Malacopedia

São Paulo, SP, Brazil
Volume 3(1): 1-9

ISSN 2595-9913
Feb/2020

Gastropod pallial siphons and siphonal canals

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Abstract

Siphons and siphonal canals evolved independently several times along the phylogeny of Gastropoda. They can be divided into three categories: 1) a canal lacking a corresponding pallial siphon in the mantle edge, as in some cerithioideans and stromboideans; 2) a canal with a corresponding pallial siphon, as seen in Siphonogastropoda; and 3) same, but almost entirely occluded inside a tubular canal, as seen in some tonnoideans and stenoglossan neogastropods. Siphons originating from the head-foot integument also exist, and can be found in some vetigastropods and basal caenogastropods (ampullarioideans and viviparoideans); in this case, they consist of a pair of structures (incurrent and excurrent) and have no corresponding canal. All this information is explored in a phylogenetic scenario. Other types of siphons are also discussed.

DOI: 10.13140/RG.2.2.19454.33601

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

Introduction

The pallial siphon in gastropods is an expansion of the left side of the mantle edge (Fig. 1). It is used to absorb water far from the aperture of the pallial cavity and, as explained below, as an exploratory structure. Nowadays mostly referred to simply as **siphon**, this structure is practically exclusive to some branches of the Caenogastropoda. Naturally, it only occurs in aquatic animals.

1. Crawling *Daphnella lymnaeformis* from Fernando de Noronha, Brazil (L ~10 mm); arrow showing active pallial siphon.

The siphonal canal is a shell structure located in the most anterior region of the aperture (Figs. 2-8: arrows). Despite its presence, it is not always related to a respective pallial siphon, as explained below.

2-8. Examples of caenogastropod shells with siphonal canal (arrows): 2. *Cerithium atratum* from Brazil (L ~30 mm); 3. *Telescopium telescopium* from Australia (L~50 mm); 4. *Strombus pugilis* from Brazil (L ~50 mm); 5, *Pustularia bistrinotata* from Philippines (L ~22 mm); 6, *Afrocominella capensis* from South Africa (L 21 mm); 7, *Bolinus brandaris* from Spain (L 110 mm); 8, *Fusinus crassiplicatus* from Japan (L 83 mm). Courtesy Femorale http://www.femorale.com

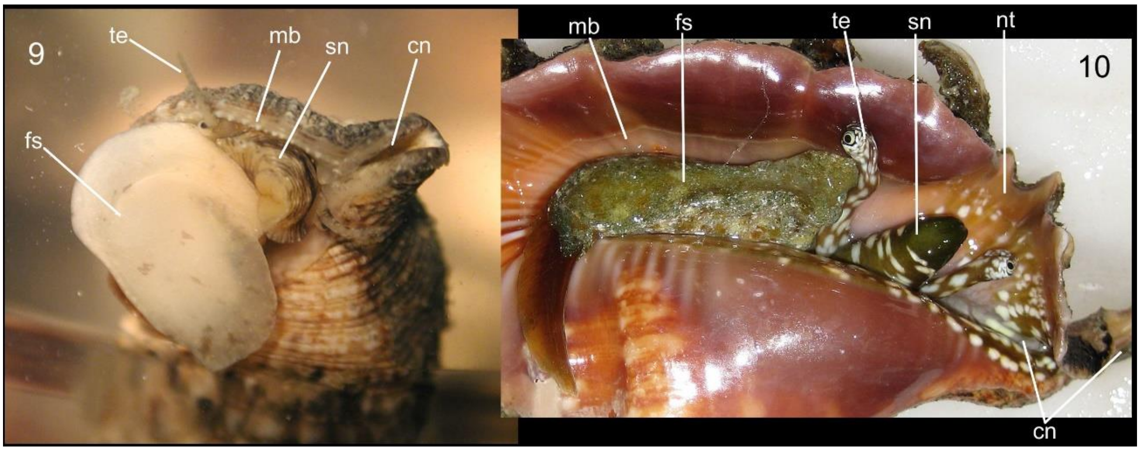
The siphonal canal, usually referred to as **canal**, is a hollow furrow or tube located in the anterior region of the shell. Its main function is to produce an anatomical conduit for incurrent water into the pallial cavity. This canal can work even in retracted or estivating animal, allowing them to breathe without having to move the shell's aperture away from the substrate (Simone, 2011).

