

## The mollusk osphradium, structure and evolution

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### Abstract

The osphradium is a molluscan olfactory organ of aquatic forms, located in the water entrance of the pallial cavity, usually in front of the gills. The structure is practically microscopic in most mollusks, but in gastropods the osphradium is macroscopic. Its morphological modifications are explored here, mainly focusing the phylogeny. It can be divided in: button-like, ridge-like, bipectinate ridge-like, bipectinate elliptical, and partial of totally monopectinate. The taxa that bear each type is informed, under a phylogenetic scenario, as well as a brief discussion of the osphradial anatomy, function, and further modifications are discussed.

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### Introduction

The osphradium is an olfactory structure expected to be present in all aquatic mollusks. As it has the function of smelling the environment, its position is invariably in the entrance of water flow in the pallial cavity. This anatomical region is the first to receive the environmental water containing detectable particles or molecules, to stimulate epithelial receptors. These chemical receptors generate a nervous impulse that is conducted through the osphradial nerve to the central nervous system for processing.

The normal model is having a pair of osphradia, usually placed in front of the gills. The structures detect water quality that will flood through gills. The pair of osphradia is anatomically similar to small buttons located in the pallial cavity entrance, hardly to be detected macroscopically. The osphradia of most molluscan classes, especially in bivalves and cephalopods, usually are individually seen in serial sections as a set of receptors only (e.g., Haszprunar, 1987; Beninger et al, 1995).

The osphradia is practically only macroscopically detected in gastropods. The aquatic forms usually have an easily identified structure in front of the gill(s). As usual, however, the structure has suffered several further specializations and modifications along with gastropod evolution, in which main types are explored herein. One of the easier modifications is the osphradial loss, which occurred in 2 special cases: 1) in air-breathing taxa, an environment in which the osphradial function for detecting molecules apparently is precluded; and 2) replacement for other olfactory structures, such as, e.g., the Hancock organ and rhinophores in aquatic heterobranchs.

The heterobranch Hancock organ and rhinophores will be explored in a future Malacopedia issue, including the possibility of being homologous structures. This one is dedicated only to the primary osphradium found in the aquatic prosobranchs.

As gastropods have a larger osphradium than the remaining mollusk classes, it is possible to infer that the organ is further important for their biology. Being a structure of detection, its contact with the environment is primordial, and the larger its surface, the more sensible the structure is. Despite being huge when compared to osphradia of other classes, the osphradium of aquatic herbivore and detritivore gastropods are the smallest. Enormous osphradia, sometimes even larger than the gill, are found in carnivorous-predatory gastropods, for the obvious reason of the necessity of prey detection. Additionally, only the external conformation is explored herein, the internal tissue organization, except for some interesting issues, is not approached, as it is only known in a few taxa (e.g., Haszprunar, 1985a).

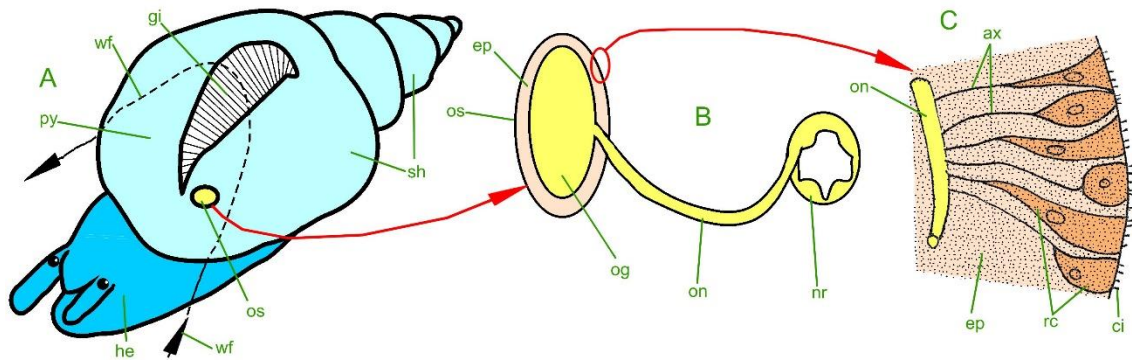
Practically all gastropod osphradium modifications occurred more than once, independently, along with the classes' evolution (Simone, 2011). By the external appearance, the gastropod osphradium can divide into the following types:

