

The Caenogastropoda mid-esophageal glands

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Abstract

The third branch of Gastropoda, so far unnamed, characterized by the complexity of the esophagus and another 11 synapomorphies by Simone (2011), is here named Trachiogastropoda. Focusing some esophageal structures, an evolutionary pathway is proposed for the unpaired mid esophageal glands of higher caenogastropods. The mid septate esophageal gland of higher mesogastropods (Naticoidea, Cypraeoidea, Tonnoidea) is homologue to the gland of Leiblein of the Stenoglossa and to the venom gland of the Toxoglossa. The reasons for these considerations are discussed, and include phylogenetic, morphological, and developmental arguments.

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Introduction

The esophagus in most animals is a simple tube connecting the oral cavity, a region in which the food is crushed and mixed with saliva, with the stomach, the region in which the food is further processed. The mollusks, in general, are not an exception, as all classes characteristically have simple, tubular esophagi. The gastropods, however, follow this rule only in the two most basal branches – the Patellogastropoda and the Cocculiniformia (Leal & Simone, 1998, 2000; Sasaki, 1998). The remaining gastropod branches, however, the esophagus becomes more than a simple tubular connection. It has chambers, diverticula, glands, papillae, pouches, gizzard, etc., i.e., additional structures that show that the esophagus plays an important role in processing the food coming from the oral cavity, furnishing to the stomach an already double processed matter. Thus, this gastropod branch is here treated as **Trachiogastropoda**, derived from Latin *trachia* meaning wind-pipe, throat, an allusion to the sophistication of the esophagus.

All kinds of esophageal modifications of the Trachiogastropoda will be treated in future Malacopedia issues. The present one the mid-esophageal glands are focused, in especial the esophageal gland of the mesogastropods, and the gland of Leiblein and the venom gland of the neogastropods, which has been shown to be homologous structures. This evolutionary pathway is explained below. Other esophageal trachiogastropod modifications that will be addressed in future Malacopedia issues include the anterior esophageal paired pouches, so typical of orthogastropod/archaeogastropod grade and some basal caenogastropods (ampullarioideans and viviparoidaeans); the stenoglossan valve of Leiblein; etc. However, an esophageal (and sometimes gastric) modification – the gizzard – was already addressed by Simone (2020).

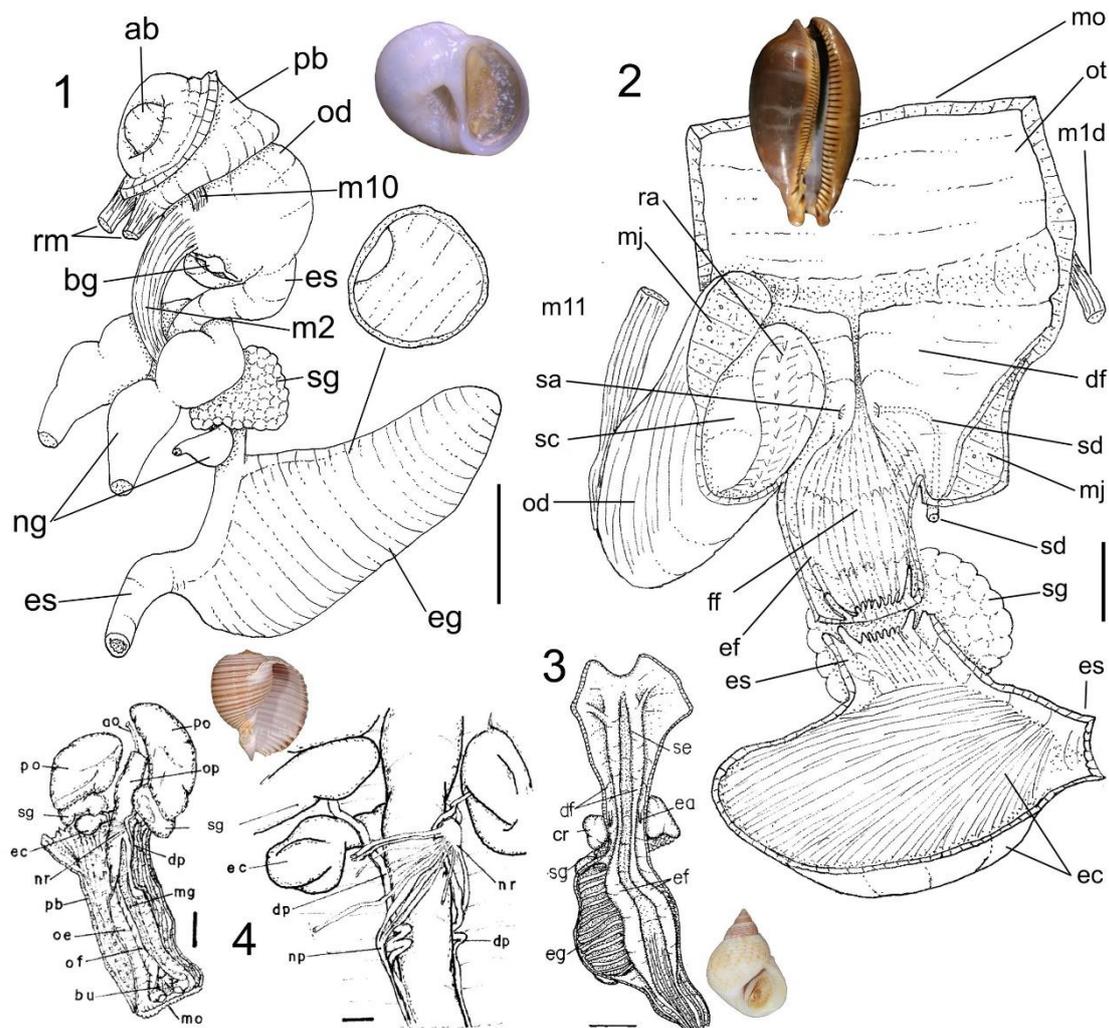
Following, the three main kinds of mid-esophageal ventral glands of caenogastropods are explained, and finally they are explained in an evolutionary-phylogenetic scenario.

