Malacopedia

São Paulo, SP, Brazil
Volume 4(2): 22-30

ISSN 2595-9913
Apr/2021

The proboscis of the Gastropoda 2: the pleurembolic proboscis further evolution

Luiz Ricardo L. Simone

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

Abstract

This second paper on proboscis focuses further modifications of the pleurembolic kind of proboscis in a comparative and phylogenetic scenario. Details of its anatomy are exposed, and its main types are: 1) minute, 2) decrease of its buccal mass portion, 3) enlargement of its buccal mass portion, and 4) permanent rhynchodeal cavity (even in protracted condition). Taxa that bear each type and its possible evolutionary pathway are concisely exposed and discussed.

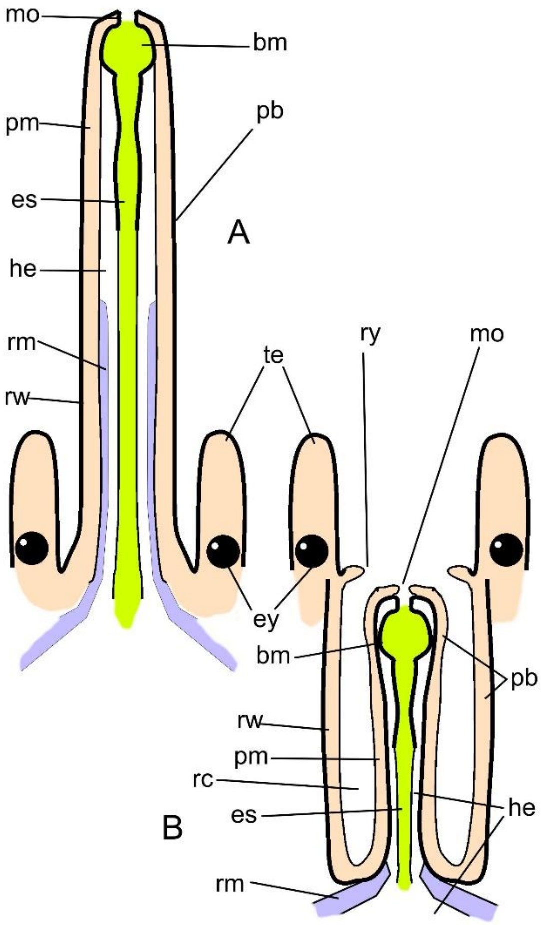
DOI: 10.13140/RG.2.2.30955.67362

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

Introduction

This paper complements the first one on gastropod proboscis (Simone, 2019), focusing on further development and evolution of the pleurembolic proboscis only, and has as base a previous scenario published in a wider Gastropoda phylogeny (Simone, 2011).

As reported in those papers, the gastropod proboscis has as main categories the acrembolic and the pleurembolic models. The acrembolic proboscis, which retracts completely, evolved independently at least in 5 gastropod branches (Simone, 2019, fig. 18). The pleurembolic proboscis, on the other hand, appeared evolutionarily only once in a branch of the Caenogastropoda, named, because of it, Rhynchogastropoda (Simone, 2011, 2019), being a conspicuous exclusive character, i.e., a synapomorphy of this taxon. Differently from the acrembolic proboscis, the pleurembolic one



1. Schematic representation of a usual pleurembolic proboscis in dorsal view, sectioned longitudinally: **A**. extended condition; **B**, retracted condition Lettering: bm, buccal mass; es, esophagus; he, haemocoel; mo, mouth; pb, proboscis; pm, proboscis buccal mass; rc, rhynchodeal cavity; rm, proboscis retractor muscle; rw, rhynchodeal wall; ry, rhynchostome; te, cephalic tentacle.

has only partial capacity of retraction; its distal portion remains non-retracted, sheltered inside its basal portion in recalled condition (Simone, 2019, figs 14-17) called rhynchodeal cavity.

The anatomical conformation of the pleurembolic proboscis has as an advantage of saving inner space for sheltering it, and less time for retraction. As rhynchogastropods are a huge group, the pleurembolic proboscis suffered all kinds of further modifications, except its disappearance. The structure diminished in some groups, greatly enlarged in others, as well as modified some of its components, and gained some annexed structures, sometimes mischaracterizing it for easy recognition. This paper deals exactly with this, the main kind of modifications that pleurembolic proboscis underwent along with the rhynchogastropods evolution.

