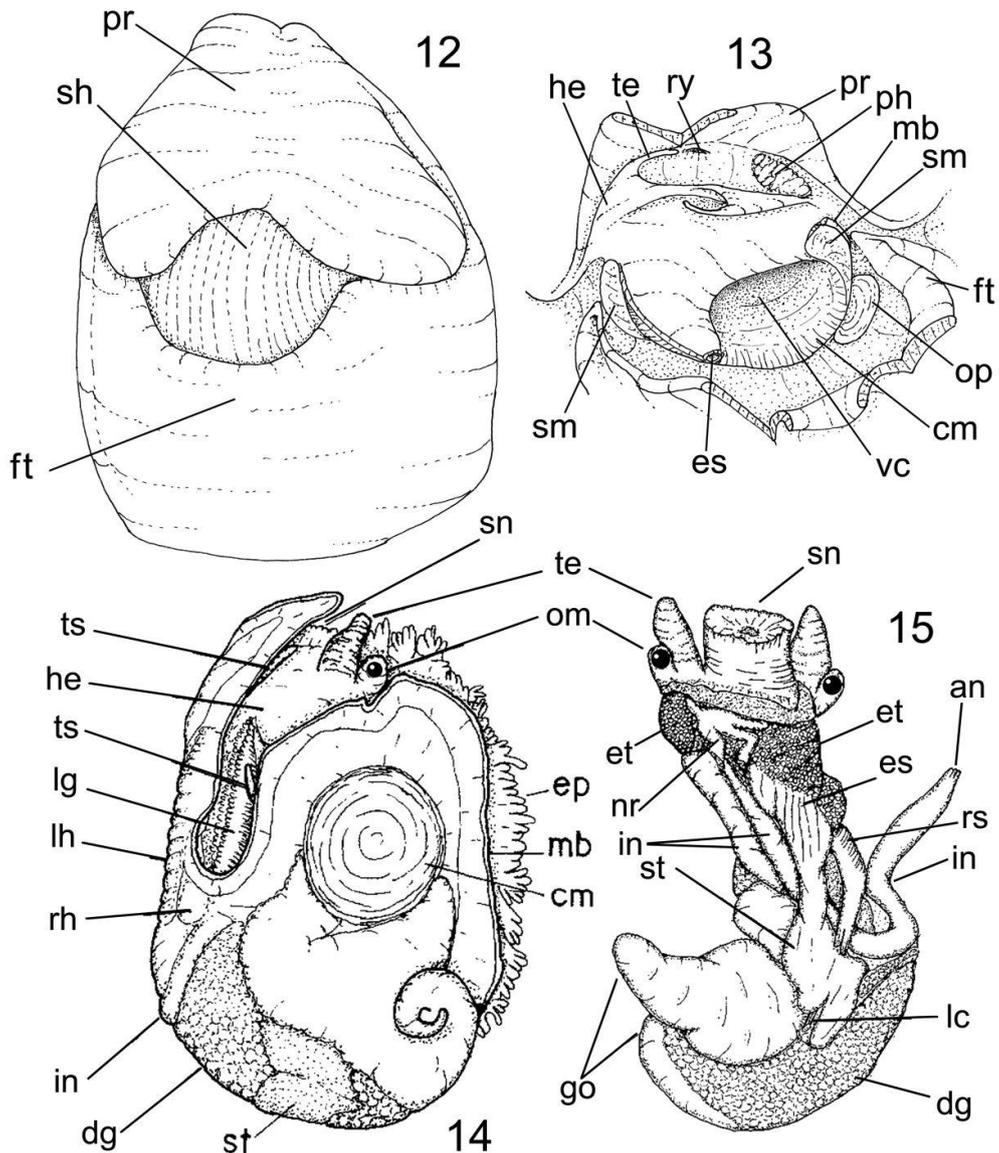
Limpetization degree 1 – ear-shell (Figs. 30-32):

Degree 1 limpets have a shell with a very wide aperture, but with a clear and yet small spire. The general shell shape barely resembles a human ear, which is why they are commonly known as ear-shells. Some examples in the Vetigastropoda are the haliotids (abalones) (Fig. 8), and stomateline (Fig. 9) and fossarine trochids. In the Caenogastropoda we have the sinine naticids (Fig. 10) and *Concholepas* (Fig. 11), a muricid.



8- 11. Shells of ear-shelled species, degree 1 of limpetization. 8, *Haliotis aurantium* from Brazil (L 26 mm); 9, *Stomatella planulata* from Japan (L 20 mm); 10, *Sinum cf. perspectivum* from Brazil (L 34 mm); 11, *Concholepas concholepas* from Chile (L 110 mm). All courtesy of Femorale.

The anatomical attributes of these ear-shelled species are peculiar. The visceral mass is encased in the small shell spire, but this space is not sufficient to shelter it completely, and part of it is dislocated to the posterodorsal region of the head-foot. The dislocation of the visceral mass in the Caenogastropoda produces a concavity located just posterior to the end of the head-foot hemocoel (Fig. 13: vc), as the diaphragmatic septum obstructs the incursion of visceral structures into the hemocoel (Simone, 2011). While in other groups, particularly of the archaeogastropod grade and in heterobranchs, which lack septum, the reallocation of the visceral structures is usually into the hemocoel (Fig. 15).



