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The proboscis of the Gastropoda 1: its evolution

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Abstract

The proboscis is a remarkable feature developed by some branches of the Gastropoda. The structure is an elongation of the snout associated to the capacity of retraction inside haemocoel, adaptations which are explained in an evolutionary and phylogenetic scenario. Two basic kinds of proboscis exist: the pleurembolic proboscis, which have only partial capacity of retraction, ass synapomorphy of the caenogastropod Rhynchogastropoda; and the acrembolic proboscis, which occur as convergence at least in some basal heterobranchs, in pulmonate Streptaxidae, and in caenogastropod ctenoglossans. The acrembolic proboscis has total capacity of retraction and is usually related to parasitism.

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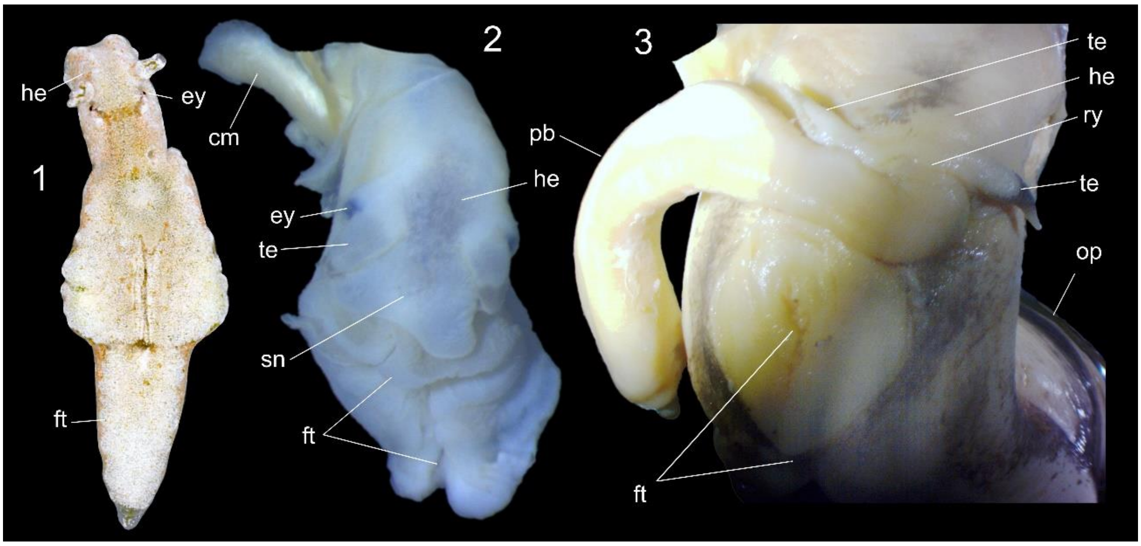
Introduction

Any elongation of the anterior region of the face of any animal can be called proboscis. An example is the mammalian order Proboscidea, i.e., proboscis-bearing afrotherian, elephant and elephant-like animals with snout modified as trunk. Another example is the protobranch bivalves, their proboscis is a prolongation of the labial palps that is used for food capture in the sediment, nothing homologous to the gastropods. In the gastropods, however, a more detailed terminology must be coined, in order to demonstrate analogous or homologous structures. Gastropod heads can be divided in 3 types: 1) a plane head; 2) a head with snout; and 3) head having proboscis.

The plane head (1) is mostly usual in heterobranchs and consists of a head that is not protruded, with surface uniform with remaining parts of the body (Fig. 1). The head having a snout (2), on the other hand, has an anterior protuberance, in such the mouth stays at its tip. This kind of head is the usual in more basal gastropods, including all taxa of the archaeogastropod grade, and the basal caenogastropods. The snout obviously has a capacity of certain movements independent from remaining body, mainly in exploratory and feeding activities. However, snouts have no capacity of retraction inside the head-foot, i.e., a snout never disappear from the snails' face.



1. *Elisia orientalis*, lacking snout and proboscis (L ~6 mm) (courtesy Hilton Galvão Fo); **2**, *Parachondria neglectus*, with snout (L ~10 mm); **3**. *Buccinanops gradatus*, specimen preserved with extended proboscis (L ~50 mm). Lettering: **ey**, eye; **ft**, foot; **he**, head; **op**, operculum; **pb**, proboscis; **ry**: rhynchostome; **sn**, snout; **te**, tentacle.

