

Male copulatory organs in gastropods

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Abstract

Male copulatory organs evolved independently in several gastropod lineages, evidencing a clear evolutionary trend. They can be divided into the following categories: (1) exophalic penis; (2) retractile penis; (3) pallial penis; (4) copulatory cephalic tentacle; and (5) snout penis. Details of their structure, occurrence, evolution, and development are addressed herein. Possible convergences are discussed in a phylogenetic context.

DOI: [10.13140/RG.2.2.25285.06882](https://doi.org/10.13140/RG.2.2.25285.06882)

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

Introduction

The advantages of a transition from external to internal fertilization are quite intuitive. External fertilization requires that gametes meet randomly in an open, often hostile environment. The production of gametes consumes a considerable amount of energy and a large number of these cells may be necessary to guarantee reproduction under these circumstances. Internal fertilization, however, reduces the number of gametes needed by concentrating them directly in a structure that promotes fertilization. This type of evolutionary pathway seems to have occurred several times in Mollusca: it appears in all classes and is especially evident in gastropods and cephalopods.

The present work deals with Gastropoda, in which evolution towards internal fertilization seems to have occurred independently several times. Internal fertilization can occur without the development of a copulatory organ, as in some archeogastropods and caenogastropods (for example, Cerithioidea – Simone, 2001). In some vetigastropods, the male gamete is released inside the female's pallial cavity, which seems to be an attempt at internal fertilization. This procedure eliminates the need for gametes to seek their counterpart in an open environment, and also reduces their volume. In cerithioideans, individuals mate through spermatophores, that is a sac containing gametes, the male transfers them into the bursa copulatrix of females. This transfer happens even

in the absence of clear copulatory structures, via ciliary paths with the aid of both participants, leading the spermatophore towards its final destination in the female genital tract.

Internal fertilization of groups in which male copulatory structures are absent is not addressed in the present paper. Herein, the focus is made on male copulatory structures, which appeared several times throughout the evolution of gastropods, in different ways, places and conformations. These structures also have several distinct designations in the literature, e.g., penis, verge, phallus, etc., but in the current context, the term “penis” is chosen.

Gastropod copulatory organs can be didactically divided in the following categories:

- 1) Exophalic penis
- 2) Retractable penis
- 3) Pallial penis
- 4) Copulatory cephalic tentacle
- 5) Snout penis

Considering the vast diversity of the Gastropoda, the present survey is not exhaustive. Nevertheless, the main branches are addressed below regarding the presence of copulatory organs.

1. Exophalic penis (Fig. 9)

The exophalic penis is permanently protruded, i.e., it cannot be retracted, and is usually



1. Example of exophalic penis *Siratus consuela* from Brazil, Shell (right) (L ~40 mm) and extracted head-foot, dorsal view. Arrow indicated penis.

rooted behind the right cephalic tentacle in the nuchal region of the head-foot (Fig. 1). It is an elongated, rather cylindrical muscular structure, which is stored inside the pallial cavity and is easily visible when the male’s head-foot protrudes further outside of the shell. In groups that have this structure, by positioning the snail with the shell aperture facing upwards, and waiting for the animal to begin its shell-righting behavior, anyone can easily pinpoint its sex.

Ontogenetically, the exophalic penis first appears as a small wart behind the right cephalic tentacle, and grows along with the animal’s development. In most species, the penis of young and mature specimens is quite in size and shape (Figs. 3-4). Exophalic penises are clearly a specialization of the integument of the pallial cavity’s floor. It is a muscular, mobile structure used by the male to conduct sperm towards the females’ genital tract, usually into the bursa copulatrix. There is no such thing as an erection, however. Nevertheless, the ontogenetic growth of the penis begins at the end of a sperm groove, which is usually located at the