22-15. Anatomical structures of ear-shelled species. **12-13**, *Sinum cf. perspectivum* from Brazil exemplifying a caenogastropod (L ~40 mm); **12**, whole specimen, dorsal view; **13**, detail of head-foot with removal shell, visceral mass and pallial structures removed, dorsal view, showing visceral concavity (vc), some portions of foot sectioned and only partially shown. **14-15**, *Haliotis aurantium* from Brazil, exemplifying a vetigastropod (L ~20 mm) (from Simone, 1998); **14**, whole dorsal view, shell removed; **15**, head and haemocoel structures as in situ, ventral view, foot removed. Lettering: an, anus; cm, columellar muscle; dg, digestive gland; ep, epipodium; es, esophagus; et, esophageal pouch; ft, foot; he, head; in, intestine; lc, left columellar muscle; lg, left gill; lh, left hypobranchial gland; mb, mantle border; ph, penis shelf; pr, propodium; om, ommatophore; op, operculum; rh, right hypobranchial gland; rs, radular sac; ry, rhynchostome; sh, shell; sm, shell muscle; sn, snout; st, stomach; te, cephalic tentacle; ts, mantle tentacle; vc, visceral concavity.

Since the taxa of the archaeogastropod grade, in particular, the vetigastropods and neritimorphs, still have a pair of columellar muscles, the limpetization degree 1 causes the separation and asymmetry of both muscles (Simone, 1998). The right one becomes larger and more dorsal-centrally positioned (Fig. 14: cm), with a round outline in a cross-section. The left columellar muscle, on the other hand, diminishes and becomes more ventral (Fig. 15: lc), thin, and elliptic.

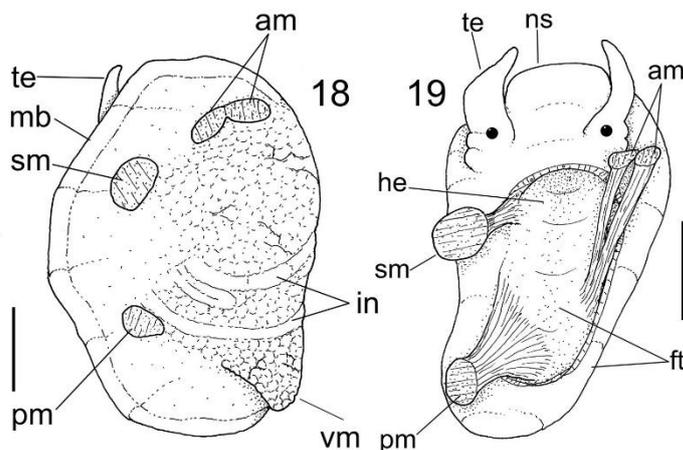
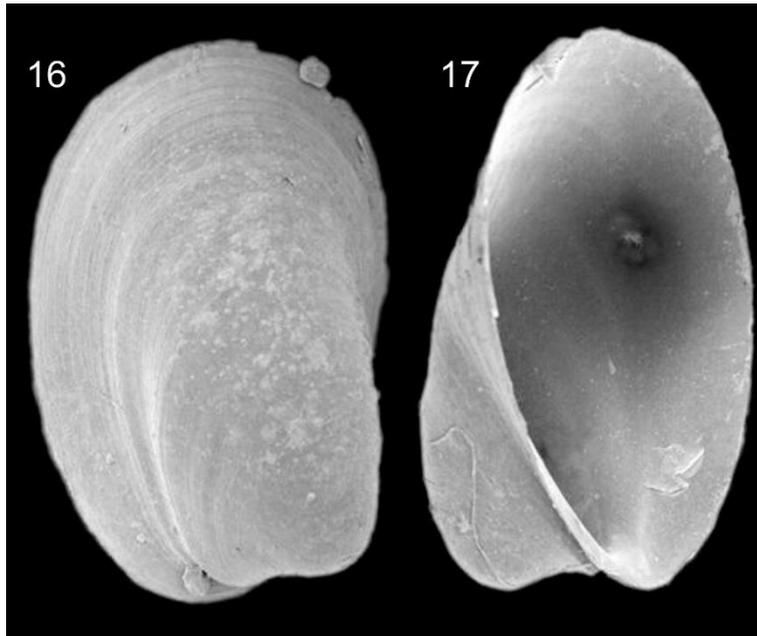
A single (right) columellar muscle is one of the synapomorphies in the Apogastropoda (Heterobranchia + Caenogastropoda), after the archaeogastropod grade (Simone, 2011). The adaptations to the limpetization degree 1 produce a columellar muscle slightly horseshoe-shaped in cross-section (Fig. 13: cm), with thickened lateral ends (Fig. 13: sm), and a thin middle region.

All these modifications in the head-foot musculature are reflected in the shell's inner scars, being usually easily detectable in their inner surface.