To put it simply, there are three types of canals: 1) one that lacks a corresponding pallial siphon; 2) one that shelters a corresponding pallial siphon; and 3) the same, but almost entirely occluded as a tube. These three types are explained in more detail below.

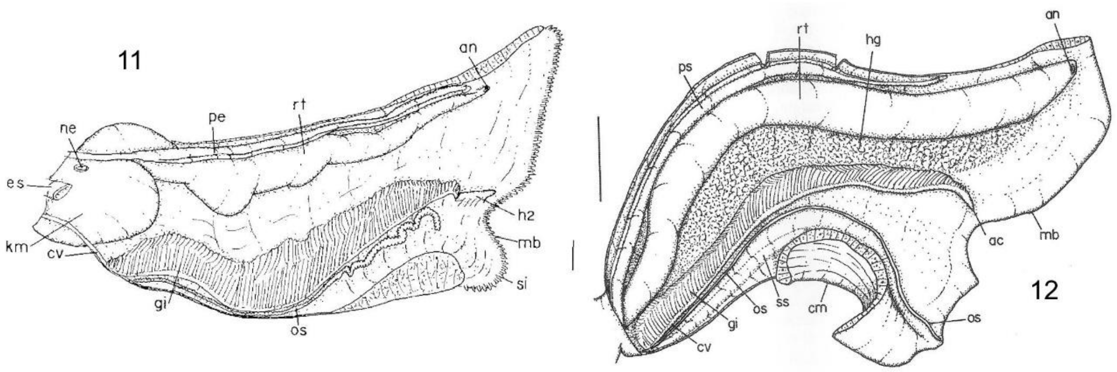
Canal lacking a pallial siphon

Some gastropod taxa developed a siphonal canal in the anterior region of the peristome. However, it does not shelter a developed siphon formed from the adjacent mantle edge. This kind of canal is, then, only produced as an undulation, a wide groove of the mantle, into which the flow of water can be directed (Figs. 9-10: cn).

Two groups of caenogastropods developed siphon-less canals: one of them are the Cerithioidea, including families such as Cerithiidae (Fig. 9), Potamididae, Cerithiopsidae, and Triphoridae (both last ones considered cerithioideans herein, which will be explained in future papers). The other group are the Stromboidea, strombids in particular (Fig. 10). In both groups, the mantle edge is relatively thick and undulated around the siphonal region, originated from it, is wanting (Figs 11, 12).



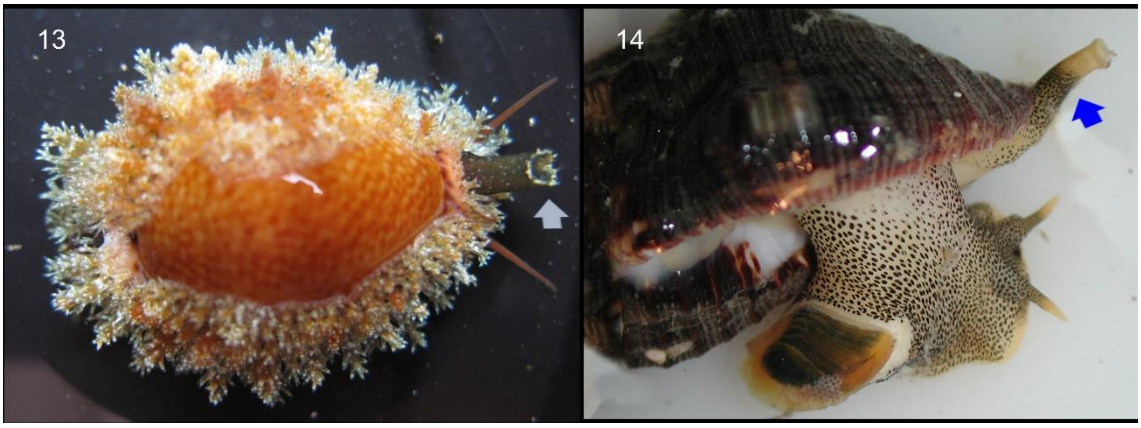
9-10. Examples of species with a siphonal canal, but lacking a pallial siphon, both in apertural view. **9**, cerithiid *Cerithium atratum*, from Brazil (L~30 mm); **10**, strombid *Lambis* sp, from Philippines (L ~100 mm), courtesy Gijs Kronenberg. Lettering: cn, canal; fs, foot sole; mb, mantle edge; nt, stromboid notch; sn, snout; te, cephalic tentacle.