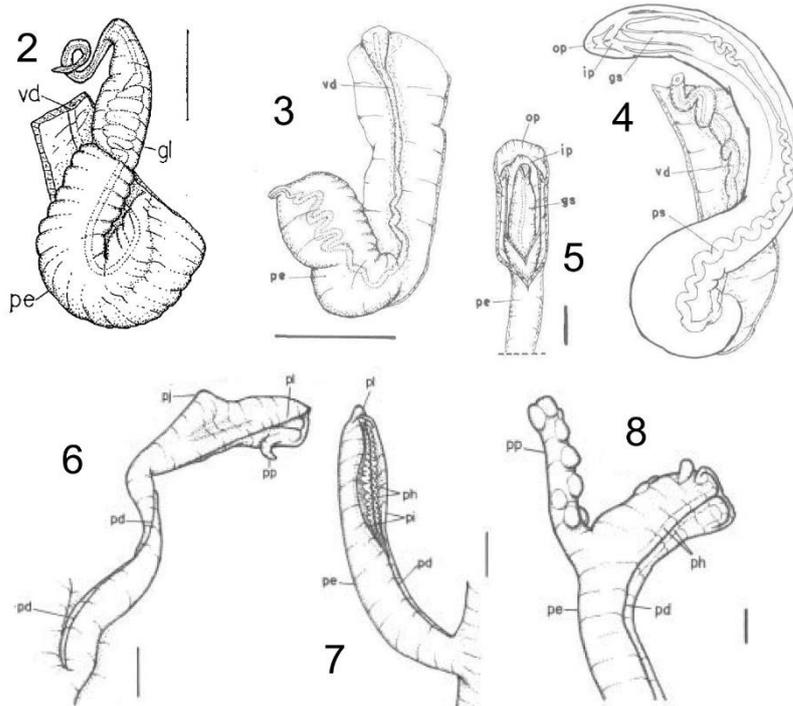
end of the male pallial genital tract. The sperm groove begins on the roof of the pallial cavity, extends to its floor, and runs towards the right cephalic tentacle. A very common additional state stems from the closure of the sperm groove, which effectively becomes a duct called pallial vas deferens. The sperm groove also extends along the penis itself, becoming a penis groove (Figs. 6-8: pd). This groove also commonly becomes a duct in several taxa, called penis duct (Figs. 2-4: ps). The penis duct can have a terminal or subterminal opening.

The closure of the sperm groove into a vas deferens can be partial, and can vary between different species within a same genus. Usually, a species has it characteristically it opened (groove) or closed (duct). More rarely intraspecific variation occurs, e.g., some species of the olivid genus

Agaronia and the volutid genus *Zidona* appear to present both states (personal obs.).

Exophalic penis can be simple, i.e., a cylindrical structure (Fig. 1), tapering along its length towards the tip, which can be from blunt to sharp. However, penises very frequently bear several accessory structures, like glands, projections, terminal or secondary papillae, etc. (Figs. 2-8).

Exophalic penis appeared in the Cyclophoroidea and in the Hypsogastropoda (Ponder & Lindberg, 1997; Simone, 2004), thus emerging twice along the