Beyond the above-mentioned muscle modifications, the reallocation of structures is important in the limpetization process. The head-foot and pallial structures become totally located in the body-whorl, more specifically, in the apertural region. The visceral structures, on the other hand, are only partially sheltered inside the shell spire. The anterior region of the visceral mass, as referred above, bulges through the head-foot space, also toward the shell's last whorl. Lacking the diaphragmatic septum (Simone, 2011), visceral structures can be displaced to the head-foot hemocoel in archaeogastropods and heterobranchs. The ear-shells have visceral structures located inside the hemocoel, running alongside the esophagus (Fig. 15). This visceral displacement is precluded in caenogastropods, which have a diaphragmatic septum. As mentioned above, the migration of visceral structures is, then, done by means of a separated concavity (Fig. 13: vc) located in posterior region of the head-foot, ventrally and to the right protected by the columellar muscle, and anteriorly and left by the integument of the haemocoel itself (Fig. 13: cm, es).

Limpetization degree 2 – almost-limpets (Figs. 33-35):

Degree 2 limpets are practically a “true” limpet, except for two main features: (1) the apex of the shell slightly dislocated to the right (in dorsal view) (Figs. 16, 35) and (2) the shell muscles are not horseshoe shaped.



Some classic examples of degree 2 limpets are the Ancylineae planorbids (Figs. 16-19) (Basch, 1959; Simone et al, 2012). These normally tiny freshwater limpets fulfill the above-mentioned attributes and can be considered almost-limpets in the present rank. Their shells have the apex slightly dislocated to the right (Figs. 16, 17, 35), showing a vestigial coiling (despite some

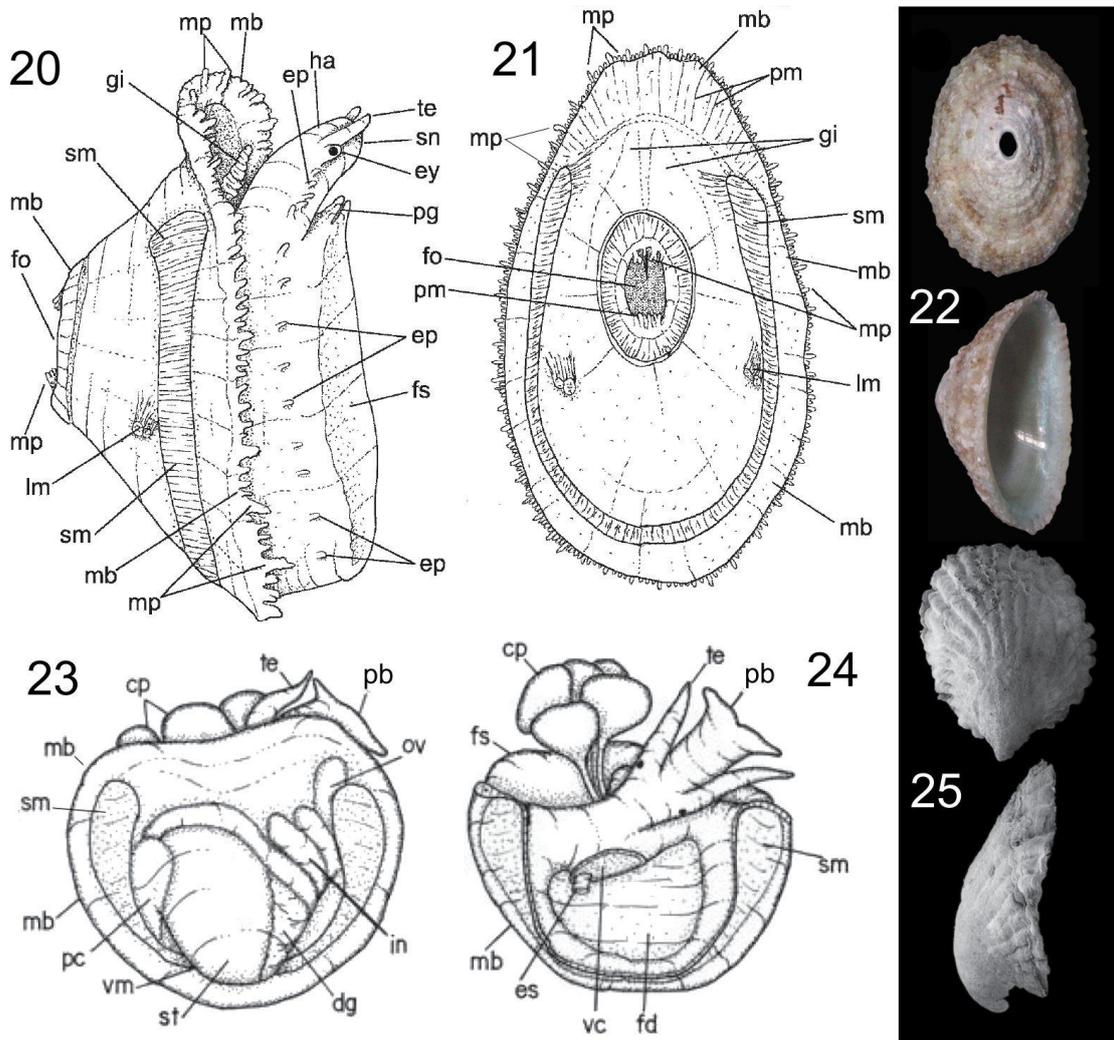
16-19. Example of a degree 2 of limpetization: *Gundlachia ticaga* from Brazil, an ancyline planorbid (from Simone et al, 2012). **16**, SEM of shell (MZSP 63654, L 2 mm), dorsal view; **17**, same, right-slightly ventral view; **18**, specimens removed from shell, whole dorsal view; **19**, head-foot, dorsal view, pallial and visceral structures removed, mainly showing shell muscles. Scales= 0.5 mm. Abbreviations: am, anterior-right shell muscles; ft, foot; he, haemocoel; in, intestine; mb, mantle border; ns, snout; pm, postero-left shell muscle; sm, left-anterior shell muscle; te, cephalic tentacle; vm, visceral mass.

ancylines not being tall enough to display a clear apex asymmetry).