1. Mesogastropod grade's esophageal gland

In the phylogenetic pathway based on phenotypic characters (Simone, 2011, and subsequent papers), the pair of large esophageal pouches that is one of the synapomorphies of the here named Trachiogastropoda, is present in all branches of the archaeogastropod grade, entering in the caenogastropod two first branches – Cyclophoroidea and Ampullarioidea (Simone, 2004a). The pair of esophageal pouches is lost in Epiathroidea (Simone, 2011). However, another kind of important gland appeared in Adenogastropoda – the esophageal gland (Figs. 1-4: eg, ec).

The esophageal gland, or mid-esophageal gland, is a large diverticulum-like or sometimes just a swollen stretch of the esophagus in the region between the nerve ring and the stomach. This gland is different from other diverse types of glands, pouches and chambers that are so common in trachiogastropods' esophagus, because it is ventral, unpaired, and is fulfilled by a series of transverse septa. Each septum is a thin flap with glandular cover in both surfaces, its edges are attached to esophageal walls, except for a small dorsal area, in which a canal or the esophageal lumen itself runs (see transverse section in Fig. 1). All septa are located close from each other along the gland, in such a way that they produce an almost massive glandular set, in which glandular product flows through the narrow hollow dorsal area. This esophageal region, Marcus (1957), for example, called “foliate stomach”.

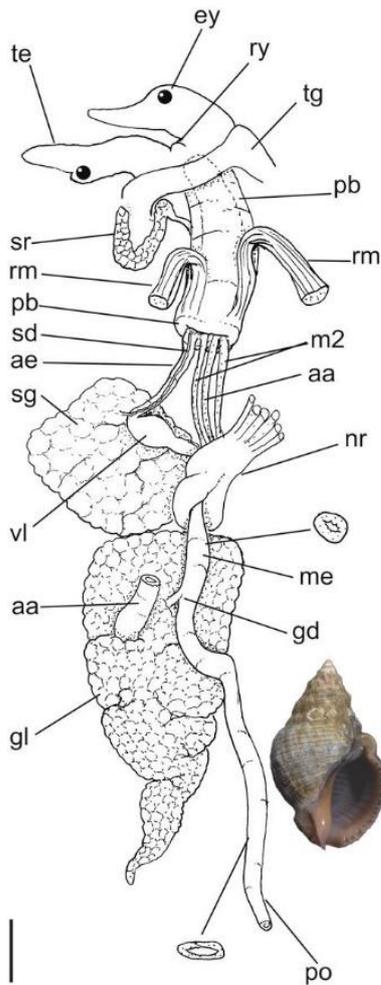
Esophageal glands are present in practically all members of the 3 first branches of the Adenogastropoda so far known, and they are relatively similar in overall features. Of course, they have some variation, sometimes the gland is small or even lost, as, e.g., in pedicellariids (Simone, 2004b), and sometimes large (e.g., some cypraeids Simone & Cavallari, 2020, Fig. 2: ec). Sometimes the gland is only an esophageal enlargement (Fig. 2), it is diverticulum-like (Fig. 1), or it is even sac-like, simulating a structure with a duct as in some tonnoideans (Fig. 4). The esophageal gland has a single series of septa in Naticoidea and Cypraeoidea, but has two parallel series, separated by a longitudinal septum in Tonnoidea (Simone, 1995, 2011). Despite the esophageal gland as described here is a Adenogastropoda synapomorphy, a strikingly similar one is found in Rissooidea branch Littorinidae (Fig. 3: eg – Simone, 1998, 2006), a branch relatively distant. This is certainly a remarkable convergence.