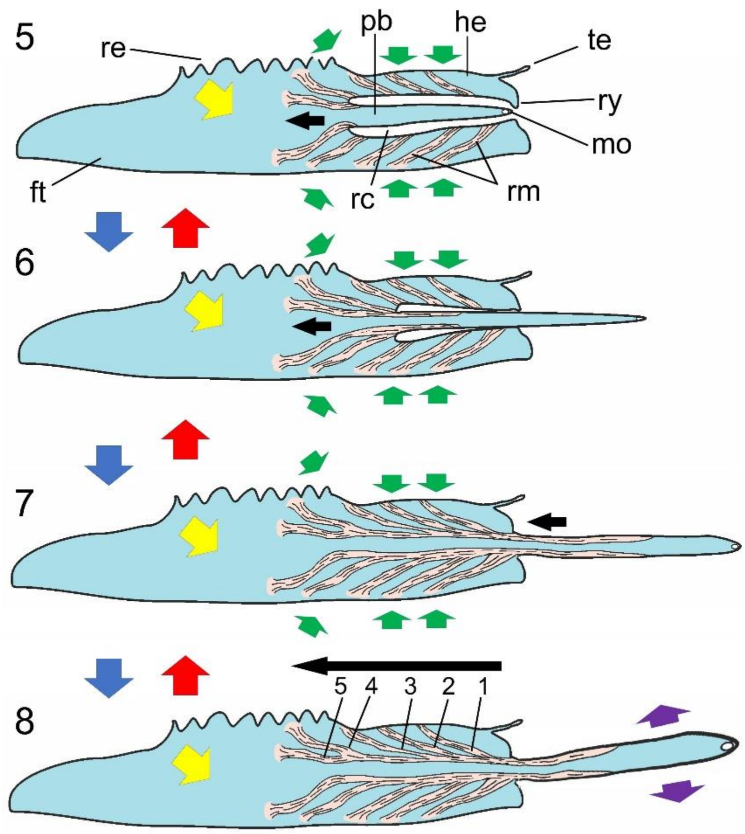
Snouts have all kinds of modifications, they can be very short, as most Rissooidea, and very long, simulating a proboscis, as in Strombidae (Fig. 4). Snouts can have secondary appendices, such as papillae in several Vetigastropoda, and lateral expansions in Ampullariidae. Snouts modifications and adaptations are matter for a future paper.

4. *Strombus alatus*, alive, note long **snout** that can extend and move independently, but has not capacity of retraction inside the head-foot (L ~60 mm) (from Wikipedia).

Gastropods that have proboscis (3), their head can change considerably in shape according to the degree of contraction of the organ. If the proboscis is fully extended; the head's shape is if the animals have an elongated snout. On the other hand, if the proboscis is fully retracted, the head looks like a plane head. Proboscis can be in any intermediary position between fully extended to totally sheltered in preserved animals, but normally the organ is retracted.

How does proboscis work?

In simple words, the proboscis is protruded by toothpaste effect, i.e., head-foot and cardiac pressure press the liquid (blood) inside the proboscis to push it out, to be exteriorized and extended. The retraction back of the proboscis in only provided by proboscis retractor muscles. The Figs. 5-8 are schematic representations of a generic proboscis-bearing gastropod. In the Fig. 5 the proboscis (pb) is fully retracted, sheltered inside a space called rhynchodeal cavity (rc), a space that disappear when the organ is protruded. To start the proboscis protrusion, the proboscis retractor muscles relax, the head-foot's walls musculature contracts in order to augment the hydraulic pression inside haemocoel. This pression increment is also helped by the cardiac pression (yellow arrow), as