The shell musculature of the ancylines also show a barely “U” or horseshoe-shaped organization, which is however incomplete, since only some muscle regions are present (Figs 18-19: am, sm, pm). These two features might be clues of a limpetization process still in progress.

Beyond the planorbids and the Ancylineae, other examples of degree 2 limpets are the also freshwater Latiidae (Meyer-Rochow & Moore, 1988) from New Zealand, and the deepwater marine vetigastropods Lepetodrilidae (McLean, 1993; personal obs.). These taxa also usually have asymmetrical limpet-like shells, and the shell musculature have an incomplete horseshoe shape.

Limpetization degree 3 - true limpets (Figs. 36-38):

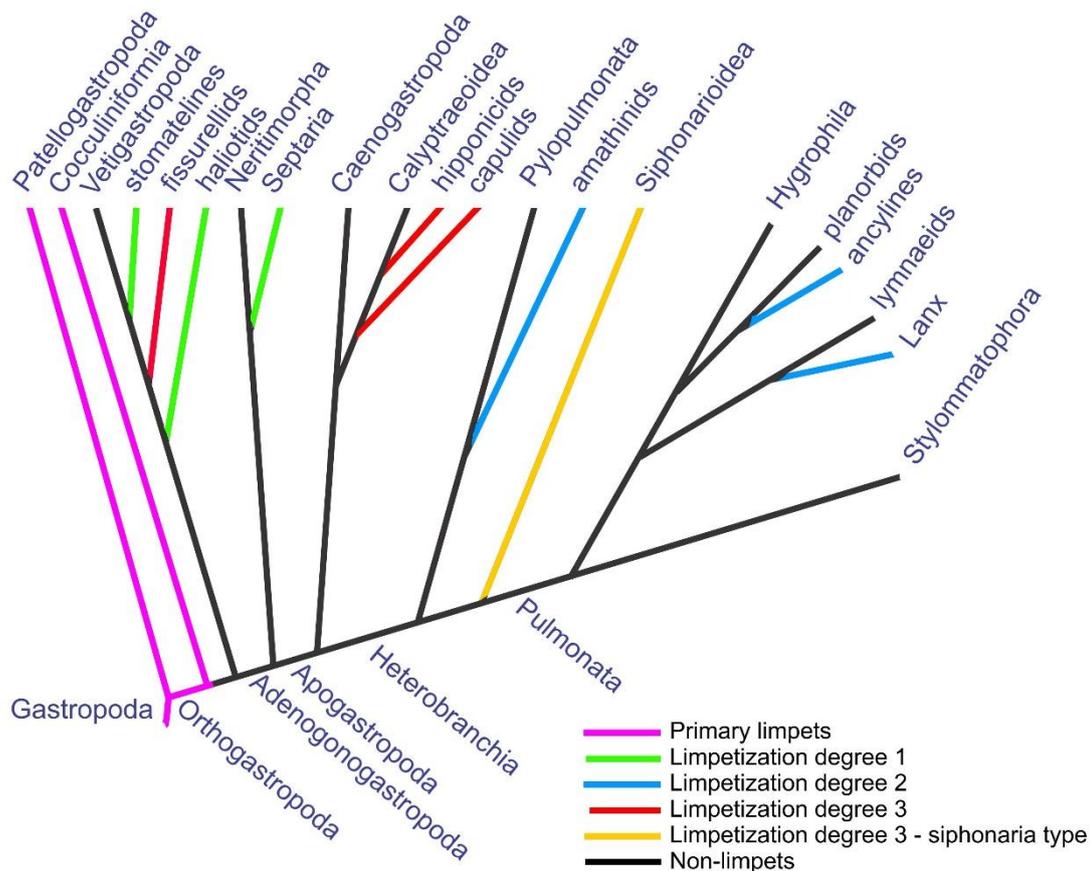


20-25. Examples of degree 3 of limpetization (both L ~20 mm): **20-22** *Fissurella mesoatlantica* from Brazil, a vetigastropod (from Simone, 2008); **20**; specimen extracted from shell, right view; **21**, same, dorsal view; **22**, shell of holotype MZSP 87462, dorsal and right-slightly ventral views; **23-25**, *Hipponix costellatus* from Brazil, a calyptraeoid caenogastropod (from Simone, 2002); **23**, specimen extracted from shell, dorsal view; **24**, head-foot, female, dorsal view; **25**, shell of MZSP 28498, dorsal and right views. Abbreviations: cp, egg capsules; dg, digestive gland; ep, epipodial tentacles; es, esophagus; ey, eye; fd, foot dorsal surface; fo, foramen; fs, foot sole; gi, gill; ha, head; in, intestine; lm, lateral shell muscle; mb, mantle border; mp, mantle papillae; ov, pallial oviduct; pb, proboscis; pc, pericardium; pg, pedal gland furrow; pm, mantle muscles; sm, shell muscle; sn, snout; st, stomach; te, cephalic tentacle; vm, visceral mass.