1-4. Foreguts, examples of mid esophageal glands (eg, ec) in mesogastropods. 1, *Microlinices latiusculus* (Naticidae), shell (W= 4 mm), foregut, left view, and transverse section in indicated level of esophageal gland (from Simone, 2014; scale= 0.5 mm); 2, *Macrocypraea mammoth* (Cypraeidae), shell (L 133 mm), foregut opened longitudinally, ventral view, odontophore deflected to left, transverse section preceding gland (from Simone & Cavallari, 2020; scale= 5 mm); 3, *Littoraria flava* (Littorinidae), shell (L 12 mm, from Femorale), foregut opened longitudinally, ventral view, odontophore extracted (from Simone, 1998; scale= 1 mm); 4, *Tonna galea* (Tonnidae), shell (L 180 mm, from Femorale), foregut, dorsal view, with anterior region opened anteriorly, including adjacent proboscis (left, scale= 10 mm), and detail of its middle region (right, scale= 2 mm) (from Simone, 1995). Lettering: ab, accessory boring organ; ao, aorta; bg, buccal ganglion; bu, buccal complex; cr, esophageal pouch; df, dorsal fold; dp, salivary duct; ea, pouch aperture; ec-eg, esophageal gland; ef, esophageal fold; es, esophagus; ff, esophageal folds; m1, jugal muscles; m2, buccal retractor muscle; m10, ventral protractor muscle; mg, mid esophageal groove; mj, jaw and peribuccal muscles; mo, mouth; ng, nervous ganglia; nr, proboscis nerve; nr, nerve ring; od, odontophore; oe, anterior esophagus; of, esophageal folds; ot, oral tube; pb, proboscis; po, proboscis gland; ra, radula; rm, proboscis retractor muscles; sa, salivary aperture; sc, subradular cartilage; sd, salivary duct; se, dorsal buccal chamber; sg, salivary gland.

2. Stenoglossa gland of Leiblein

The gland of Leiblein (Figs. 5-6: gl) is typical of the stenoglossan neogastropods – Stenoglossa. It is a gland located in the head-foot haemocoel, usually with a conic format, solid-glandular, beige to pale brown in color, posteriorly pointed, increasing gradually towards anterior, being broad in its anterior region, in the place in which it has the duct connecting it to the esophagus. Mostly, the gland is folded in on itself and in the last, anterior, larger fold the aorta crosses it (Fig.



5. Foregut with typical gland of Leiblein.

Thaisella guatemalteca (Muricidae) (from Simone, 2017); shell (L ~29 mm); foregut uncoiled, with transverse sections in indicated regions. Lettering: aa, anterior aorta; ae, anterior esophagus; ey, eye; gd, duct of gland of Leiblein; gl, gland of Leiblein; m2 odontophore retractor muscles; me, mid esophagus; nr, nerve ring; pb, proboscis; po, posterior esophagus; rm, proboscis retractor muscle; ry, rhynchostome; sd, salivary duct; sg, salivary gland; sr, accessory salivary gland; te, tentacle; tg, integument; vl, valve of Leiblein.