Firstly, a basal anatomical terminology is necessary to be stated in an average pleurembolic proboscis. Fig. 1 represents a usual pleurembolic proboscis in dorsal view and opened longitudinally, showing some internal structures like buccal mass and esophagus (green). The proboscis (beige) is represented extended (Fig. 1A) and fully retracted (Fig. 1B), a movement mainly provided by the pair of retractor muscles (rm). More details can be found in Simone (2019), including the usually multiple insertions of the proboscis retractor muscles, represented single in Fig. 1 as a didactic simplification. The retracted condition (Fig. 1B) remains with a distal portion of the proboscis non-retracted; this portion is called **proboscis buccal mass** (pm). The remaining, proximal or basal proboscis portion forms the **rhynchodeal wall** (rw), which surrounds the **rhynchodeal cavity** (rc), only present in retracted condition and disappearing in extending one (Fig. 1A). Other structure that only appears in retracted condition is the **rhynchostome**, or rhynchodeum (Fig. 1B: ry). The rhynchostome simulates the mouth in retracted proboscis, and it is even called “external mouth” in some old papers. The true mouth lies in the proboscis' tip (mo). All these structures are important for the understanding of successive proboscis modifications explored below.

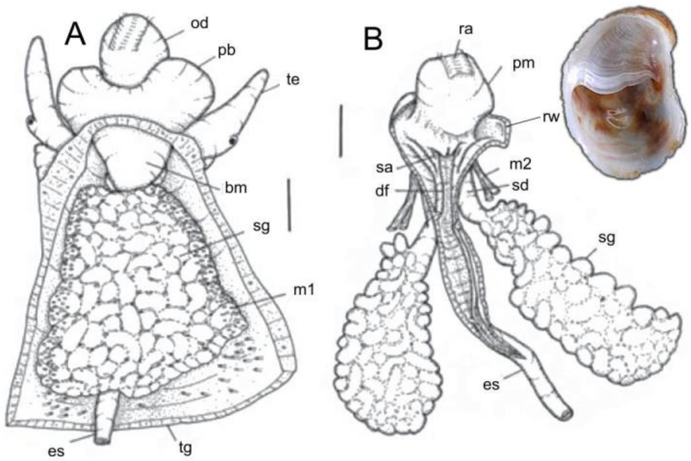
From the above schematized pleurembolic proboscis model, a series of additional modifications occurred along with the rhynchogastropods evolution. The main modifications are explained in the topics below. In the end, a phylogenetic approach is given, showing which main branches evolved to each kind of modifications.

Several different kinds of gastropod proboscis classifications exist in the literature (e.g., Ball et al., 1997; Strong, 2003), however, all types of reported categories actually are derived from

3 main types: 1) an elongated snout (not a proboscis) (e.g., of stromboideans), 2) acrembolic, and 3) pleurembolic. Details on this issue are found elsewhere (Simone, 2011, 2019), thus a long debate on proboscis classification is not performed here, as the main concern is those proboscis models derived from the pleurembolic type, some of which have been reported as different categories.

1) Proportional minute pleurembolic proboscis

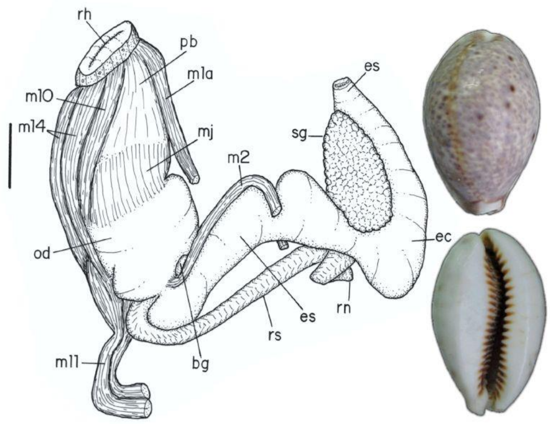
The pleurembolic proboscis is small in the most basal branch of the rhynchogastropods – the Calyptraeoidea (Simone, 2002, 2011, 2019) (Fig. 2). The minuteness and the commonly extended proboscis in preserved specimens raise confusion with a simple snout. However, the morphological conformation of the structure and the capacity of retraction permit its classification as a pleurembolic proboscis, small, but a proboscis, as can be seen in Figs. 2A (pb) and 2B (pm, rw).