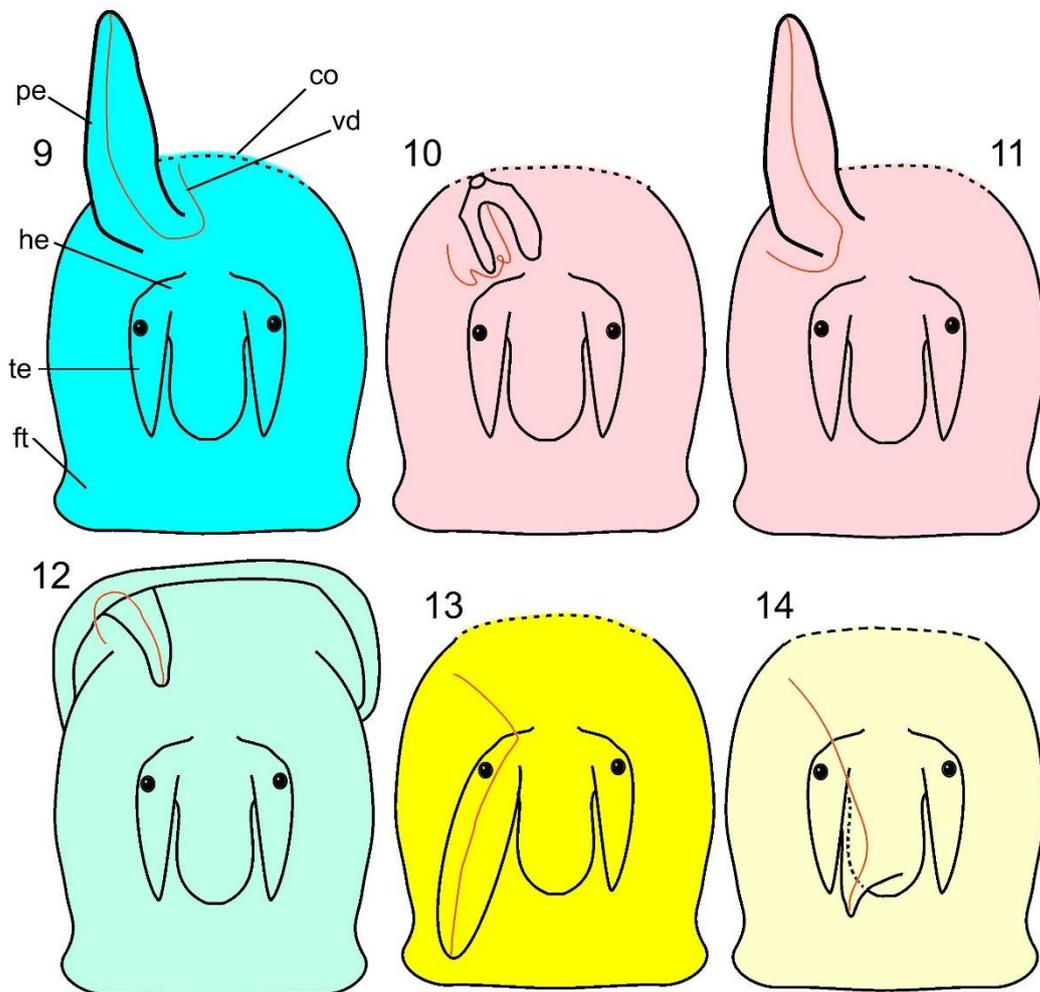
2-8. Examples of peculiar exophalic penises in some caenogastropods. **2**, *Littoraria flava* (by Simone, 1998), scale= 1 mm; **3-5**, *Cochlespira elongata* (by Simone, 1999); scales= 1 mm; **3**, immature specimen; **4**, mature specimen, structures seen by translucence; **5**, dissected tip; **6-8**, strombids (by Simone, 2005); **6**, *Strombus pugilis* scale= 5 mm; **7**, *Eustrombus goliath*, scale- 10 mm; **8**, *Tricornis raninus*, tip only, scale= 2 mm. Lettering: gl, glans; gs, glans; ip, inner lip; op, outer lip; pd, groove; pe, penis; ph, distal folds; pi, inner folds; pj, projection; pl, longitudinal fold; pp, papilla; ps, penis duct; vd, vas deferens.

evolution of the Caenogastropoda (Simone, 2011). Nevertheless, it is one of most important synapomorphies of Hypsogastropoda, and, as far as surveyed, was never reverted (lost) in any internal branch. Hypsogastropods are a penis-bearing group, preceded in the phylogeny by several branches lacking penis (Simone, 2011). However, in the most basal branch of Caenogastropoda – the Cyclophoroidea (s.l., sensu Simone, 2004, 2011) – there are taxa with a very similar exophalic penis. Cyclophoroideans are terrestrial gastropods with obscure known internal relationships. Some of its branches lack a penis, e.g., diplommatinids (Martins & Simone, 2014), while others have it, e.g., neocyclotids (Simone, 2004), in an interesting convergence with hypsogastropods. However, in cyclophoroideans, emergence of the penis seems to be a complex pathway, as some rare penis-bearing diplommatinids do exist (*Habeastrum* – Simone et al, submit.). This enigma only will only be clarified when a phylogeny of the Cyclophoroidea will be available.

Among hypsgastropods, the exophalic penis evolved as a synapomorphy and was not reversed in any internal branch (Simone, 2011), even in sessile taxa (e.g., capypraeoideans – Simone, 2002) and in inner coral parasites (e.g., *Leptoconchus*, a muricid – pers. obs.). This resource possibly contributed to the Caenogastropoda becoming the most biodiverse group within Mollusca.