5-8. Schematic representation of a generic head-foot of a proboscis-bearing gastropod in sagittal section. **5**, proboscis fully retracted; **6**, proboscis in mid-way to be protruded; **7**, proboscis fully extended; **8**, extended proboscis showing lateral movements. **Blue arrows**: sequence of protraction; **red arrows**: way back to retraction; forces to proboscis protraction: **green arrows**: forces of head-foot muscular walls, **yellow arrow**: cardiac pressure; **black arrow**: forces for proboscis retraction produced by proboscis retractor muscles; **purple arrow**: extra movements of proboscis by intrinsic muscles of its walls. Lettering: **ft**, foot; **he**, head; **mo**, mouth; **pb**, proboscis; **rc**, rhynchodeal cavity; **re**, remaining animal portions (pallial cavity and visceral mass); **rm**, proboscis retractor muscles; **ry**, rhynchostome; **te**, cephalic tentacle; **1 to 5**, gradation of successive contraction of muscles for proboscis retraction. **Light blue color**: blood inside haemocoel. **Beige**: muscles.

mostly proboscis-bearing gastropods have large hearts. This pression increase causes inflation of the internal proboscis blood, forcing it outwards though the rhynchostome (ry). This protrusion is accompanied by the diminishment of the rhynchodeal cavity and by the gradual entrance of the retractor muscles inside proboscis cavity (Fig. 6). Of course, all organs and structures which are in the base of the proboscis gradually also go inside it, mostly the foregut, which must be connected to the mouth at proboscis' tip. They are not represented in the Figures.

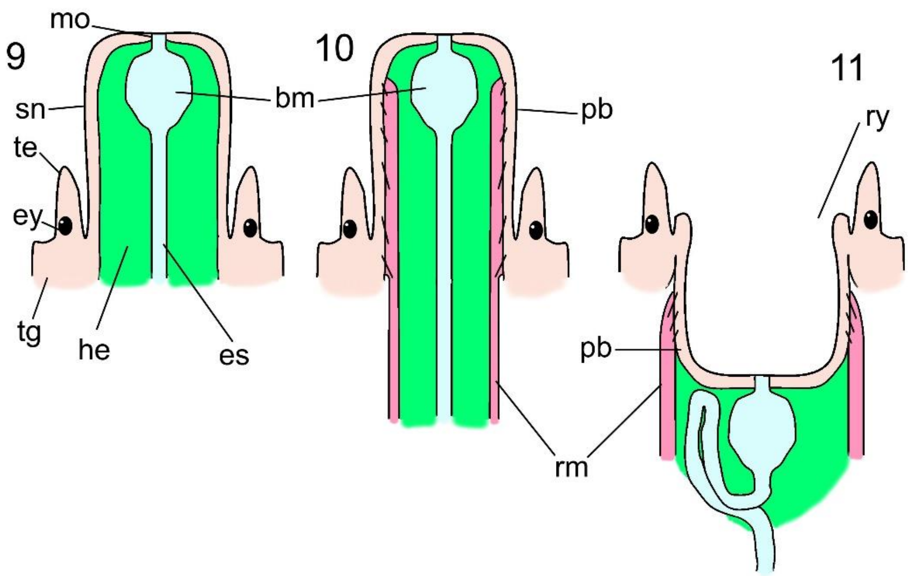
The Fig. 7 represents a totally protracted proboscis, ready for its action of exploring, attacking and eating. The proboscis retractor muscles are all stretched inside the structure. The proboscis is maintained extended by the constant contraction of the haemocoel wall muscles. The Fig 8 represents the remaining proboscis movements, such as bending, lateralization, elevation, winding, etc., all them provided by the proboscis intrinsic muscle layers at its walls. Normally the proboscises have successive layers of circular, oblique and longitudinal muscles which can be differentially contracted to produce different forms and elongations. Then, the succession of protrusion events is represented in the Figs. 5-8 following the blue arrows.

The retraction of the proboscis is represented following the red arrows in Figs. 8-5. The proboscis retraction is only made by the retractor muscles, which normally are a pair (left and right), but with multiple origins, from anterior to posterior. The Fig. 8 shows a hypothetic gastropod having 5 successive origins, the numeration shows the order of contraction while the proboscis is being retracted, represented by the black arrow. The anterior-most pair of muscles (1) contracts first, being gradually succeeded by the more posterior ones (2 to 5). The number of origins of each retractor muscles is not constant, can vary or being fused, i.e., represented by wide, elongated sequence of muscles; they usually are also asymmetric and twisted. This sequence of contraction is important to put the proboscis and adjacent structures in their correct place inside haemocoel, otherwise some structure can be displaced or wrinkled by the others, a physiological problem for contractile organisms. The reallocation of structures is also helped by the net of jugal muscles that connect all haemocoelic structures. According the proboscis is being retracted, the rhynchodeal cavity reappears, and is used to shelter it.