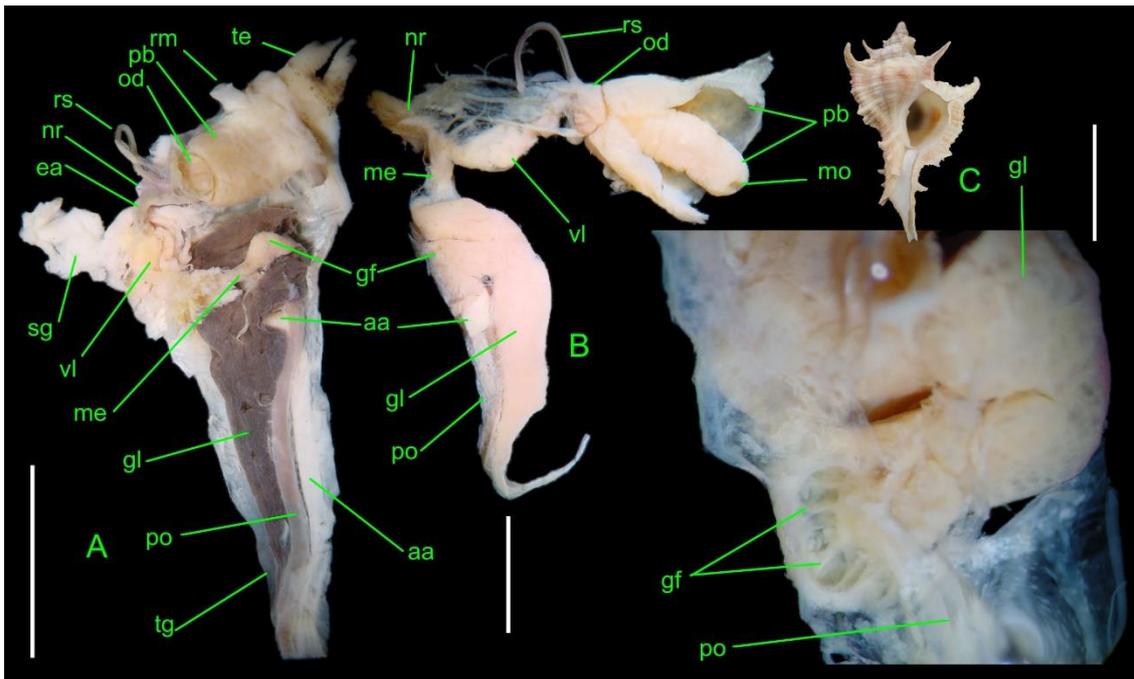
6: gf) is a small gland located between the gland of Leiblein and the esophagus, along the duct of the gland of Leiblein. If its glandular tissue is carefully removed, a series of small transverse septa remains (Fig 6C: gf), truly resembling a miniature of the mesogastropods' esophageal gland described above. Analyzing these features, it is not difficult to deduce that the gland of Leiblein is derived from the mesogastropods esophageal gland, as the localization is the same, and the internal structure is also similar. The muricids, and possibly other basal stenoglossans, still have vestiges of the septa in their anterior region, but the middle and posterior regions evolved to a solid, bulge gland in which product flows via a duct. Most stenoglossans lost the remains of the septate portion, possessing only the glandular portion – the gland of Leiblein itself.

6A: aa). Of course, this typical pattern is modified in the myriad of the stenoglossan diversity, including its decrease (e.g., *Buccinanops* – Pastorino & Simone, 2021), until the complete loss (e.g., some cancellariids and harpids – Simone, 2011; and mitrids – Simone & Turner, 2010).

As most stenoglossan neogastropods, beyond the gland of Leiblein also possess the valve of Leiblein, another *Stenoglossa* synapomorphy that will be treated in a future Malacopedia issue, the esophagus is divided into 3 regions (Fig 5): 1) anterior esophagus (ae): from the mouth to the valve of Leiblein (vl); 2) mid esophagus (me): from the valve of Leiblein to the duct of the gland of Leiblein (gd); and 3) posterior esophagus (po): from that duct to the stomach.

The complexity of the stenoglossan foregut is usual for carnivore animals, which contrasts with the usual simplicity of mid and hindguts. The structures, chambers, glands, tubes, ducts, muscles, odontophore, etc., are all coordinated by the central nervous system that is usually large and concentrated in these animals (Fig. 5: nr). Their functions are not totally well understood, including those of the gland and the valve of Leiblein, but certainly they are connected to the predatory (prey numbness?) and digestive activities (see discussion for more details).

Most of the gland of Leiblein tissue is a solid glandular matter. Its duct, however, is a hollow tube that constantly and relatively uniformly has successive ramifications up to its periphery. The duct is connected directly to the esophagus ventral surface. Sometimes, the inner surface between the duct and the esophagus has a special arrangement of folds and grooves that may bypass the gland's secretion directly to the oral cavity (e.g., in volutids). These features will be treated in future Malacopedia issues. However, in the present context, a remarkable feature is present in some muricids, especially in Muricinae – the gland “framboise” (Pastorino, 2002; Simone, 2011). The gland framboise (Fig



6. *Siratus senegalensis* (Muricidae, Brazil) MZSP 55955. Example of a specimen having gland framboise (gf); shell (L ~60 mm); (A) head-foot, ventral view, showing haemocoel inner structures as in situ, foot and columellar muscle removed, some ventral structures deflected to left (scale= 10 mm); (B) foregut removed and uncoiled (other specimen), most ventral view, proboscis partially opened longitudinally (scale= 10 mm); (C) same, detail of region of connection between gland of Leiblein and esophagus, gland framboise (gf) and adjacencies dissected, its inner glandular tissue removed in order to shown septa (Scale= 2 mm). Lettering: aa, anterior aorta; ea, anterior esophagus; gf, gland framboise; gl, gland of Leiblein; me, mid esophagus; nr, nerve ring; od, odontophore; pb, proboscis; po, posterior esophagus; rm, proboscis retractor muscle; rs, radular sac; sg, salivary glands; te, tentacle; tg, integument; vl, valve of Leiblein