2. Retractable penis (Figs. 10, 11)

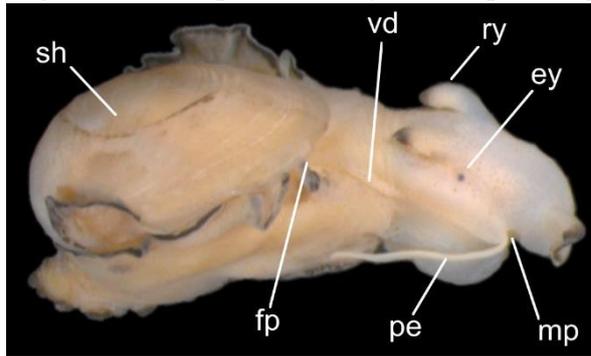
As the name implies, the retractile penis can be retracted into the body, disappearing from external view, except for a small aperture called male or genital pore (Fig. 10). During copulation, the retractile penis is externalized via hydraulic pressure much like a proboscis (details in Simone, 2019) (Fig. 11).



9-14. Schematic representation of head-foot of dextral gastropods with emphasis in the different types of penis, no accurate proportions nor shape of head, frontal view. **9**, exophalic penis; **10-11**, retractile penis; **10**, penis contracted; **11**, penis protruded; **12**, pallial penis; **13**, copulatory cephalic tentacle; **14**, snout penis (neritids). Lettering: co, connection with visceral mass; ft, foot; he, head; pe, penis; te, right cephalic tentacle; vd, vas deferens or sperm groove.

A retractile penis is one of the synapomorphies of Heterobranchia, which are characteristically hermaphrodites. In most heterobranchs, the penis is located behind the right cephalic tentacle, while the female pore is located much more posteriorly, but also on the right side, being called female or hermaphrodite pore (Fig. 15). The connection between the female/hermaphrodite pore

and the penis can be external, through a ciliary tract (e.g., aplysiomorphs) (Fig. 15: vd) or a duct (e.g., basommatophorans). Stylommatophoran pulmonates are exclusive in having both female/male pores merged into a single genital pore, usually posterior to the right ommatophore.



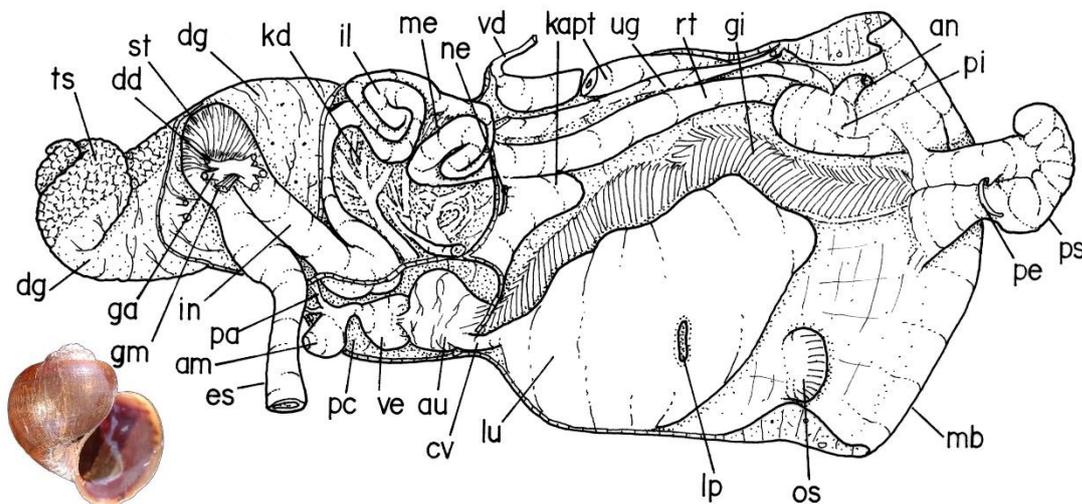
15. *Aplysia parvula* as example of retractile penis. Fixed specimen with protruded penis (L ~10 mm). Courtesy Carlo M. Cunha. Lettering: ey, eye; fp, female/hermaphrodite pore; mp, male pore; pe, penis; ry, rhinophore; sh, shell; vd, seminal groove connecting both pores.

The development of a retractile penis is related to the remaining genital structures, which lie along the head-foot haemocoel, free from the integument (as in an exophalic penis) (Figs, 10-11) aside from the Heterobranchia.