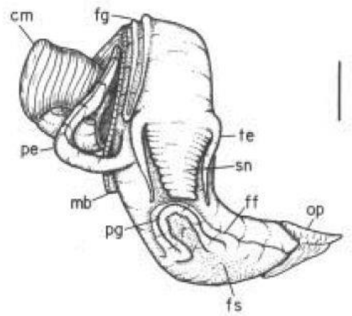
The degree of retraction of the proboscis depends how inside is the last retractor muscle. If it is placed in the middle, the proboscis only retracts halfway of its length. In this case, the distal half of proboscis remains not retracted, permanently sheltered inside the rhynchodeal cavity; this kind of proboscis is a typical **pleurembolic** proboscis. On the other hand, if the last retractor muscles are inserted close to the proboscis' tip, the proboscis can be retracted totally, being stored entirely inside out; this kind of proboscis is the typical **acrembolic** proboscis.

Proboscis evolution

The gastropod proboscis is clearly a modification and a specialization of the snout. For the transformation of a snout can occur, two basic adaptations should happen: (1) the development of retractor muscles, in such origin should be more posterior than snout's base, and (2) the appearance of a space inside haemocoel to shelter it. This suggested evolution is represented in the Figs. 9-11. These Figures are transverse section in the frontal plane just in the level of the tentacles, in a dorsal view. The Fig. 9 shows an ordinary snout-bearing gastropod, as occur in all archaeogastropods and basal caenogastropods. The snout has some capacity of shortening, stretching, and moving independently from the remaining head-foot. However, it has no capacity to be retracted inside, i.e., it never disappears. The Fig. 10 represents another step towards a proboscis – the appearance of a pair of lateral retractor muscles (rm). The origin of these muscles is along the dorsal surface of the foot (inside haemocoel) and in the lateral walls of the haemocoel;



9-11. Schematic representation of anterior region of a generic gastropod head, and the suggested evolution of the proboscis; frontal section, dorsal view. **9**, a snout; **10**, an extended proboscis; **11**, a retracted proboscis. Lettering: **bm**, buccal mass; **es**, esophagus; **ey**, eye; **he**, haemocoel; **mo**, mouth; **pb**, proboscis; **rm**, proboscis retractor muscles; **ry**, rhynchostome; **sn**, snout; **te**, cephalic tentacle; **tg**, integument.