2. *Bostrycapulus odytes* as example of small pleurembolic proboscis (shell in right-superior corner, ventral view, ~20 mm): **A**, head-foot, ventral view, foot removed, proboscis extended; **B**, foregut, ventral view, mostly opened longitudinally. Lettering: bm, buccal mass; df, dorsal fold of oral cavity; es, esophagus; m1, jugal muscles; m2, buccal mass retractor muscle; od, odontophore; pb, proboscis; pm, buccal mass proboscis portion; ra, radula; rw, rhynchodeal wall; sa, salivary aperture; sd, salivary gland duct; sg, salivary gland; te, cephalic tentacle; tg, integument. (shell courtesy Femorale – www.femorale.com) (drawings modified from Simone, 2002); scales= 1 mm.

This minuteness of proboscis can be primary in calyptraeoideans, as the following rhynchogastropod branch – the Adenogastropoda – has more elongated proboscises. Only a few other caenogastropods bear small proboscis, and, in those cases, it can be called reduced. Examples are the neogastropod deep-sea benthobiids (Simone, 2003, e.g., fig. 7F).

2) Small buccal mass portion of pleurembolic proboscis



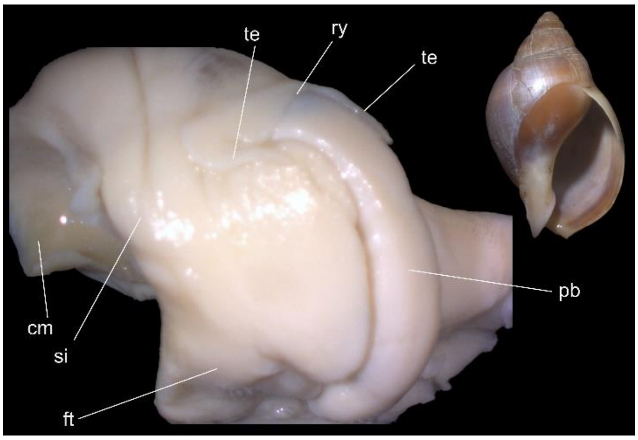
3. *Lyncina linx* as example of pleurembolic proboscis with small buccal mass portion (shell in right, dorsal and ventral views, ~20 mm): foregut, left view. Lettering: bg, buccal ganglion; ec, esophageal gland; es, esophagus; m1a, dorsal buccal mass retractor muscle; m2, buccal mass retractor muscle; m10+m14, ventral buccal mass retractor muscles; m11, ventral radular tensor muscle mj, peri-buccal muscles; od, odontophore; pb, proboscis; rh, rhynchostome; rn, radular nucleus; rs, radular sac; sg, salivary gland (modified from Simone, 2004); scale= 1 mm.

Some taxa have the buccal mass portion of the pleurembolic proboscis ("pm" in Fig. 1) reduced (Figs. 3, 7C). This condition simulates an acrembolic proboscis, as apparently the proboscis retracts completely. However, the pleurembolic condition is regarding a small distal portion of the buccal mass still protruding inside rhynchodeal cavity even in a fully retracted structure (Fig. 7C). This condition is not found in any truly acrembolic proboscis.

A small buccal mass portion of pleurembolic proboscis is notorious in naticoideans (Simone, 2011), but it is also found in more advanced cypraeoideans, i.e., ovulids+cypraeids (Simone, 2004: fig. 531 – node 12). Interestingly, the more basal cypraeoideans (velutinids, eratoids, triviids, pediculariids) have an elongated pleurembolic proboscis of a usual model (represented in Fig. 1).