The retractile penis is only found in a single group in a non-heterobranch gastropod, in a subgroup of the caenogastropod Naticoida (Simone, 2011), such as, e.g., *Sinum* and allies.

3. Pallial penis (Figs. 12)

the pallial penis is exclusive to the Ampullarioidea (Simone, 2004). These freshwater caenogastropods have genital structures running along the right side of the pallial cavity as in all caenogastropods, but instead of going towards the pallial floor, the ampullarioideans maintain the genital tract on the pallial roof (Fig. 16).



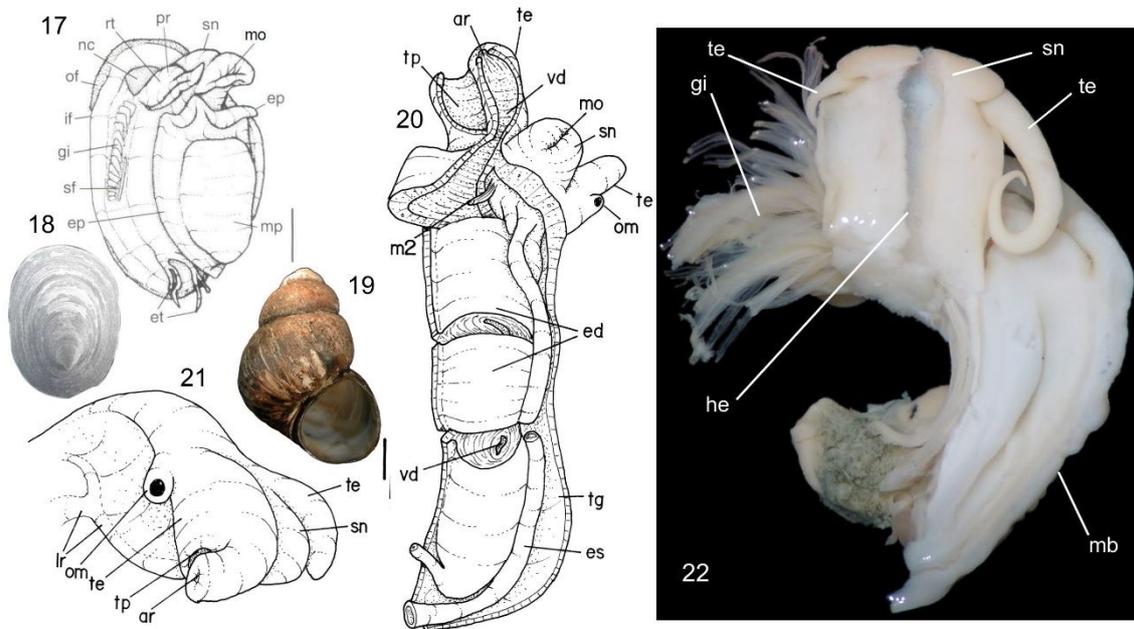
16. Example of pallial penis in *Pomacea sordida*, shell in inferior-left corner (L~40 mm); pallial cavity and uncoiled visceral mass, ventral view; scale= 2 mm (from Simone, 2004). Lettering: am, ampulla; an, anus; au, auricle; cv, ctenidial vein; dd, duct to digestive gland; dg, digestive gland; es, esophagus; ga, gastric ventral chamber; gi, gill; gm, gastric muscle; il, intestinal loops; in, intestine; ka, membrane kidney-pallial cavity; kd, kidney; lp, pneumostome; lu, lung; mb, mantle border; me, mesentery; ne, nephrostome; os, osphradium; pa, posterior aorta; pc, pericardium; pe, penis; pi, penis sac; ps, penis shield; pt, prostate; rt, rectum; st, stomach; ts, testicle; ug, urinary gutter; vd, vas deferens, ve, ventricle.

A pallial penis actually stays coiled inside a penis sac (Fig. 16 pi). The easily visible structure is the penis shield (ps), which is located on the right side of the pallial edge (mb). The penis shield is easily visible in the living animal, which allows to verify its gender (absence of a penis shield means female). The penis itself is very slender, and is externalized only during copulation, with the

aid of the penis shield. The ampullariid penis shield has different arrangements of shape, glands, projections, notches, etc., exclusive to each species, thus being relevant in the group's taxonomy.