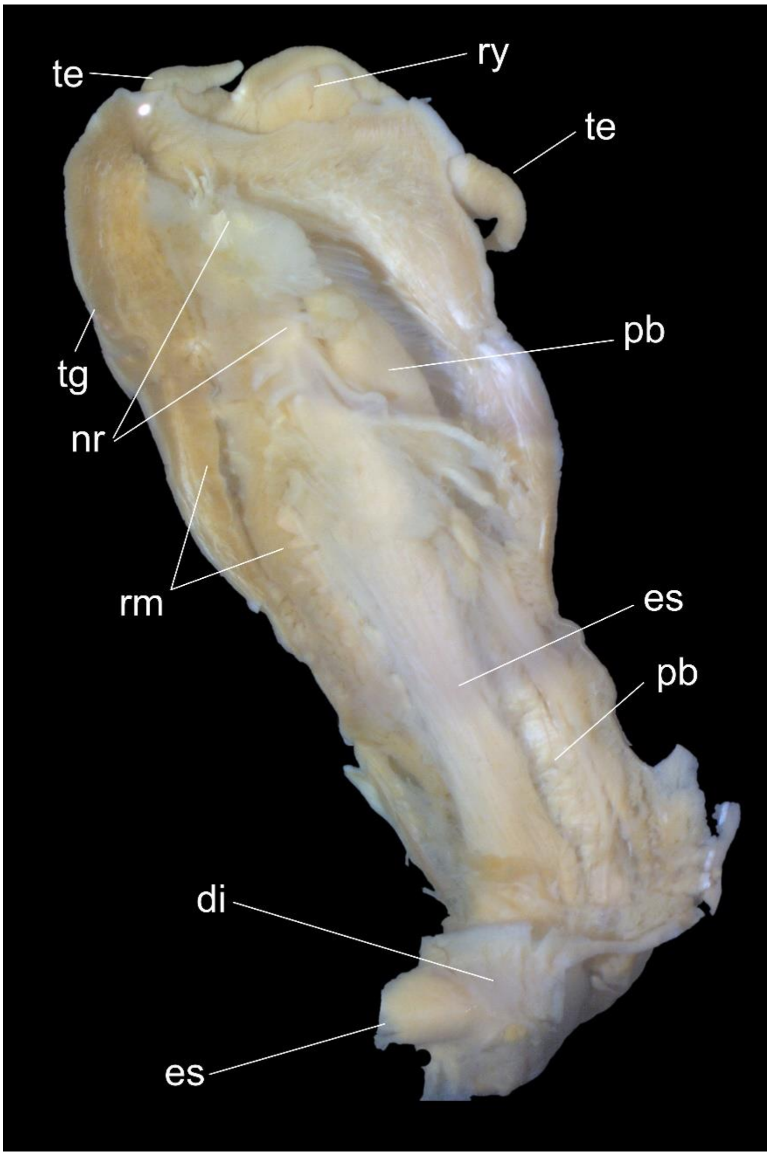


12. *Tylospira scutulata* (Struthiolariidae), isolated male head-foot, frontal view. Lettering: **bm**, buccal mass; **cm**, columellar muscle; **es**, esophagus; **ff**, foot groove; **fg**, food groove; **fs**, foot sole; **mb**, mantle border; **op**, operculum; **pe**, penis; **pg**, pedal gland furrow; **sn**, snout; **te**, cephalic tentacle. Scale= 5 mm.

their insertion is along the lateral snout inner surface. When these muscles contract, they pull the structure inside (Fig. 11). In the classification by Simone (2011), the pair of retractor muscles appeared in the Strombogastropoda, i.e., in the branch preceding Stromboidea in caenogastropod phylogeny (Simone, 2011: fig. 21). The stromboideans have the pair of retractor muscles mostly immersed in the innermost muscular layer of the snout walls. This gives a capacity of shortening their snouts; this is particularly clear in struthiolariids, in such the snout has a high capacity of lengthening, but it must be retracted in emergencies, being stored with several successive folds, but, as snout, remains outside of the head (Fig. 12).

The final evolutionary step towards a proboscis only appeared in the Rhynchogastropoda (Simone, 2011), i.e., the space inside haemocoel to store it, permitting its retraction inside haemocoel and its complete disappearance in external view when contracted (Fig. 11). All rhynchogastropod taxa bear proboscis, although some of them have short ones, such as the calyptraeoideans.

The above-mentioned proboscis evolutionary pathway is relevant to the main caenogastropod taxa, studied by Simone (2011) – the pleurembolic proboscis. However, proboscises also appeared in other taxa inside and outside Caenogastropoda, as it will be explained below.