3. Toxoglossa venom gland

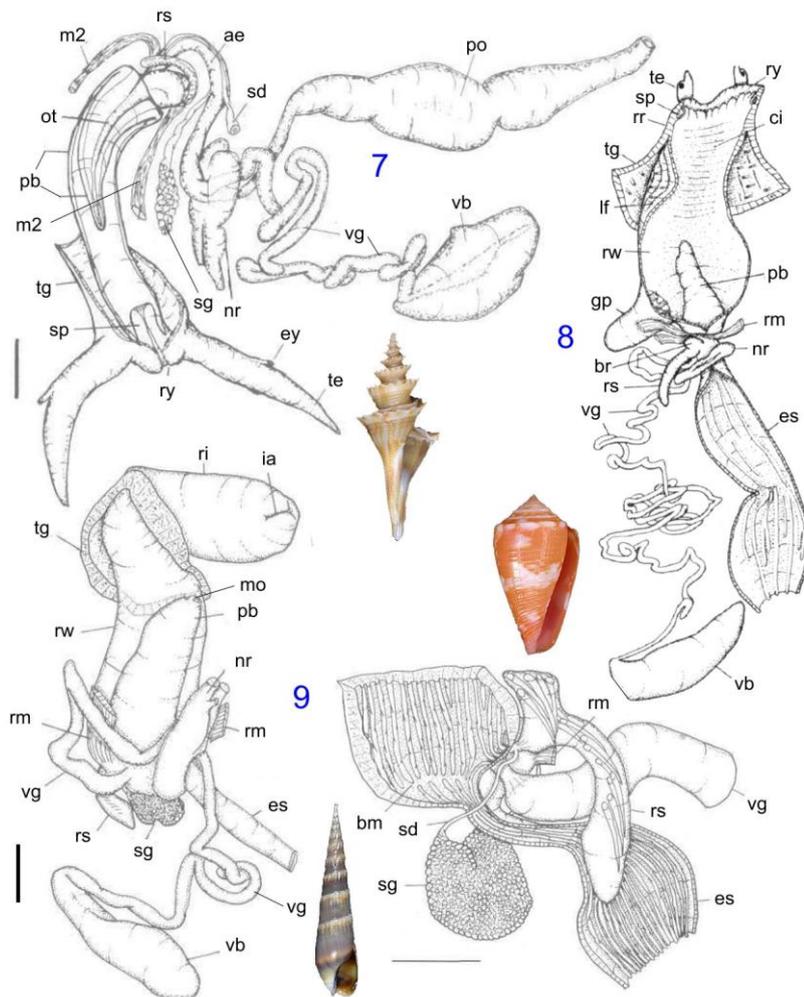
Toxoglossa until some decades ago had only 3 families: Turridae, Conidae and Terebridae. Turridae, however, have been revealed to be a polyphyletic taxon (e.g., Simone, 2011) and it has split into several families in a number that varies according to the author. MolluscaBase (2022), for example, considers in Conoidea nothing more than 18 families; maintaining Conidae and Terebridae, all remaining 16 were once considered Turridae. As discussed elsewhere in Simone (2021), Conoidea is the single superfamily of the neogastropod subdivision called Toxoglossa.

The Toxoglossa/Conoidea branch possesses nothing less than 61 morphological synapomorphies supporting it (Simone, 2011, 2021), one of them is the venom gland (Figs. 7-9: vg). The venom gland is a very long, slender, and convoluted glandular tube located in the haemocoel, having in its distal end the venom bulb and in the proximal end usually connected to the buccal mass. The venom bulb (Figs. 7-9: vb) is a large, elliptic, hard, iridescent structure that possesses 2-3 thick layers of muscles; its lumen is narrow (Fig. 7); its contraction promotes the venom through the venom gland to the buccal mass.

The complex structures that constitute the venom apparatus of the conoideans, and its variation (including loss), is also issue of a future Malacopedia issue and is not the scope of the present one, but, in a simplistic way, at least in the conids and terebrids (Figs. 8-9) a harpoon-like radular tooth (inside radular sac – rs) is placed at the tip of the proboscis. It is introduced to the prey. The venom bulb contracts injecting the venom in the prey, which quickly dyes. It, thus, can

be consumed more easily. Crustaceans, polychaetes, other mollusks and even fishes are common prey of the conoideans.