11-12. Examples of species with siphonal canal in shell, but lacking pallial siphon. Pallial cavities in ventral-inner view. **11**, cerithiid *Cerithium atratum* (by Simone, 2001, scale-= 1 mm); **12**, strombid *Strombus pugilis* (by Simone, 2005, scale= 10 mm). Lettering: ac, anterior gill projection; an, anus; cm, columellar muscle; cv, ctenidial vein; es, esophagus; gi, gill; h2, projection anterior to gill; hg, hypobranchial gland; km, kidney membrane; mb, mantle edge; ne, nephrostome; os, osphradium; pe, pallial spermoduct; ps, pallial spermoduct; rt, rectum; si, siphonal region; ss, style sac.

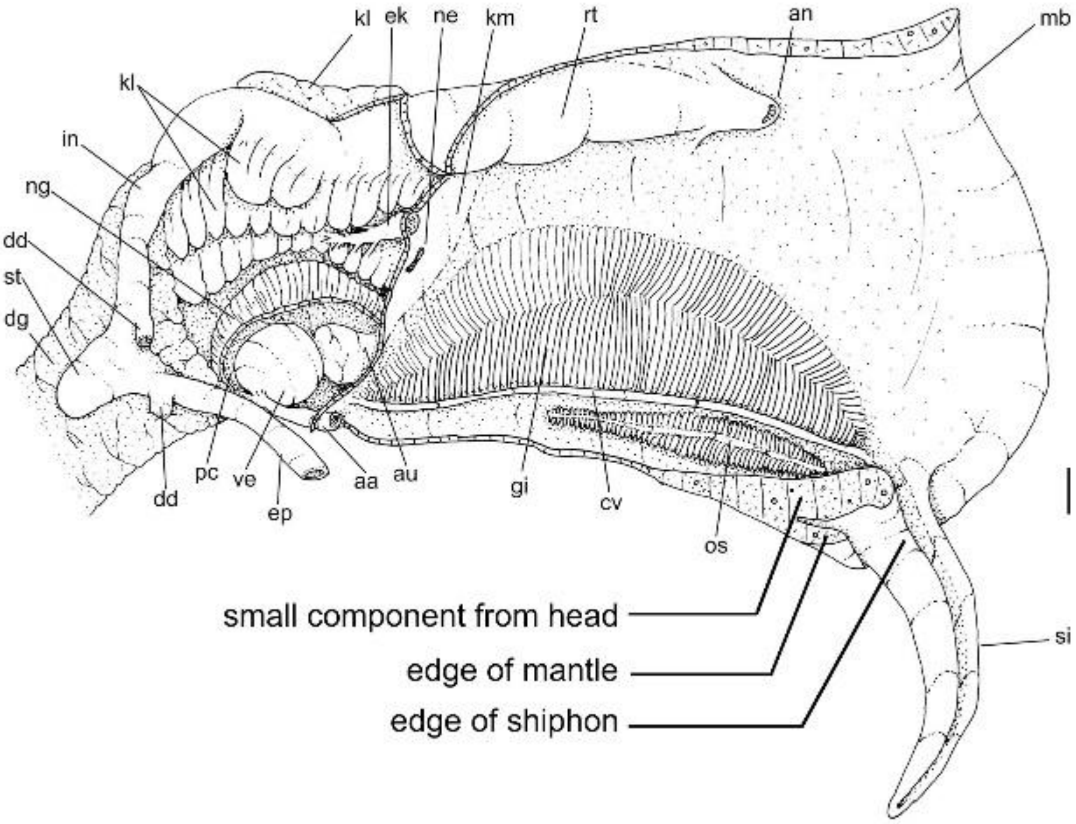
Canal with a corresponding pallial siphon