4) Copulatory cephalic tentacle (Fig. 13)

The copulatory cephalic tentacle, which is usually the right one, is relatively common within several groups in the archaeogastropod grade. It is relatively rare in vetigastropods, e.g., the genus *Neomphalus* (Fig. 22), but it is practically a rule amongst the Cocculiniformia.



17-22. Examples of copulatory tentacles. 17-18, cocculiniform *Copulabyssia riosi* (from Leal & Simone 2000); 17, head-foot and adjacent mantle edge, right-slightly ventral view, scale = 0.5 mm; 18, shell, dorsal view (L 3 mm); 19-21, caenogastropod *Viviparus acerosus* (from Simone, 2004); 19, shell, frontal view (L ~35 mm); 20, head and haemocoel, ventral view, foot and columellar muscle removed, some transverse section artificially done in some portions of sperm duct; 21, head, right-slightly anterior view, scales= 1 mm; 22, *Neomphalus fretterae*, head-foot, ventral view, some adjacent structures also shown, foot and haemocoelic structures removed (L ~20 mm). Lettering: ar, mantle pore; ed, ejaculatory duct; ep, epipodium; es, esophagus; et, epipodial tentacles; gi, gill; he, head; if, inner mantle fold; lr, head lobe; m2, buccal mas retractor muscle; mb, mantle border; mo, mouth; mp, mesopodium. nf, nuchal cavity; of, outer mantle fold; om, ommatophore; pr, protuberance; rs, right cephalic tentacle; sn, snout; sf, fold of gill; te, tentacle; tg, integument; tp, distal chamber; vd, vas deferens.

Neomphalus fretterae has been considered an aberrant organism, separated from other gastropods at the subclass level – Neomphaliones (MolluscaBase, 2020). However, its anatomical characters (McLean, 1981; pers. obs. – Fig. 22) are relatively similar to Vetigastropoda. Although this conclusion has not yet been published, the analysis of morphological attributes of *Neomphalus* indicates that it is indeed related to vetigastropods. Thus, it is treated here in this way, but further information will be given in a future paper. Undoubtedly, *Neomphalus* is a very strange organism, and it is a rare case when the left tentacle (Fig. 22: te - on the right side) was modified, becoming a penis. The very large left tentacle has a central dorsal groove used to conduct sperm. The gender name *Neomphalus*, by the way, means "new penis".

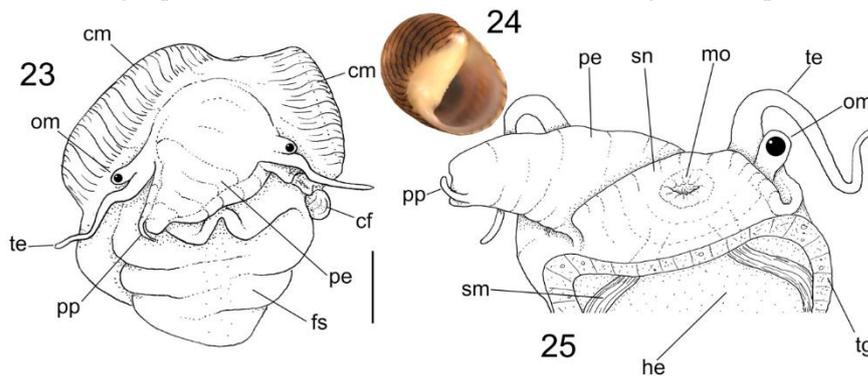
As mentioned above, cocculiniforms have the right tentacle modified into copulatory structure in most groups. Some have an apparently regular tentacle (symmetrical with its pair), e.g., *Addisonia* (Simone, 1996), while others have a much enlarged right tentacle than its counterpart,

e.g., the pseudococculinid *Copulabyssia* (Leal & Simone, 2000) (Figs. 17-18). The copulatory function of this tentacle can be inferred from the presence of a ciliary furrow connecting the genital aperture to the base of the right tentacle. This furrow mostly runs along the tentacle (fig 17: rt). Certainly, the development of a copulatory right tentacle happened several times along the archaeogastropod grade, but it is possibly one of the cocculiniform's synapomorphies. On the other hand, Cocculiniformia has recently been dismantled, with some taxa incorporated into Vetigastropoda, while other in Neomphaliones (MolluscaBase, 2020), based on molecular analyses.