Analyzing the venom gland of the more derived conoideans, it is difficult to infer any correlation between it and the mesogastropod esophageal glands and stenoglossan gland of Leiblein. However, the venom gland of more basal conoideans like cochlespirids (Fig. 7), which have a proboscis similar to other caenogastropods (pb), the venom gland has some resemblance with the gland of Leiblein, as it is connected to the esophagus posteriorly to the nerve ring (nr), also in ventral position. Cochlespirids have, thus, the anterior esophagus (ae). The other conoideans, however, the anterior esophagus was shortened, taking the venom gland insertion from a posterior region in the esophagus



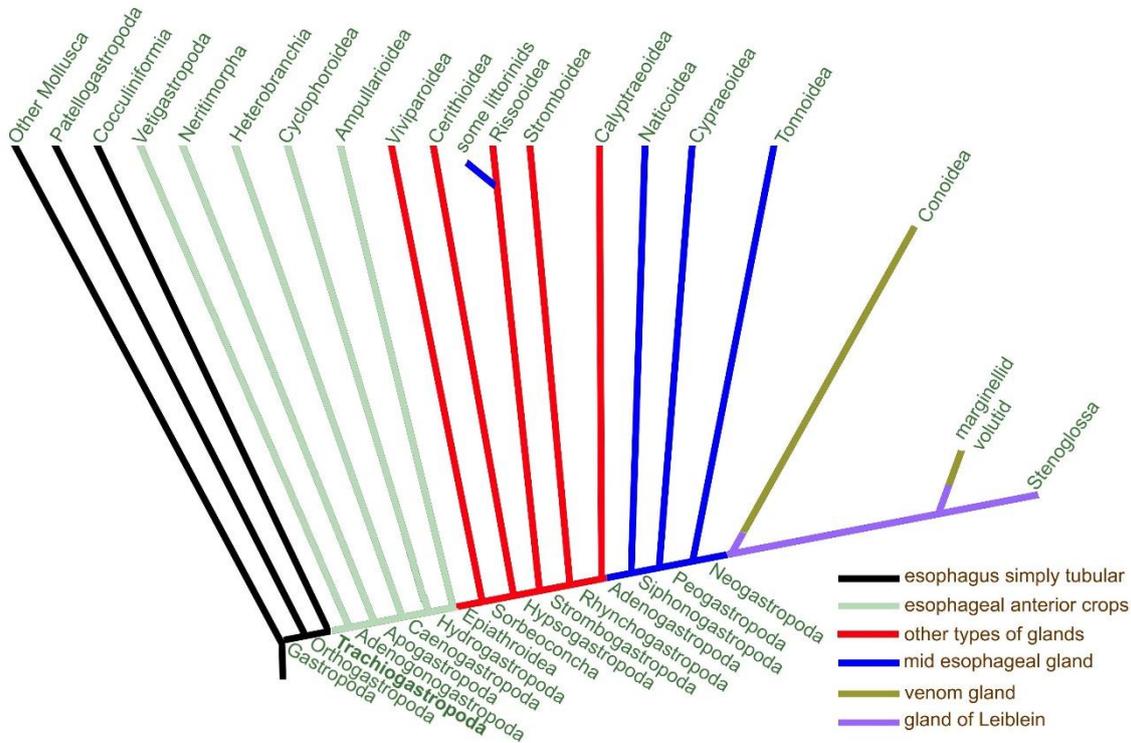
7-9. Examples of *Toxoglossa* foreguts. 7, *Cochlespira elongata* (Cochlespiridae, from Simone, 1999b), shell (L 28 mm), head and uncoiled foregut, ventral view, scale= 0.5 mm; 8, *Poremskiconus archetypus bertarollae* (Conidae, from Costa & Simone, 1997), head and uncoiled foregut, ventral view, (L of venom bulb= 0.5 mm); 9, *Hastula cinerea* (Terebridae, from Simone, 1999a), shell (L 35 mm), uncoiled foregut, ventral view (left), and detail of proboscis base opened longitudinally (right), scales= 1 mm, Lettering: ae, anterior esophagus; bm, buccal mass; br, bulged region of radular sac; ci, circular muscle fibers; es, esophagus; ey, eye; gp, proboscis gland; ia, introvert aperture; lf, longitudinal muscle fibers; m2, buccal mass retractor muscle; mo, mouth; nr, nerve ring; ot, oral tube; pb, proboscis; po, posterior esophagus; ri, rhynchodeal introvert; rm, proboscis retractor muscle; rr, rostrum; rs, radular sac; rw, rhynchodeal wall; ry, rhynchostome; sd, salivary duct; sg, salivary glands; sp, rhynchostome sphincter; te, tentacle; tg, integument; vb, venom bulb; vg, venom gland.

to a position direct in the buccal mass (Figs. 8-9). As a vestige of its previous condition, the venom gland always passes through the nerve ring (nr). Admirably, some stenoglossans converged to a gland of Leiblein similar to a conoidean venom gland, being an elongated tubular gland with a bulb in its distal end. This is particularly found in some volutids, marginellids and mitrids (Simone, 2011). But, despite being similar, these stenoglossans do not develop a real multi-layered muscular terminal bulb, neither the glands central region is so cylindric.