A single branch of Caenogastropoda developed a pallial siphon, and received the name after this conspicuous structure, the **Siphonogastropoda**, related to node 117 in the phylogeny by Simone (2011). Despite being partially rooted in the nuchal-left region of the head, the siphon is called pallial because of its main origin from the pallial margin. A clear siphon is found in Cypraeoidea (Simone, 2004b) (Fig. 13), but it becomes longer, and is used as an exploratory structure a branch after – in the **Hypsogastropoda** – which includes Tonnoidea and the Neogastropoda (Figs. 1, 16).



13-14. Examples of species with siphonal canal in shell and also a pallial siphon (arrows). Living crawling specimens. **13**, cypraeid *Naria acicularis* from Fernando de Noronha (L ~ 25 mm); **16**, buccinid *Gemophos auritulus* from Ilhabela, Brazil (L ~ 30 mm).

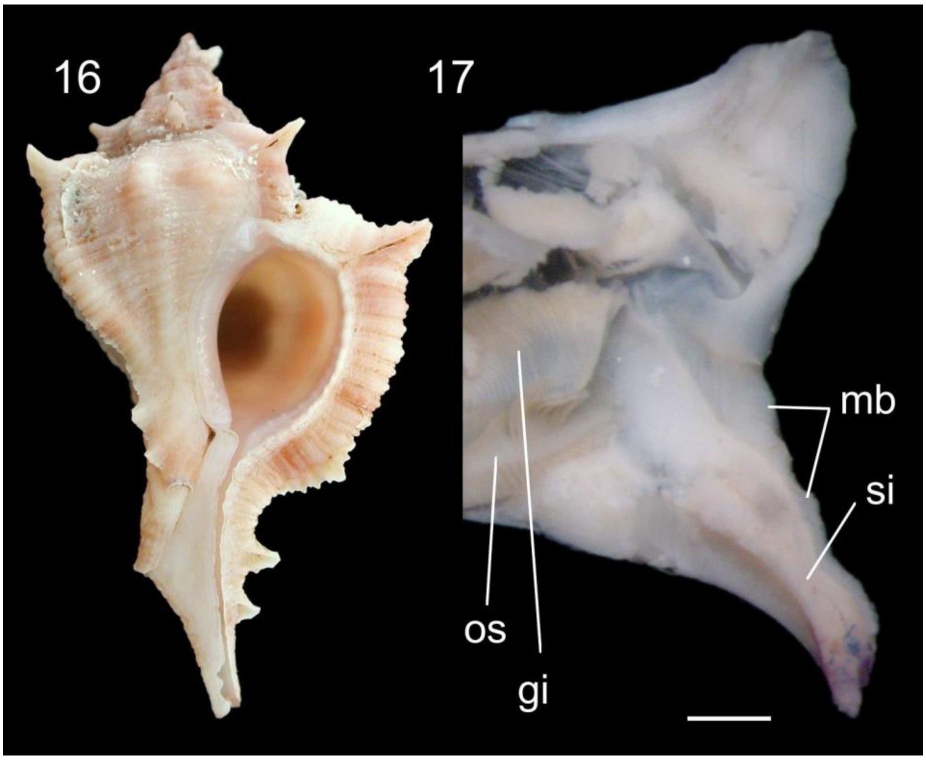
Different from the siphon-less canal groups mentioned above, the anatomical pallial siphon has its edges separated from the mantle edge. Independent of its size, shiphonogastropods always have two edges in the incurrent end of the pallial cavity. The internal edge can be short to very long, sometimes even longer than the animal's body length. Examples of short siphons are cypraeoideans, like eratoids and ovulids. Examples of very long siphons are mostly conoideans and parasite stenoglossans like cancellariids and colubrariids.