Despite the primary limpets (Patellogastropoda and Cocculiniformia) are true limpets as defined them, the so-called secondary limpets would be those that are closest to them morphologically. The secondary limpets, however, evolved from coiled ancestors. Their shells are symmetrical and the columellar muscle became horseshoe-shaped, which is the main character of a “true limpet”. The visceral hump migrated totally forwards and is usually sheltered below the shell’s apex. Like almost all limpets, the true-limpets also have differences in the visceral placement between the caenogastropods and the other gastropods (heterobranchs and archaeogastropod grade). As mentioned above, the caenogastropods have a diaphragmatic septum, which blocks the migration of visceral structures to the head-foot hemocoel. Therefore, the visceral structures become located in a concavity surrounded by the hemocoel (Fig. 24: fd). In other gastropods, part of visceral structures migrates to the inner parts of the hemocoel, covering the posterior region of the esophagus.

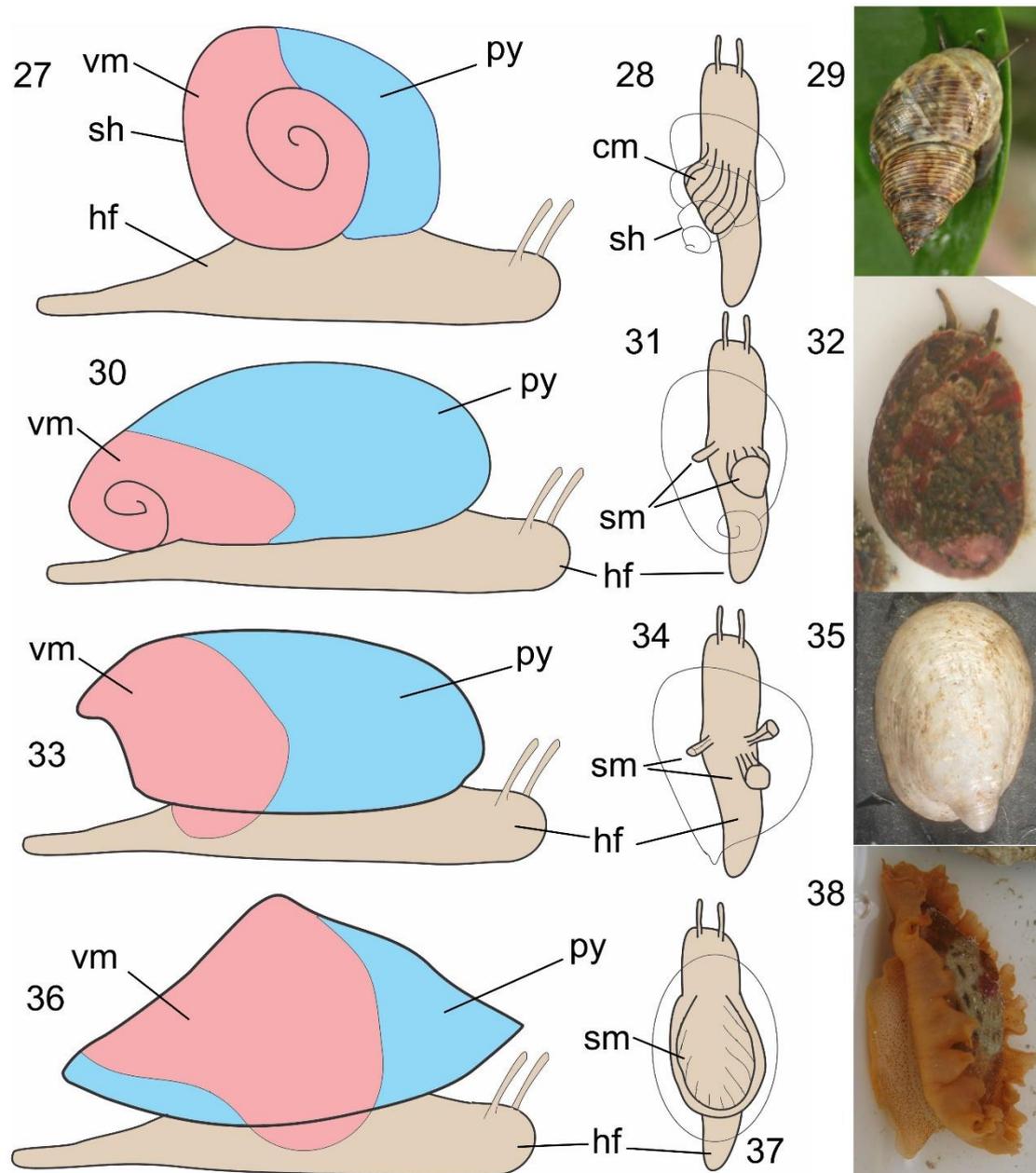
In true limpets, the visceral mass is not coiled anymore, and becomes a mold of the inner shell surface, mainly in the region surrounding the apex. The gonad, the digestive gland, the stomach, and adjacent intestinal loops are usually located in the postero-dorsal half of the limpet. The pallial cavity occupies the dorso-anterior region, while the ventral half is usually occupied by the head-foot musculature (Fig. 36).