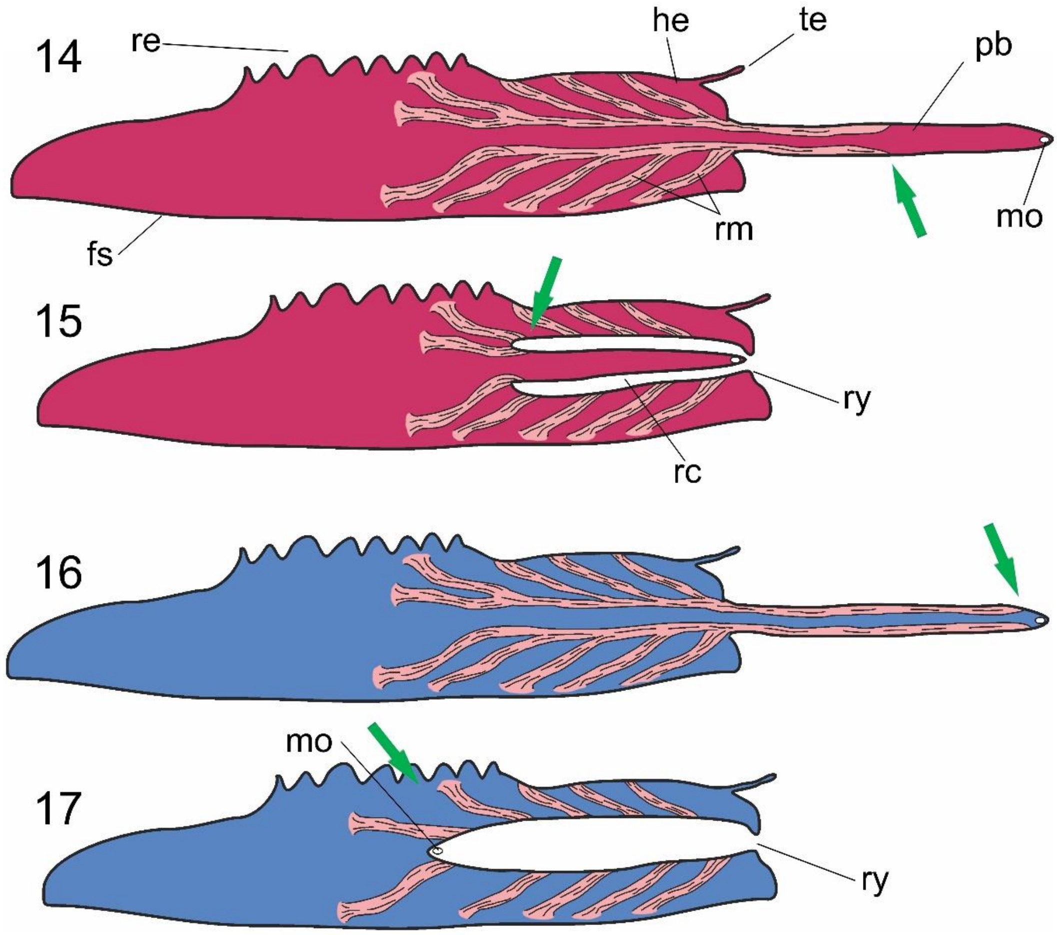


13. *Buccinanops gradatus* (Dorsaniidae), isolated haemocoel, ventral view, inner structures as in situ, foot and columellar muscle removed (L ~30 mm). Lettering: **di**, diaphragmatic septum; **es**, esophagus; **nr**, nerve ring; **pb**, proboscis; **rm**, proboscis retractor muscles; **ry**, rhynchostome; **te**, cephalic tentacle; **tg**, integument.

Another relevant matter related to the proboscis is the presence of the **diaphragmatic septum**, a caenogastropod synapomorphy (Fig. 13: di). This septum located in the haemocoel transition to visceral mass block entirely the blood fulfilling head-foot haemocoel (mostly only referred as the "haemocoel"), avoiding its leaking to visceral cavity. This improves considerably the hydrostatic operation of the proboscis, as the contraction of the head-foot wall musculature becomes more efficient, pushing the proboscis out. This is the possible reason for the caenogastropods possess the more impressive proboscises, mainly in the predatory groups such as the tonnoideans and several neogastropods. This also promoted the appearance of proboscises in other caenogastropod, non-rhynchogastropod taxa, as reported below. Beyond the caenogastropods, proboscises are rare, which can reinforce the importance of the septum.

Proboscis types

There are two basic types of proboscises: (1) pleurembolic (Figs. 14-15); (2) acrembolic (Figs. 16-17).



14-17. Schematic representation of a generic head-foot of proboscis-bearing gastropods in sagittal section. **14-15**, pleurembolic (exclusive of the Rhynchogastropoda); **14**, proboscis fully extended; **15**, proboscis fully retracted; **16-17**, acrembolic proboscis; **16**, proboscis fully extended; **17**, proboscis fully retracted. **Green arrows**: more distal level of insertion of proboscis retractor muscles. Lettering: **fs**, foot sole; **he**, head; **mo**, mouth; **pb**, proboscis; **rc**, rhynchodeal cavity; **re**, remaining animal portions (pallial cavity and visceral mass); **rm**, proboscis retractor muscles; **ry**, rhynchostome; **te**, cephalic tentacle.