15. Pallial cavity hoof and anterior portion of adjacent visceral mass of nassariid *Buccinanops cochlidium* from Argentina, ventral view, showing anatomically defined pallial siphon (si) (scale= 5 mm). Lettering: aa, anterior aorta; an, anus; au, auricle; cv, ctenidial vein; dd, gastric duct to digestive gland; dg, digestive gland; ep, posterior esophagus; ek, efferent renal vessel; gi, gill; in, intestine; kl, kidney lobe; km, kidney membrane with pallial cavity; mb, mantle border; ne, nephrostome; ng, nephridial gland; os, osphradium; pc, pericardium; rt, rectum; si, siphon; st, stomach; ve, ventricle.

During dissection, removing the entire pallial cavity of these taxa, requires prior removal of the base of the siphon, which must be sectioned from the left region of the nuchal head's surface (Fig. 15). In this kind of approach, the anatomical individuality of the siphon becomes very clear (si). The incurrent mantle edge (bm) surrounds the siphon's base (Fig. 15); the siphon, on the other hand, has two edges. The right edge originates in the pallial roof, close to the mantle edge, and it usually separates the anterior end of osphradium from that of the gill. The left edge has a double origin, partially from the mantle, analogous to the right edge, and also from the nuchal region of the head. This kind of siphon has very thick muscular walls, but distinct muscular layers are rarely detectable. Certainly, there are longitudinal, circular and oblique fibers, since the siphon is a very mobile structure. The muscles of the left siphonal edge spread and mix with the head muscles. Fig. 15 shows the above-mentioned components.

Pallial siphons sheltered inside an almost closed-tubular canal



16-17. Examples of muricids with almost tubular siphonal canal in shell. **16**, shell of *Siratus senegalensis* from Brazil, MZSP 33110 (L ~ 55 mm); **16**, *Muricopsis zeteki* from W Panama (L ~ 30 mm), pallial cavity roof, anterior third, scale= 1 mm. Lettering: gi, gill; mb, mantle edge; os, osphradium; si, siphon.

Species that bear an almost tubular siphonal canal are mostly neogastropods, usually muricids (Figs. 7, 16, 17).

Most of the siphonal structure is similar to that described above for taxa having pallial siphons. The main difference is the mantle edge lying along the entire, or almost entire siphonal edges (Fig. 17: mb + si). As the mantle builds the tubular structure to protect the siphon, the mantle edge must go along with the siphon.

Nevertheless, tubular canals are not common. Beyond the above-mentioned muricids (mostly muricines), tubular siphons can be found in some fasciolariids (e.g., *Fusinus* – Fig. 8), colubrariids (e.g., *Columbarium*), and some cymatiids (e.g., *Biplex, Ranularia*), among others.

Different types of gastropod siphons

As mantioned above, pallial siphons and canals are normally associated with caenogastropods, and, at least the pallial siphons, appear to be a synapomorphy (exclusivity) of the Siphonogastropoda (Simone, 2011). However, a myriad of other gastropods also developed some kind of siphons, that is convergent, and not related to the above-mentioned ones.

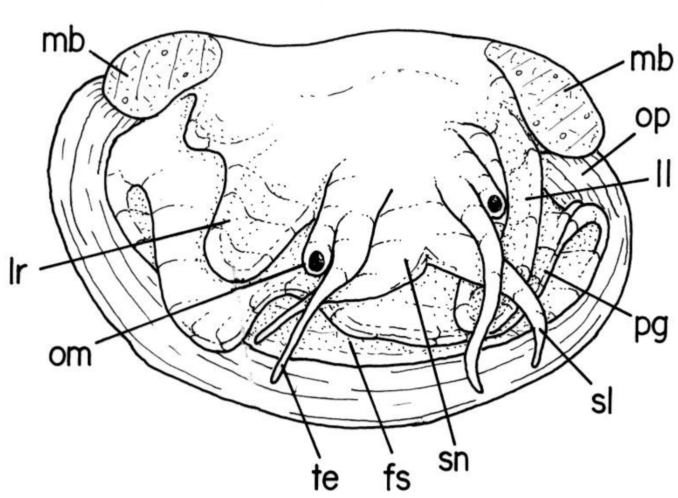
Some marine slugs and semi-slugs have highly muscular mantle edges and foot projections, which can form incurrent and excurrent siphons, like, e.g., the aplysiid *Aplysia* and *Bursatella*, siphons that disappear in fixed samples. However, a noteworthy type of siphon is the **head-foot siphon**. This type originates in the nuchal region of the head and is not related to the mantle edge.