Main branches that suffered limpetization.



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

The Fig 26 shows an unpretentious cladogram representing the main branches of the gastropod phylogeny in which a limpetization process occurred to any degree. The two first branches



27-38. Schemes summarizing the limpetization process; left column crawling snails in right view; middle column crawling snail in dorsal view, focus on head-foot structures, shell is transparent (outlined); right column photos of actual examples. **27-29**, recent coiled snail; **27**, main body portions; **28**, detail of ordinary columellar muscle; **29**, *Littorina angulifera*, from Florida (L 25 mm); **30-32**, degree 1 of limpetization; **30**, main body portions; **31**, showing modification of columellar muscle into shell muscle; **32**, *Halio tis coccinea*, from Azores (L 40 mm); **33-35**, degree 2 of limpetization; **33**, main body portions; **34**, multiple shell muscles; **35**, *Ancylus rudolffi*, from Chile (L 6 mm, syntype); **36-38**, degree 3 of limpetization; **36**, main body regions; **37**, modification to a true, horseshoe-shaped shell muscle; **38**, *Lucapina* sp, from Fernando de Noronha, Brazil (L 35 mm). Abbreviations: hf, head-foot; py, pallial cavity; sh, shell; sm, shell muscle(s); vm, visceral mass.

(purple) represent primarily limpet taxa, i.e., those that do not descend from coiled ancestors. The Vetigastropoda is the first branch that includes limpetized taxa, particularly the trochid Stomatelinae and the haliotids (Simone, 1998) at degree 1, with the Fissurellidae reaching the apothotic degree 3 (Simone, 2008), which can also be attributed to Neomphalidae (not shown). Amid the Adenogonogastropoda, the Neritimorpha have the single neritid genus *Septaria* in the degree 1. In Apogastropoda, only two families have degree 3 limpets, the calyptraeoidaeans Hipponicidae,

and Capulidae (Simone, 2002), by convergence. Within the Heterobranchia, the Amathinidae also have degree 2 of limpetization. Amongst the Hygrophila, two independent degree 2 lineages are the planorbid Ancylineae, and in the lymnaeid genus *Lanx*. As told above, this survey is not exhaustive, and some few taxa are missing, like, e.g., some hot-vent taxa with a still obscure anatomy.

It is interesting to realize that several branches of Gastropoda converged into different degrees of limpetization. Additionally, the taxa having the degree 3 of limpetization are not preceded by taxa with the degree 2, and as such are also not preceded by the degree 1, at least in the living, detectable taxa. It is theorized that a higher degree of limpetization must be preceded by lower levels of it during evolution, as ontogeny seems to suggest (Vermeij, 2017). A more complete survey, including fossil taxa, is provided by Vermeij (2017).

The evolution of the columellar muscle (Fig. 28: cm) into the horseshoe-shaped shell muscle (Fig. 37: sm) possibly is preceded by the conditions in which the columellar muscle is divided (Figs. 31, 34), obeying the physical need of attachment, the torque, in order to optimize the shell holding and its compression to the substrate.