3) Extreme elongated buccal mass portion of pleurembolic proboscis

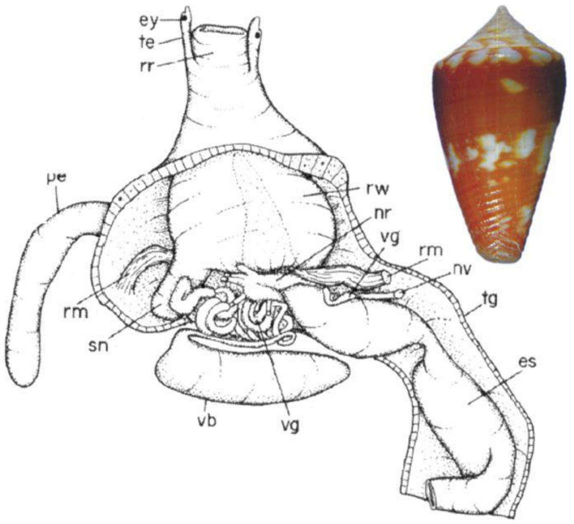
On the contrary to the previous condition, some taxa overly developed buccal mass portion of the pleurembolic proboscis ("pm" in Fig. 1). That portion becomes so elongated that it no longer easily fits inside the rhynchodeal cavity. Some specimens having this condition can retract the buccal mass portion inside, but this capacity demands an additional convolution of it. Other specimens simply maintain a portion of the proboscis permanently protruded (Figs. 4, 7D).



4. *Buccinanops paytensis* as example of pleurembolic proboscis with very large buccal mass portion (shell in right, apertural view, ~30 mm): extracted head-foot of fixed specimen, dorsal-slightly right view (partially shown). Lettering: cm, columellar muscle; ft, foot; pb, proboscis; ry, rhynchostome; te, cephalic tentacle; si, siphon.

Several rhynchogastropods developed this condition, the more usual ones are the tonnoideans (almost as a whole), and several buccinoideans (Fig. 4). The exaggerated development of the buccal mass portion of the proboscis sometimes also simulates an acrembolic type or even an elongated snout. Both references are found in literature, including classifications putting it apart from pleurembolic type (e.g., Ponder & Lindberg, 1997), however, the morphological structure clearly shows the usual conformation of a pleurembolic proboscis.

4) Pleurembolic proboscis with permanent rhynchodeal cavity



5. *Dauciconus ziczac bertarollae* as example of pleurembolic proboscis with permanent rhynchodeal cavity (shell in right, dorsal view, ~25 mm): head-foot, ventral view, foot and columellar muscle removed, buccal mass portion of proboscis seen by translucency. Lettering: es, esophagus; ey, eye; pe, penis; nr, nerve ring; nv, verve; rm, proboscis retractor muscle; rr, rostrum; rw, rhynchodeal wall; sn, snout gland; te, cephalic tentacle; tg, integument; vb, venom bulb; vg, venom gland. (from Costa & Simone, 1997)

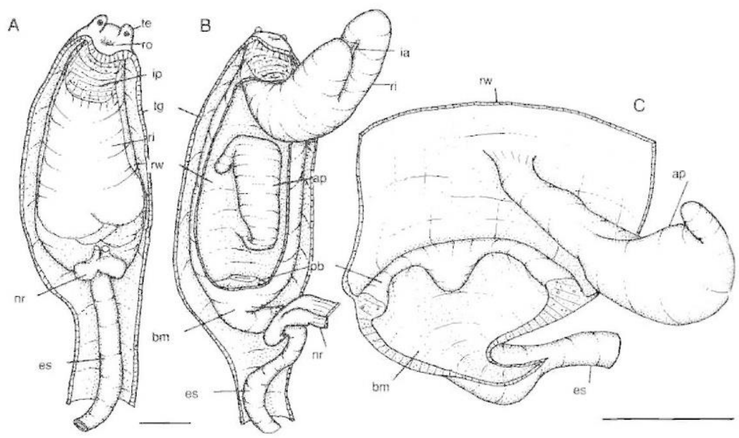
Based on the retracted usual pleurembolic proboscis represented in Fig. 1B, with special reference to the rhynchodeal cavity (rc), flanking by rhynchodeal wall (rw), some taxa evolved to bear a permanent rhynchodeal cavity. In this condition, the rhynchodeal wall (rw), despite being the basal portion of the proboscis, becomes translucent, thin-walled, wide (Fig. 5: rw), and no more it is exteriorized. The remaining proboscis portion – the buccal mass portion (seen by translucency in Fig. 5, 7D) – becomes the main portion that is protruded.

The buccal mass portion of the proboscis can be greatly elongated, exiting through the rhynchostome for the prey capture. The prey can thus be brought inside the permanent rhynchodeal cavity to be consumed. The protrusion of the buccal mass portion of the proboscis is provided by simple hydraulic pressure, as usually occurs in the proboscises (Simone, 2019). Its retraction, however, is provided by a pair of lateral proboscis retractor muscles, which originate in the middle level of the haemocoelic wall (Fig. 5: rm); a mechanism also similar to a usual pleurembolic proboscis. As the insertion of the pair of retractor muscle is dislocated further posteriorly, the proboscis proximal portion is more difficultly exteriorized, becoming a permanent inner cavity.