18-19. Examples of snails with siphons originated from head (red arrows). **18**, calliostomatid *Calliostoma javanicum* from Caribbean (W ~ 20 mm), courtesy www.caribbeanreeflife.com; **19**, ampullariid *Pomacea* sp (L ~ 40 mm), from http://creationwiki.org/File:Island_Apple_Snail.jpg by Paul Williams.

Two main taxa developed head-foot siphons instead of pallial siphons. One of them is part of the vetigastropods, chiefly those with single gill, like trochids (Smith, 2012), tegulids (Dornellas et al., 2019), calliostomatids (Fig. 18), phasianellids, etc. They usually have a well-developed epipodium, bearing well-developed tentacles. The epipodium usually becomes the **nuchal lobes** on both sides of the head, ending at the base of the tentacles. The pair of nuchal lobes are usually simple flaps that living animals use as siphons (Fig. 18); the left the incurrent one, and, consequently, the right one is excurrent.

The other main taxa that developed head-foot siphons (certainly a convergence), are the basal caenogastropod Ampullarioidea and Viviparoidea. Both taxa are sometimes included in the same group, an arrangement that was shown to be paraphyletic (Simone, 2004a, 2011).

Much like to the above-mentioned vetigastropods, the ampullarioideans and viviparoideans have a pair of **nuchal lobes** (called head-foot lobes in Simone, 2004a) on both sides of the head, close to the base of the cephalic tentacles (Fig. 20: lr, ll). The left lobe usually is longer than the right one, as it works as an incurrent siphon. It can be remarkably long (Fig. 19), sometimes touching the water surface and opening to the air. Ampulariids can breathe air as they also have a lung beyond the gill, and the left nuchal lobe's base is very close to the lung's pneumostome. This strategy is used by the ampullariids in stressing situations, when the O2 level in the water is too



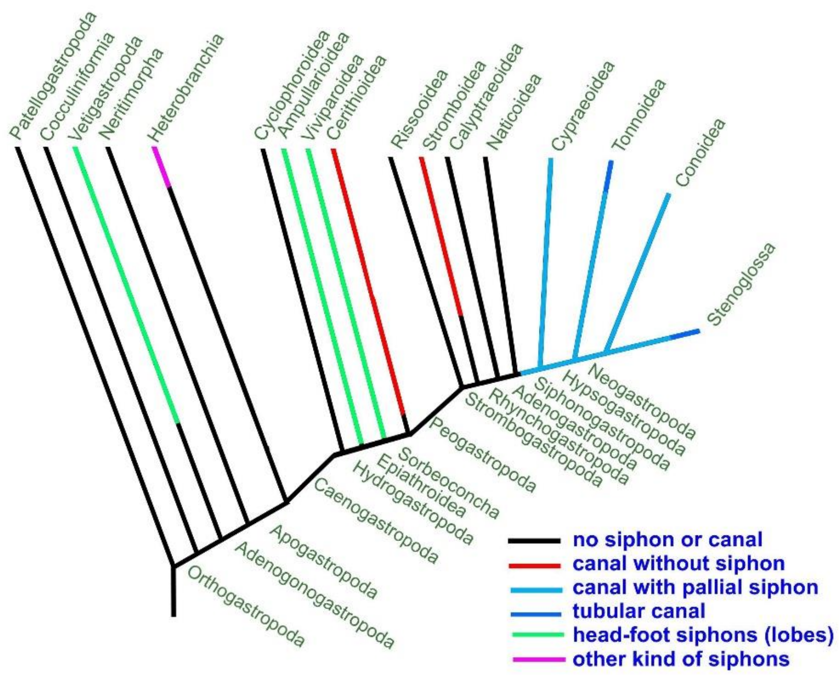
20. *Pomacea crosseana* from Brazil, isolated head-foot, frontal view, showing nuchal lobes (lr, ll) which work as siphons (W ~ 30 mm) (from Simone, 2004a). Lettering: fs, foot sole; ll, left nuchal lobe; lr, right nuchal lobe; mb, mantle border (sectioned); om, ommatophore; op, operculum; pg, pedal gland anterior furrow; sl, snout tentacle; sn, snout; te, tentacle.