The conoideans are a mega-diverse group, and, thus, have an enormous variation of the venom apparatus. Some of them even lost it at all, and the foregut became a simple tube connecting

the mouth, at the proboscis' tip, to the stomach (e.g., *Daphnella*), lacking any kind of gland or additional structure. But, as referred above, this will be treated in a future Malacopedia issue.

4. Phylogenetic inference of mid esophageal glans

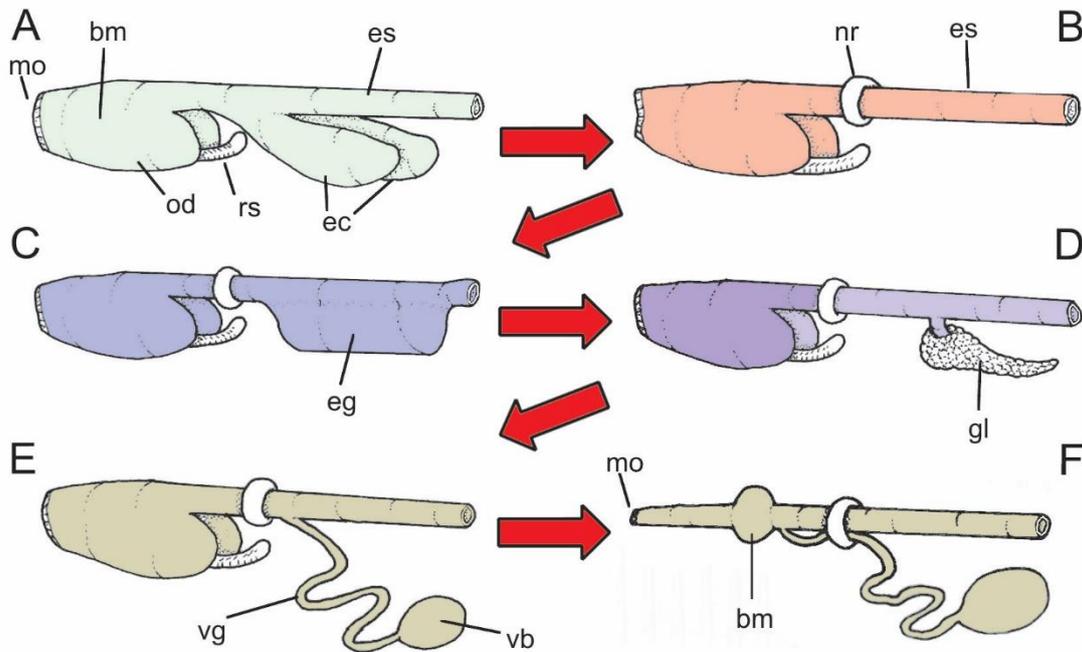


10. Phylogenetic representation of Gastropoda mostly based on Simone (2011) with special concern to the type of mid esophageal glands indicated by colors

Based on the phylogeny of the Gastropoda by Simone (2011), corroborated by subsequent papers, the phylogenetic representation focusing the esophageal glands is represented in Fig. 10. In that, the 2 first branches (black) are represented the taxa that possess only tubular esophagus, similar to the usual model of remaining mollusks. The following branch, here named Trachiogastropoda, the esophagus became more complex, being this a notable synapomorphy. This branch corresponds to the node K by Simone (2011: fig 20), which is supported, in total, by 12 synapomorphies (page 309 of that paper, discussed in page 225); it was not named that time, but, as this branch was not challenged so far, it deserves to be named (Trachiogastropoda). The identity and set of synapomorphies supporting Cocculiniformia, the second gastropod branch, will be subject of future papers and a Malacopedia issue.