The model of pleurembolic proboscis having a permanent rhynchodeal cavity is usual in Conoidea, excepting its first branch – the Cochlespiridae. A similar conformation is also found in other neogastropods, notoriously in several Marginellidae (Simone, 2011; Souza & Simone, 2019, e.g., fig. 87: node 4) and some Mitridae (person. obs.). The conoidean kind of proboscis has been classified as "intraembolic", apart from the pleurembolic type (e.g., Miller, 1989), and sometimes only the buccal mass portion has been referred to as "proboscis" (e.g., Taylor et al., 1993).

5) Further modifications of the pleurembolic proboscis

The modifications of the pleurembolic proboscis explained above are only the main tendencies. In a taxon as huge as the rhynchogastropods, all kinds of proboscis modifications are expected. Only its total reduction was not found, but a reduction of some of its parts is not rare. Also, the appearance of annexed structures is found in several taxa. Noteworthy in proboscis oddities are the conoideans, particularly the Terebridae (Simone, 1999, 2000) and some turriform branches (Simone, 2011).

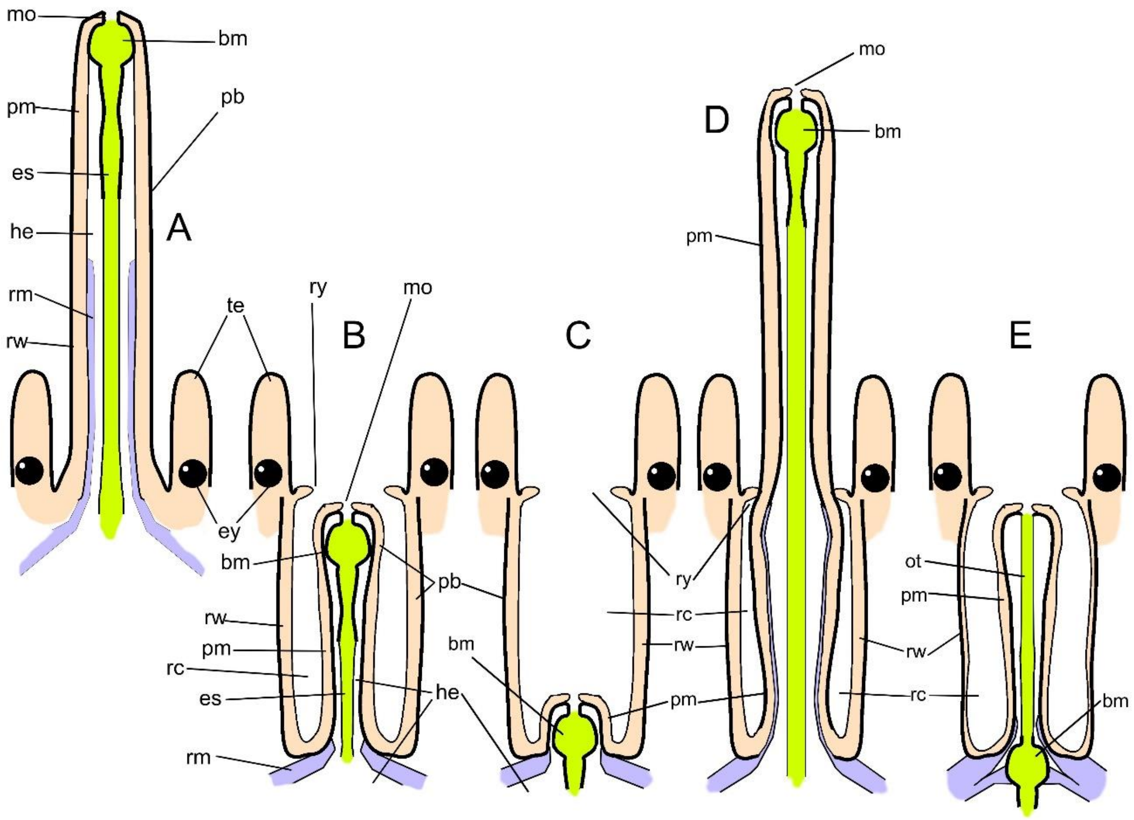


6. *Neoterebra brasiliensis* as example of weird pleurembolic proboscis: **A**, head-foot, ventral view, foot and columellar muscle removed, inner proboscis structures seen by translucency; **B**, same, ventral portion of rhynchodeal wall remoded, introvert deflected upwards; **C**, same, detail of reminiscent proboscis buccal mass portion opened longitudinally (scales= 0.5 mm). Lettering: ap, accessory proboscis structure; bm, buccal mass portion of proboscis (slightly reduced); es, esophagus; nr, nerve ring; ro, rhynchostome; ia, introvert aperture; ip, insertion in foot musculature; ri, rhynchodeal introvert; rw, rhynchodeal wall; te, cephalic tentacle; tg, integument. (from Simone, 1999).

Some interesting terebrid proboscis structures can be found elsewhere (Simone, 1999, 2000, and references therein), but a good example is *Neoterebra brasiliensis* (Fig. 6). The pleurembolic proboscis is modified as a permanent, thin, translucent rhynchodeal wall (rw) and a reduced buccal mass portion (bm). The species completely lost the venom apparatus and odontophore. Additionally, an interesting great introvert is present (ri), a structure that can be exteriorized (it is shown retracted, inside-out in the specimen) and becomes a wide, muscular cone expanding the rhynchostome. The introvert is analogous (homologous?) to the rostrum of the conids (Fig. 5: rr), but, differently, the conid rostrum cannot be retracted (Simone, 2011). The introvert is an interesting synapomorphy of the Terebridae. Furthermore, *N. brasiliensis* has an accessory proboscis structure, or appendix (Figs. 6B, C: ap). Proboscis appendices and accessory structures are relatively common in terebrids. Usually, they have a mucous epithelium and a muscular structure, and they can even be branched. Nothing similar is found in conids; on the other hand, conids commonly have glandular annexed structures in the proboscis (e.g., Fig. 5: sn) (Simone, 2011). A myriad of proboscis modifications is also found in turriform conoideans, which have since species with usual pleurembolic proboscis (as *Cochlespira*, see below) up to, e.g., *Daphnella*. This genus completely atrophied all foregut structures, only the rhynchodeal wall remained, connected directly to the esophagus (Simone, 2011).

The Rachiglossa (i.e., non-conoidean neogastropods, mostly stenoglossans) does not have the same level of proboscis oddities as the conoideans. Despite several kinds of modifications are found, they mostly are only quantitative, i.e., hypotrophy or hypertrophy of some of the proboscis parts. Rarely novelties appear. One of the few examples is found in Mitridae. The family is noteworthy in having an **epiproboscis**, a secondary protractile projection developed to exteriorize the salivary secretion (Ponder, 1972, Simone & Turner, 2010). The structure is a stem that runs through odontophore and proboscis and has a pair of salivary grooves.

Confrontation amongst the diverse main types of pleurembolic proboscis



7. Schematic representation of main types of pleurembolic proboscis in dorsal view, sectioned longitudinally: **A**. medium elongated proboscis, extended condition; **B**, same, retracted condition; **C**, proboscis with small buccal mass portion, retracted condition; **D**, proboscis with enlargement of buccal mass portion, retracted condition; **E**, proboscis with permanent rhynchodeal cavity and buccal mass at base of buccal mass portion of the proboscis. B-D have a similar aspect as represented in A in extended condition, while E remains with the rhynchodeal cavity (rc). Lettering: bm, buccal mass; es, esophagus; he, haemocoel; ot, oral tube; mo, mouth; pb, proboscis; pm, proboscis buccal mass; rc, rhynchodeal cavity; rm, proboscis retractor muscle; rw, rhynchodeal wall; ry, rhynchostome; te, cephalic tentacle. Not all structures indicated, but easily inferred.