low. In normal conditions, the left lobe works as an incurrent siphon, and the right one is the excurrent one, helping to promote water flow in the pallial cavity. The viviparids possibly have a comparable strategy, as the anatomy of their lobes is similar.

As mentioned above, the nuchal lobes of vetigastropods and basal caenogastropods are convergent, despite having similarities. The vetigastropod lobes are derived from the epipodium, which is a vetigastropod synapomorphy. The lobes of the ampullarioideans and viviparoideans, on the other hand, are especial modified muscle of the pallial floor integument.

Moreover, different from the pallial siphons, the head-foot siphons leave no trace of a canal in the shell's peristome.

Evolution of the gastropod siphons



21. Morphology-based gastropod phylogeny, mostly based on Simone (2011), showing different types of siphons as indicated by the colors (see text for details).

Siphons appear to be important in aquatic gastropod physiology, as they enable the intake of water coming far from the animal's excreta. Additionally, siphons permit to the animal to scent via osphradium if it is sufficiently long for foraging movements.

From morphology-based cladogram (mostly based on Simone, 2011) (Fig. 21), it is possible to infer that siphons appeared several times and in different ways along the gastropod evolution. Some

22. Alplysiid *Phyllaplysia engeli* from Brazil, crawling, with siphons produced by the edge of the parapodia (arrows) (L ~10 mm)

siphon types, such as head-foot siphons, appeared three times (some vetigastropods and two basal caenogastropods) (Fig. 21: light green), and the canal-lacking pallial siphons appeared twice, in the cerithioideans and stromboideans (Fig. 21: red). The ordinary pallial siphon appears to have evolved only once in the Siphonogastropoda (Fig. 21: pale blue), although its derived condition in a tubular canal evolved independently in the Tonnoidea and the stenoglossan neogastropods (Fig. 21: dark blue).

Other types of siphon-like structures appeared in diverse gastropods taxa, mainly in aquatic slugs and semi-slugs. Some patent examples are some aplysiids, in which siphons are mostly formed by the parapodia (Fig. 22: arrows): the anterior siphon is incurrent, while the posterior one is excurrent. Aplysiids that possess paired siphons, e.g., *Phyllaplysia* and *Bursatella*, were observed alternating their openings while breathing.

Even though siphons and canals are related to aquatic forms, some kinds of canals and tubes are rarely found in terrestrial animals as well. The shell of some cyclophoroideans (basal caenogastropods), for example, have an anterior canal (e.g., *Pupina*), while others have posterior anal tubes close to the peristome (e.g., *Rhiostoma*). These structures allow the animal to breathe even with the aperture completely closed by the operculum.

Discussion

The gastropod siphon is an important comparative structure in gastropod evolution, even considering occasional convergences. All things considered, they are important synapomorphies that support several taxa, sometimes higher taxa or, occasionally, only a small branch inside a larger lineage.

It is essential to note that a canal-bearing shell does not always shelter a corresponding pallial siphon. Similarly, pallial siphons can also occur without a matching shell structure. These events are yet another reminder of the importance of a holistic approach, which allows for more secure results and interpretations in comparative biology.

Acknowledgements

I am thankful to Daniel C. Cavallari, Faculdade de Filosofia, Ciências e Letras de Ribeirão Preto, USP, for the general suggestions and review. To Mickey Charteris for permission to use the photo in the Fig 18.

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