A single group of caenogastropods developed a right tentacle with copulatory function: the freshwater Viviparoida (Simone, 2004). In viviparoidans, the right tentacle is not only enlarged, but also bears accessory structures (e.g., papillae, glands, etc.) and a closed duct running along it, with an opening located at the tentacle's tip (Figs 20-21: vd).

5. Snout penis (fig. 14)

Copulatory structures sometimes appear in groups that characteristically do not have penis, such as the ones discussed above. Some remarkable examples can be found in some Neritimorpha, particularly the marine groups of the family Neritidae. Copulatory projections are found in some genera. For example, in *Vitta virginea*, there is a pointed projection on the right side of the snout's edge (personal obs.); while in *Neritina zebra* (Fig. 24) the penis is a flap, in which the edge



23-25. *Neritina zebra* as example of peculiar penis (from Barroso et al, 2012). **23**, head-foot, anterior view, scale= 2 mm; **24**, shell, apertural view (L ~25 mm); **25**, head, ventral-slightly anterior view, foot removed, scale= 1 mm. Lettering: cf, cephalic lappet; cm, columellar muscles; fs, foot sole; he, haemocoel; mo, mouth; om, ommatophore; pe, penis; pp, penis papilla; sm, snout retractor muscle; sn, snout; te, tentacle; tg, integument.

is separated from the snout, and is located below the right tentacle (Figs. 23, 25: pe).

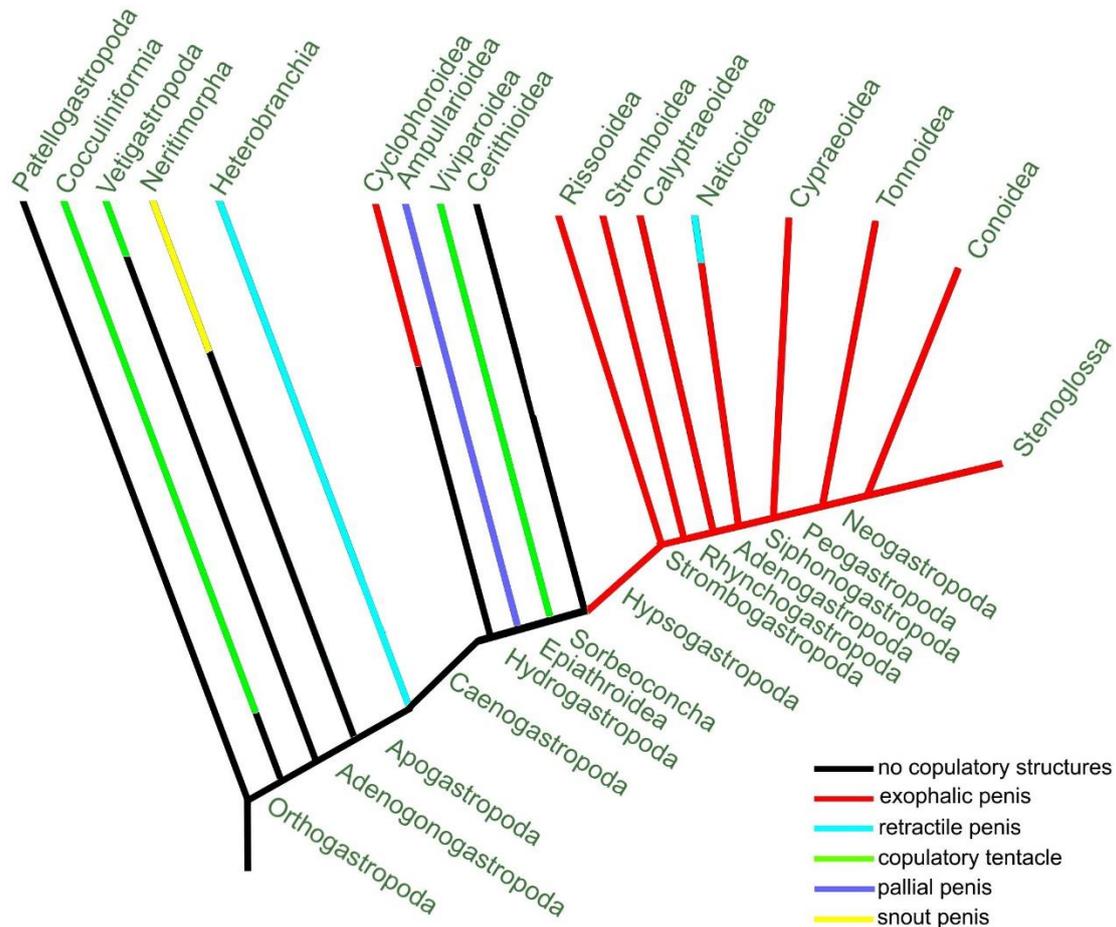
The penis of *N. zebra* is a new acquisition that is very distinct from other gastropods. It has no duct, but does have a longitudinal groove running up to its tip (Fig. 23).