Special case of the Siphonarioidea

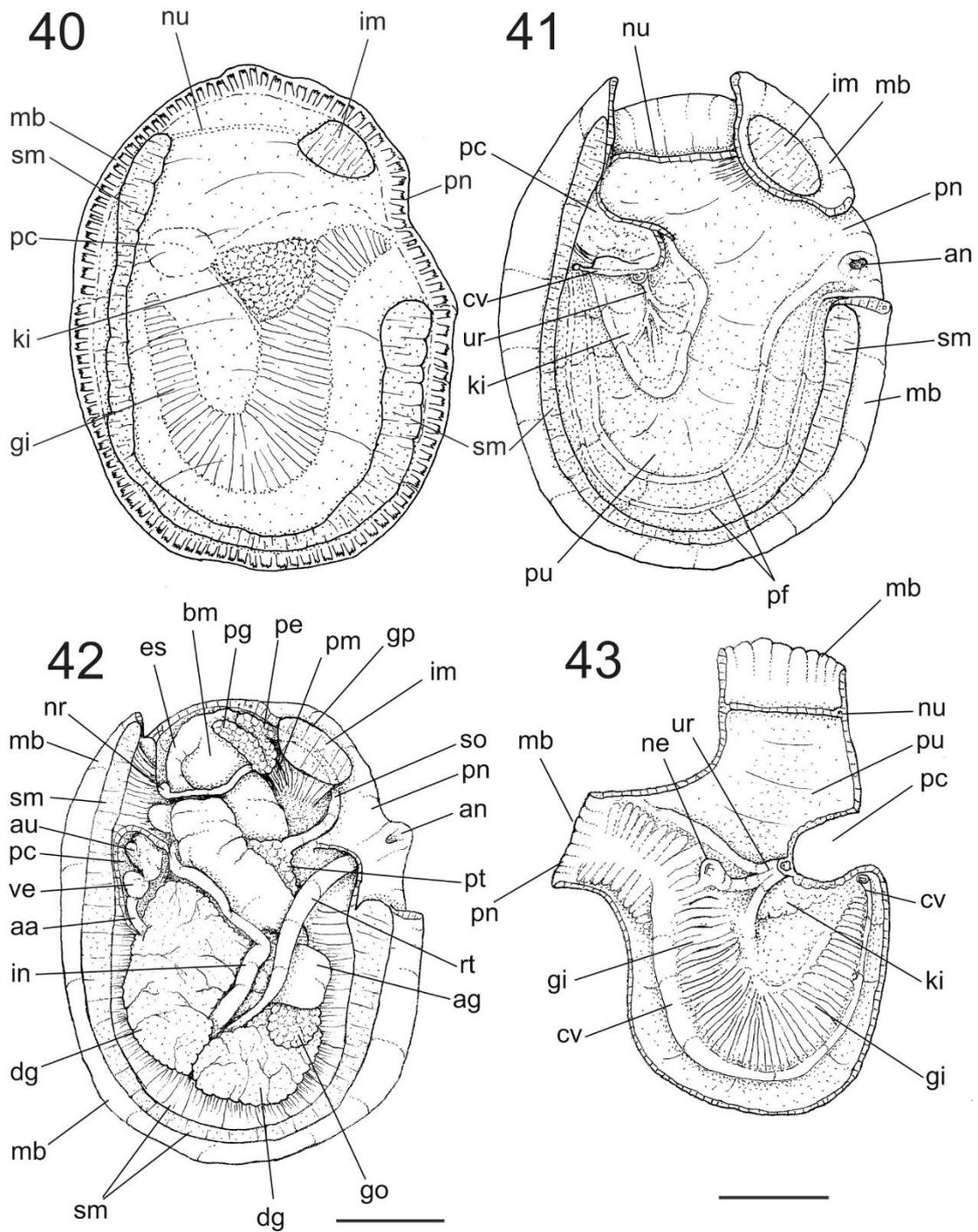
The siphonarioideans are true limpets in almost every sense of the term. However, some particular features are unlike any other limpets. Details on the siphonarioidean idiosyncrasies are explored elsewhere (Simone & Seabra, 2017), and are summarized below (Figs, 40-43):

The shell muscle has a slightly horseshoe-shaped outline, but its right branch is interrupted by the pallial cavity (Marcus & Marcus, 1960; Simone & Seabra, 2017) (Fig. 40-41: im, sm). The pneumostome is located in the right interspace between both muscles, which in these basal taxa is not contractile like those of higher Pulmonata.

The visceral hump is totally located inside the head-foot's hemocoel and only a small portion of the reno-pericardial region reaches the dorsal surface (Figs. 40, 41: pc). Almost the totality of the dorsal region, in the space between both branches of the shell muscle, is empty, constituting the pulmonary (mantle) cavity. In a different way, in the remaining limpets, the shell apex is internally filled by visceral structures, and the pallial cavity surrounds it at some anterior distance.



39. Living *Siphonaria pectinata* from Portugal, ventral view (L 30 mm) (courtesy Seabra).



40-43. Anatomical features of *Siphonaria pectinata* from Portugal (extracted from Simone & Seabra, 2017). **40**, complete specimen extracted from shell, dorsal view; **41**, same, pallial roof extracted (shown in Fig. 43); **42**, same, pallial floor removed, haemocoel structures seen as in situ; **43**, pallial cavity hoof, ventral view. Scales= 5 mm. Abbreviations: aa, anterior aorta; ag, albumen gland; an, anus; au, auricle; bm, buccal mass; cv, ctenidial vein; dg, digestive gland; es, esophagus; gi, secondary gill; go, gonad; gp, genital pore; im, isolated portion of shell muscle; in, intestine; ki, kidney; mb, mantle border; ne, nephropore; nr, nerve ring; nu, nuchal connection of mantle; pc, pericardium; pe, penis; pf, ventral pair of pulmonary folds; pg, penis gland; pm, penial/copulatory organ muscle; pn, pneumostome; pt, prostate; pu, pulmonary (mantle) cavity; rt, rectum; sm, shell muscle; so, spermatiduct; ur, urethra; ve, ventricle.

Pseudo-limpets

Gastropoda is a megadiverse group, and evolution produced a wide range of different shell conformations (including its loss), some of them weird enough to be unclassified. Strange shell conformations will be deeper addressed in future papers. Some shell forms are similar to a limpet, but they are structurally different. These shells that look superficially similar to a limpet can be called **pseudo-limpets**. One of the main groups that developed pseudo-limpets are the calyptraeoidae. As stated elsewhere (Simone, 2002), the oldest calyptraeoidae lineages are ordinary, coiled snails; this “normal” fashion was drastically modified, including two true limpets mentioned above (hipponicids and capulids). Some calyptraeoidae shells have a shape similar to a limpet, e.g., *Cheilea*, *Crepidula*, *Crucibulum*, etc. But in these cases, the shell (columellar) muscle is weak, and the shell has ventral appendices or chambers, showing that their shape does not result from limpetization.