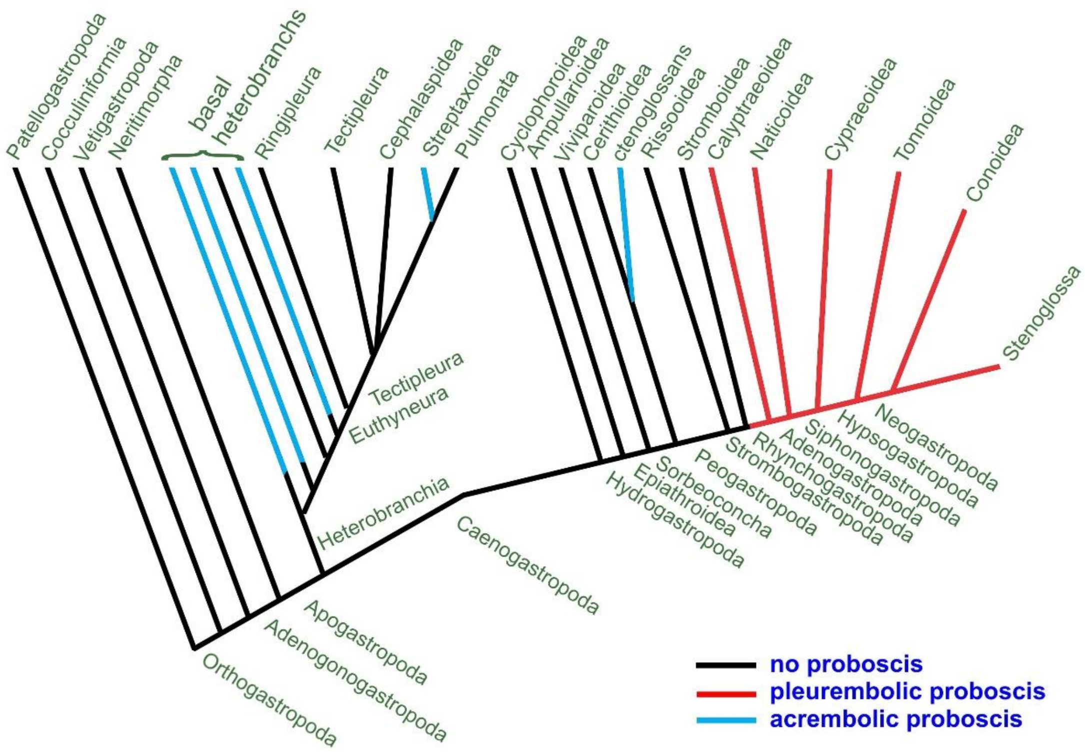
The **pleurembolic** proboscis is that which does not retracts completely inside the haemocoel in an inverted way. It has, then, more distal part of it sheltered inside itself (Fig. 15), in a so-called rhynchodeal cavity (rc). The rhynchodeal cavity is, literally, the cavity of the proboscis. This is the case of the proboscis represented in the Figs. 5, 15. In those cases, the proboscis is only half retracted inside haemocoel, the other half is maintained non-retracted inside the proximal half, the rhynchodeal cavity (rc), with the mouth, located at proboscis tip (mo), located relatively close to rhynchostome (ry). The non-retractile portion of the pleurembolic proboscis can be short, very shorter than the retracted portion, such as in naticoideans, cypraeoideans and calyptraeoideans. On the other hand, that portion can be very long, sometimes it may not fit inside the rhynchodeal cavity, as in most tonnoideans, buccinoideans, etc. the different kind of modifications of the pleurembolic proboscis is aim of another paper especially on it.

The pleurembolic proboscis evolved only once in the gastropod lineage, in the Rhynchogastropoda (Simone, 2011).

The **acrembolic** proboscis has the internal retractor muscles inserted much closer to the mouth, located at its tip (Fig. 16). In fully retracted condition, the acrembolic proboscis becomes completely inverted (Fig. 17). The mouth (mo) is, then, located very far from rhynchostome (ry).