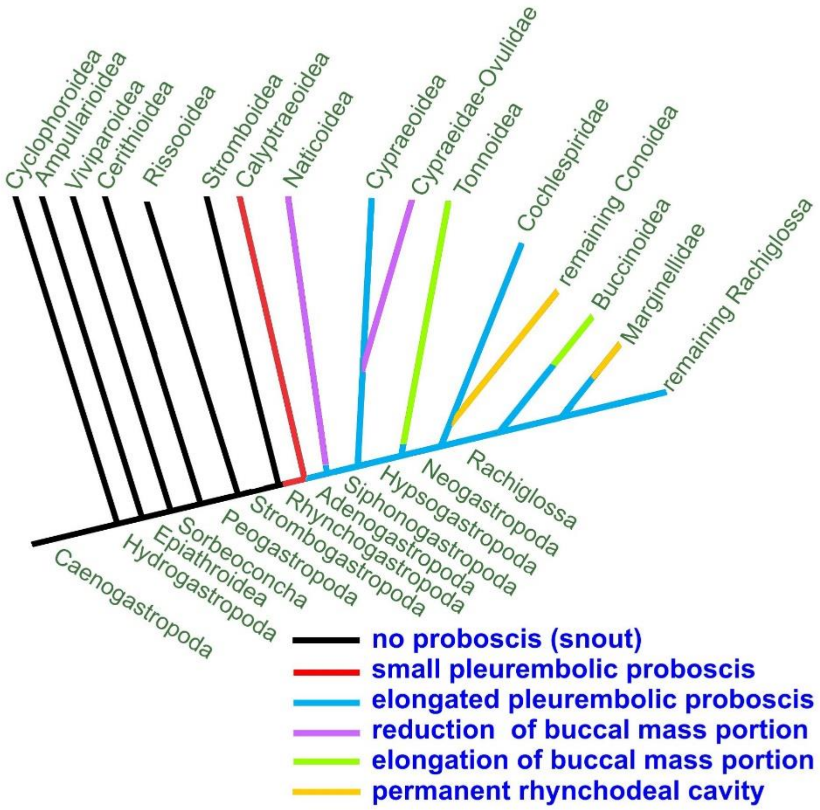
The anatomical analysis of the rhynchogastropod proboscis clearly shows that they are all clearly derived from the pleurembolic model. The Fig. 7 makes it easier to understand, as shows the different components in a similar position. The homologue structures are relatively easy to check, and the main differences are basically quantitative, i.e., augmenting or reducing some part of the proboscis. The small-sized pleurembolic proboscis is not represented in the Fig. 7, because it is simply like that represented in Fig. 7A-B, but smaller. The Figs 7A-B represents an averagely elongated pleurembolic proboscis in extended (A) and completely retracted (B) condition already reported above. The pleurembolic proboscis having a small buccal mass portion is represented in Fig. 7C, in such that portion is simply reduced. The contrary happens in the pleurembolic proboscis with enlargement of buccal mass portion (Fig. 7D), in such that portion is so increased that no more, or difficultly fits inside the rhynchodeal cavity (rc). The pleurembolic proboscis having a permanent rhynchodeal cavity is represented in Fig 7E, in such the buccal mass portion of it is the main part that is exteriorized. Interestingly, usually the buccal mass stays at the base of the contracted proboscis; a very long oral tube (ot) connects it to the mouth, located at proboscis tip. The oral tube also exists in the other proboscis types, but it is short. Usually, a portion of the proboscis retractor muscles have branches connected to the buccal mass.

It is important to emphasize that the retractor muscles (rm) usually have several insertions along the proboscis inner surface. A single region is represented in Figs. 1, 7 (except for Fig. 7D) for didactic reasons only.

Despite the pleurembolic type of proboscis is exclusive (a synapomorphy) of the Rhynchogastropoda, its modifications are not exclusive, and they all happen in more than one non-related taxa. This is better explained below.

Phylogenetic inferences of the pleurembolic proboscis

The Fig. 8 represents a phylogenetic representation of the Caenogastropoda, mostly based on Simone (2011). In it, the pleurembolic model of proboscis is represented as a synapomorphy of the Rhynchogastropoda (the reason for the name of the taxon). Its first branch, the calyptraeoideans (Fig. 1), has small pleurembolic proboscises (red). The naticoideans, the second branch, have reduced buccal mass portion (purple). Moreover, all naticoideans bear an ABO (accessory boring organ), a glandular bulge located in the ventral region of the proboscis' tip. The following branch, the Siphonogastropoda, has as a rule an averagely elongated pleurembolic



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

proboscis (Figs. 1, 8A-B) (blue). This elongation is shown as a synapomorphy of the Adenogastropoda, as naticoideans have a relatively elongated proboscis, despite having a small buccal mass portion. Interestingly, the Cypraeoidea have elongated proboscis only in its basal branches. The proboscis also has a short buccal mass portion in the cypraeoidean branch encompassing Cypraeidae plus Ovulidae (Simone 2001: fig. 531, node 12) (purple), convergent with naticoideans.