The analysis of the esophageal features is somewhat complicated because it is a coiled structure, a result of the torsion. The torsion, an outstanding gastropod synapomorphy, is the rotation of 180° of the posterior region of the body, resulting, as a final consequence, the anus placed anteriorly. This issue will also be treated in the future, but it was partially addressed by Simone (2018). The schemes of Fig. 11, however, the esophageal coiling was omitted. The esophagus, there, was artificially uncoiled as a didactic device, in order to help the understanding. The usual esophageal model of the basal branches of the trachiogastropods is with a pair of anterior lateral hollow pouches (Fig. 11A: ec) (pale green) (e.g., Simone, 1997; Sasaki, 1998; Strong, 2003). These pouches,

of course, can be lost (particularly in heterobranchs) or highly modified, as well as other additional chambers can appear (particularly in vetigastropods) in the course of the evolution of each branch (Fig. 10). These pouches are only found in the two basal branches of the caenogastropods – the Cyclophoroidea and Ampullarioidea. The pouches are lost, as a synapomorphy, by the Epiathroidea. However, the esophagus rarely becomes secondarily a simple tube; other kind of glands appear, usually glandular thickness of the esophageal epithelium (Fig. 10: red. Fig. 11B).



11. Schematic representation of an uncoiled esophagus of Trachiogastropoda (modified from Simone, 2011) (color corresponding to Fig. 10). **A**, typical form of Vetigastropoda, Neritimorpha, Cyclophoroidea and Ampullarioidea, with a pair of esophageal crops; **B**, typical form lacking crops, but with other esophageal glands, of Epiathroidea; **C**, form with wide ventral esophageal gland, basing Adenogastropoda; **D**, Form with gland of Leiblein, of Stenoglossa; **E**, form with venom gland inserted posteriorly to nerve ring, found in basal Conoidea and some Marginellidae; **F**, same, with venom gland passing through nerve ring, and loss of odontophore, state found in most Conoidea, most Marginellidae and Volutidae. Lettering: bm, buccal mass; ec, esophageal pouch or glandular chamber; eg, esophageal gland; es, esophagus; gl, gland of Leiblein; mo, mouth; nr, nerve ring; of, odontophore; rs, radular sac; vb, venom muscular bulb; vg, venom gland.

The ventral mid esophageal gland, internally fulfilled by transverse septa, is a synapomorphy of the Adenogastropoda (Fig. 10: blue; Fig. 11C: eg), with a vestigial remains at least in some muricids, as gland framboise, amongst the neogastropods; and a remarkable convergent appearing in some littorinids in the Rissooidea.

In the Neogastropoda, the gland of Leiblein is typical of the Stenoglossa (Fig 10: purple; Fig. 11D: gl), while the venom gland is typical of the Toxoglossa (Conoidea) (Fig. 10: brown, Fig. 11E-F: vg). Both glands appear to be derived from the mid esophageal gland of the above-mentioned mesogastropods as discussed above, based on localization, constitution, and even development (see below). The conoidean venom gland, in particular, is connected to the esophagus posteriorly to the nerve ring in more basal branches (Fig. 11E), migrating anteriorly, to the buccal mass, in more derived ones (Fig. 11F). Remarkably, some stenoglossans have a gland of Leiblein similarly constituted to a venom gland, particularly some Marginellidae, Volutidae and Mitridae (Marcus & Marcus, 1968: fig. 10; Coover & Coover, 1995; Leal & Harasewych, 1995, Simone, 2011), certainly convergencies.

Thus, despite the differences among the distinct types of unpaired ventral esophageal glands above referred, the distribution of the taxa on the cladogram, and the equivalent topology (ventral side of the middle region of the esophagus), suggest that all of them are homologous. Additionally, studies on ontogeny (e.g., Ball et al., 1997; Ball, 2002) revealed that the development of the gland of Leiblein begins in what the authors designated as stage 8, by means of a glandular evagination in the mid esophagus, closely similar to the esophageal gland of adult Naticoidea, Cypraeoidea and Tonnoidea. Only after stage 9 the duct begins its differentiation. Such an ontogenetic data demonstrates a single evolutionary trail for these esophageal glands. Some previous literature also advocates the homology of Leiblein and venom glands (Ponder, 1970, 1974; Kantor, 2002). Additionally, Strong (2003: 504) has also considered the gland of Leiblein as homologous to the esophageal glands of mesogastropods.

Based on these data, the evolutionary scheme shown in Figs. 10-11 suggests a connection among all types of unpaired ventral esophageal glands of the caenogastropods in a single evolutionary trend.

As referred above, the usage or function of these kinds of esophageal glands is still subject of speculation, and it is possible that there is some variation of function or secretion even in homologue glands in closely related genera. Secretor, storage, as well as absorptive functions have been suggested for the gland of Leiblein of nassariids and muricids (Andrews & Thorogood, 2005, in which a wide discussion of caenogastropod esophageal glands can be found). Several of these discussions were extracted from Simone (2011).

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