Both basic kind of proboscises, pleurembolic and pleurembolic, are aim of proper issues each, as their further modifications generated the remaining types of proboscises reported in the literature.

Taxa that developed proboscis

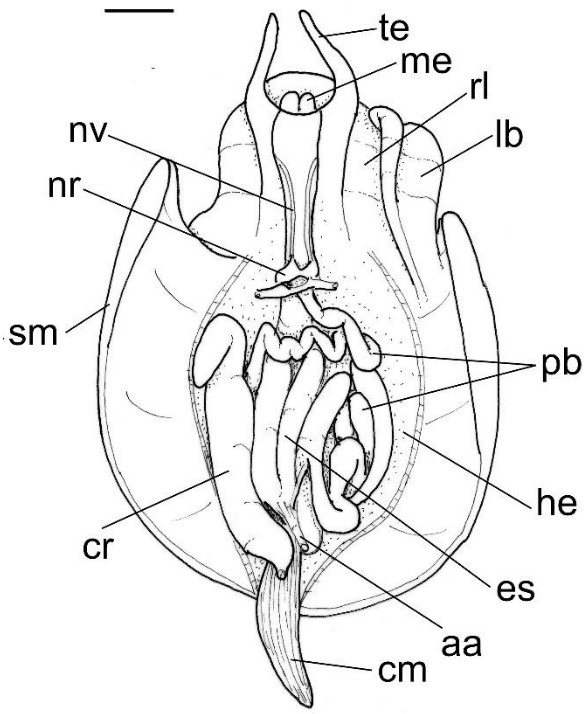


18. An unpretentious cladogram of Gastropoda, mostly based on Simone (2011) and WoRMS, showing more important taxa that have proboscis. **Black lines** represent taxa without proboscis; red: pleurembolic proboscis; blue: acrembolic proboscis. The survey is not exhaustive.

A proboscis appears to be convergent in some gastropod branches. As referred above, the pleurembolic proboscis only appeared once, in the caenogastropod branch Rhynchogastropoda, which includes Calyptraeoidea, Naticoidea, Cypraeoidea, Tonnoidea and the Neogastropoda (Simone, 2011). Although, the development of snout retractor muscle already appeared one branch earlier – in Strombogastropoda (Fig. 18). In strombogastropod first branch – the Stromboidea – the retractor muscles can shorten the snout, but they cannot retract it as a true proboscis. This capacity only appeared one branch after – Rhynchogastropoda – which literally means proboscis-bearing gastropods.

All remaining gastropods that developed proboscis have acrembolic proboscis. The basal Heterobranchia have some branches that possess proboscis, however, there is no certainty if they are related. Possibly the acrembolic proboscis are extraordinary convergences. The basal heretobranchs that are known to bear proboscis are the Amathinids (Fig. 19), Architectonicoidea, Pyramidelloidea, etc. Some of them related to parasitic habits.

Amongst the Pulmonata, at least the malacophagous predatory Streptaxoidea have something similar to a proboscis, in such the snails use to consume the prey without introduce the head inside the preys' shell (Simone, 2013).



19. *Cyclothyca pacei* (Amathinidae), head-foot, dorsal view, most of floor of pallial cavity removed to show haemocoelic structures, proboscis coiled inside (L ~20 mm). Lettering: **aa**, anterior aorta; **cm**, columellar muscle; **cr**, esophageal crop; **es**, esophagus; **he**, hemocoel; **lb**, head sole; **me**, mentum; **nr**, nerve ring; **nv**, nerve; **pb**, proboscis; **rl**, right cephalic lobe; **sm**, shell muscle; **te**, cephalic tentacle (from Simone & Bieler in prep).

Another group that developed acrembolic proboscis is inside Caenogastropoda. They are an obscure group collectively called ctenioglossans. This group so far has unclear definition, but appears to be modified cerithioideans (Simone, 2011). At least two taxa that are usually included among the ctenioglossans have acrembolic proboscis, the Epitonioidea, and the Triphoroidea. These both groups include parasitic snails, which shows the usual relation between acrembolic proboscises and parasitism.

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