An extreme elongation of the buccal mass portion of the pleurembolic proboscis is found in Tonnoidea (as a synapomorphy), and in several Buccinoidea (Fig. 4) amongst the rachiglossans (green). These are clearly convergencies. A permanent rhynchodeal cavity (orange) is found in most conoideans, excepting its first, more basal branch – the Cochlespiridae; and in some Marginellidae amongst the rachiglossans. These are certain convergencies. It is important to emphasize, anyway, that the survey is not exhaustive, some other taxa also independently developed similar kinds of pleurembolic proboscis modifications. The main intention, once more, is to show the main tendencies and that all of them have convergencies and/or reversions (i.e., homoplasies).

Acknowledgements

This paper was peer reviewed by Claudia Heromy Guimarães, Australia, in such I am grateful. I also thank the Femorale team, particularly José & Marcus Coltro, for the shell image of the Fig. 2.

References

Ball, AD; Andrews, EB & Taylor JD, 1997. The ontogeny of the pleurembolic proboscis in *Nucella lapillus* (Gastropoda: Muricidae). Journal of Molluscan Studies 63: 87-99.

Costa, PMS & Simone, LRL, 1997. A new species of *Conus* Linné (Caenogastropoda, Conoidea) from the Brazilian coast. Siratus 3(13): 3-8.

Miller, JA, 1989. The toxoglossan proboscis: structure and function. Journal of Molluscan Studies 55: 167-181.

Ponder, WF, 1972. The morphology of some mitriform gastropods with special reference to their alimentary and reproductive systems (Neogastropoda). Malacologia 11: 295-342.

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, 1999. Comparative morphology and systematics of Brazilian Terebridae (Mollusca, Gastropoda, Conoidea), with descriptions of three new species. Zoosystema 21(2): 199-248. http://www.moluscos.org/trabalhos/1999/Simone%201999%20Terebridae.pdf

Simone, LRL, 2000. A phylogenetic study of the Terebrinae (Mollusca, Caenogastropoda, Terebridae) based on species from the Western Atlantic. Journal of Comparative Biology 3(2): 137-150. http://www.moluscos.org/trabalhos/2000/Simone%202000%20Terebrinae%20phylogeny.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. http://www.moluscos.org/trabalhos/2002/Simone%202002%20-%20Calyptraeoidea.pdf

Simone, LRL, 2003. Revision of the genus *Benthobia* (Caenogastropoda, Pseudolividae). Journal of Molluscan Studies 69: 243-261.

Simone, LRL, 2004. Morphology and phylogeny of the Cypraeoidea (Mollusca, Gaenogastropoda). Papel Virtual. Rio de Janeiro, 185 pp. http://www.moluscos.org/trabalhos/2004/Simone%202004%20-%20Cypraeoidea.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%202011a%20Caenogastropoda%20Phylogeny%20LIGHT.pdf

Simone, LRL, 2019. The proboscis of the Gastropoda 1: its evolution. Malacopedia 2(4): 22-29 http://www.moluscos.org/trabalhos/Malacopedia/02-04Simone%202019%20Malacopedia-Probosis.pdf

Simone, LRL & Turner, H, 2010. Anatomical description of *Ziba carinata* from Ghana (Caenogastropoda, Mitridae). Strombus 17: 1-11. http://www.moluscos.org/trabalhos/2010/Simone%20&%20Turner%202010%20Ziba%20carinata.pdf

Souza Jr., PJS & Simone, LRL, 2019. Cladistic analysis of the family Marginellidae (Mollusca, Gastropoda) based on phenotypic features. Zootaxa 4648(2): 201-240. doi.org/10.11646/zootaxa.4648.2.1

Strong, EE, 2003. Refining molluscan characters: morphology, character coding and a phylogeny of the Caenogastropoda. Zoological Journal of the Linnean Society 137: 447-554.

Taylor, JD, Kantor, YI & Sysoev, AV, 1993. Foregut anatomy, feeding mechanisms, relationships and classification of the Conoidea (= Toxoglossa) (Gastropoda). Bulletin of the Natural History Museum of London (Zoology) 59(2): 125-170.