Other examples of pseudo-limpets are the cypraeoidae pediculariids. The shell of some species looks like a curved limpet, but the inner anatomical design is of a normally coiled cypraeoidae, with a lateral (left) muscle bundle connected to the shell (Simone, 2004: fig. 431), very similar to their coiled relatives. Also, a weird conformation is found in the heterobranch *Umbraclum*, in which the shell is extremely flattened, plane, only working as a protection to the visceral hump (Wägele et al, 2006).

Acknowledgments

The peer-reviewer of this paper was Daniel Caracanhas Cavallari, FFCLRP-USP, who I thank for comments and corrections on the text. Some comments were also made by Geerat J. Vermeij, who disagreed with the basal gastropods as primary limpets.

References

- Basch, PF, 1959. The anatomy of *Laevapex fuscus*, a freshwater limpet (Gastropoda: Pulmonata). Miscellaneous Publications of the Museum of Zoology, University of Michigan 108: 1-56.
- Beckett, TW, 1968. Limpet movements. An investigation into some aspects of limpet movements, especially the homing behaviour. *Tane* 14: 43-63.
- Leal, JH & Simone, LRL, 1998. *Propilidium curumim*, a new species of Lepetidae (Gastropoda, Patellogastropoda) from off southern and southeastern Brazil. *Bulletin of Marine Science* 63(1): 157-165.
- Marcus, E & Marcus, E, 1960. On *Siphonaria hispida*. *Boletim da Faculdade de Filosofia da Universidade de São Paulo* 260: 107-140.
- McLean, JH, 1993. New species and records of *Lepetodrilus* (Vetigastropoda: Lepetodrilidae) from Hydrothermal Vents. *Veliger* 36(1): 27-35.
- Meyer-Rochow, VB & Moore, S, 1988, Biology of *Latia neritoides* Gray, 1850 (Gastropoda, Pulmonata, Basommatophora): the only light-producing freshwater snail in the World. *Internationale Revue der Gesamten Hydrobiologie und Hydrographie* 73(1): 21-42.

- Sasaki, T, 1998. Comparative anatomy and phylogeny of the Recent Archaeogastropoda (Mollusca: Gastropoda). *Bulletin of the University Museum, University of Tokyo* 38: 1-223.
- Simone, LRL, 1998. Morphology of the Western Atlantic Haliotidae (Gastropoda, Vetigastropoda) with description of a new species from Brazil. *Malacologia* 39(1-2): 59-75.
- Simone, LRL, 2002. Comparative morphological study and phylogeny of representatives of the superfamily Calyptraeioidea (including Hipponicoidea) (Mollusca, Caenogastropoda). *Biota Neotropica* 2(2): 1-136. <http://www.molusc.org/trabalhos/2004/Simone%202004%20-%20Cypraeoidea.pdf>
- Simone, LRL, 2002. Morphology and phylogeny of the Cypraeoidea (Mollusca, Caenogastropoda). *Papel Virtual*. Rio de Janeiro, 185 pp. <http://www.molusc.org/trabalhos/2004/Simone%202004%20-%20Cypraeoidea.pdf>
- Simone, LRL, 2008. A new species of *Fissurella* from São Pedro e São Paulo Archipelago, Brazil (Vetigastropoda, Fissurellidae). *Veliger* 50(4): 292-304.
- Simone, LRL, 2011. Phylogeny of the Caenogastropoda (Mollusca), based on comparative morphology. *Arquivos de Zoologia* 42(4): 161-323. <http://www.molusc.org/trabalhos/Caenogastro/Simone%202011%20Caenogastropoda%20Phylogeny%20LIGHT.pdf>
- Simone, LRL; Bunioto, TC; Avelar, WEP & Hayashi, C, 2012. Morphology and biological aspects of *Gundlachia ticaga* from S.E. Brazil (Gastropoda: Basommatophora: Ancyliidae). *Archiv für Molluskenkunde* 141(1): 21-30.
- Simone, LRL & Cunha, CM, 2014. Taxonomical study on the mollusks collected in Marion-Dufresne (MD55) and other expeditions to SE Brazil: the Fissurellidae (Mollusca, Vetigastropoda). *Zootaxa* 3835(4): 437-468.
- Simone, LRL & Seabra, MIGL, 2017. Shell and body structure of the plesiomorphic pulmonate marine limpet *Siphonaria pectinata* (Linnaeus, 1758) from Portugal (Gastropoda; Heterobranchia: Siphonariidae) *Folia Malacologica* 25(3): 147-164.
- Vermeij, GJ, 1974. Marine faunal dominance and molluscan shell form. *Evolution* 28: 656-664.
- Vermeij, GJ, 2004. Morphological patterns in high-intertidal gastropods: Adaptive strategies and their limitations. *Marine Biology* 20(4):319-346.
- Vermeij, GJ, 2017. The limpet form in gastropods: evolution, distribution, and implications for the comparative study of history. *Biological Journal of the Linnean Society* 120: 22-37.
- Wägele, H; Vonnemann, V & Rudman, WB, 2006. *Umbraculum umbraculum* (Lightfoot, 1786) (Gastropoda, Opisthobranchia, Tyrodinoidea) and the synonymy of *U. mediterraneum* (Lamarck, 1812). *Records of the Western Australian Museum*, suppl. 69: 69-82.
- Worms – MolluscaBase (2018), <http://www.marinespecies.org/aphia.php>