Interestingly, the terrestrial neritimorphs of the family Helicinidae do not possess any copulatory structure (e.g., Simone, 2018).

Phylogenetic implications

As mentioned above, copulatory structures emerged independently in different ways in several gastropod lineages. The Fig. 26 represents the phylogeny of the Gastropoda mostly based on Simone (2011), highlighting different copulatory organs of each lineages (represented in different colors). Whenever more than one color is used in a same branch, they indicate that a given internal branch of that taxon developed the correspondent type of penis, and not the entire branch. The black lines indicate groups with external fertilization (e.g., patellogastropods) or, if internal, it is not done via copulatory structures (e.g., cerithioideans). The green branches represent taxa that

developed a right (rarely the left) tentacle as a copulatory structure. This happened in at least three groups, such as the Cocculiniformia, few vetigastropods (e.g., *Neomphalus*), and the viviparoidean caenogastropods. As far as known, all viviparids have a copulatory right tentacle; however, given the uncertainties regarding cocculiniforms, the green color does not begin at the branch base.



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

The snout penis is represented by a yellow line, and is exclusive to some marine neritimorphs. The retractile penis is represented by a blue line. It is an important synapomorphy of the Heretobranchia, with an interesting convergency with an internal branch of the naticoideans. The pallial penis is represented by a purple line, and is exclusive of the ampullarioideans. The exophalic penis is represented by a red line; it is an important synapomorphy of the hypsogastropod branch of Caenogastropoda, with a notorious convergency in some cyclophoroideans (the first caenogastropod branch), but we do not know for sure if the cyclophoroidean penis is a synapomorphy of a single branch or emerged more than a single time. Possibly this kind of penis appeared at least twice, in neocyclotids and diplommatinids.

Discussion

Despite the convergent nature of copulatory structures, such as the exophalic penis and the right copulatory tentacle, they are important synapomorphies that support valuable gastropod branches. Hence, they are of great taxonomic and phylogenetic importance. Since gastropods are not visual animals, mating activity is done through tactile and chemical senses, and gastropod copulation usually is preceded by intricate behaviors for detecting a same species' partner. Penises are part of this elaborate process which could have evolved at least partially to avoid the loss of valuable gametes.

That is the reason why the gastropod penis is more than a simple gamete conductor. It sometimes bears annexed structures, like papillae, glands, chambers, projections, branches, etc., which are apparently not related to the sperm flow. In fact, they are part of a clear key/lock mechanism that helps in the recognition of a partner, and subsequently stimulate the copulation. An interesting example are the helicids, terrestrial pulmonate snails that have a structure called style sac in the penis' tip. It is used for hurting the mate, producing hormonal stimuli. Some dorid nudibranchs also have 1 or 2 spines in the penis (e.g., Lima et al, 2016), possibly for the same reason.

In most cases, the penis appears in a location of the body where related groups do not have no structure at all. Thus, except for the right tentacle, the penis is not an adaptation of a previous structure: it develops as a muscular projection of the integument. The development of a complex structure like the penis apparently from nothing, as a true novelty, appears to be typical of the mollusks.

Acknowledgements

Thank by Daniel C. Cavallari, FFCLRP-USP, for several suggestions. I am also grateful for Carlo M. Cunha for the Fig. 15.

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