1. Button-like
2. Ridge-like
3. Bipectinate ridge-like
4. Bipectinate elliptical
5. Partial or totally monopectinate

These osphradial types are explained below, as well as the taxa that possess them are referred to. However, it is important to emphasize that the research is reasonably complete, but it is not exhaustive.

### **General anatomy of a typical osphradium**

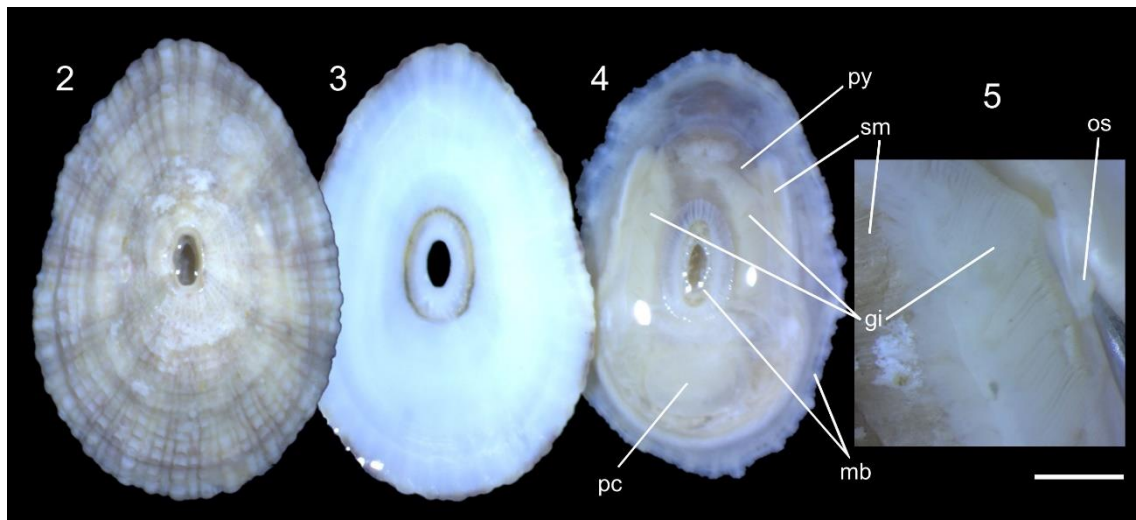
Despite the high level of modifications that the osphradium suffered in the gastropod evolution, a basic, general morphological framework is possible to establish. Fig. 1 shows the average features of the osphradium and its extrinsic structures. An ordinary dextral snail is represented crawling in Fig 1A, with some pallial cavity structures shown if the shell was translucent, its osphradium (os) usually is located as anterior-left-most structure, in the left side of the gill (gi) anterior end. Fig. 1B represents the osphradium in ventral view. In its central region lies the osphradial ganglion (og), which is its nucleus and the main portion of the organ; in the cases in such the osphradial ganglion is long, the osphradial nerve (on) usually is inserted in its middle region. The osphradial nerve usually is narrow (not so broad as represented); its usual way is going to the left, up to border between the hoof and the floor of the pallial cavity, it crosses to the floor and runs



1. Schematic representation of generic morphology of a typical prosobranch osphradium (not for scales or proportions); **A**, usual crawling snail with gill and osphradium seen by translucency, water flow within pallial cavity also indicated; **B**, detail of osphradium, ventral view, and its connection with nerve ring (epithelial thickness and nerve caliber exaggerated); **C**, microscopic detail of osphradial epithelium in transverse section, showing receptors and their axon connection to osphradial secondary nerve. Lettering: ax, axion; ci, cilia; ep, osphradial epithelium; gi, gill; mb, mantle border; he, head-foot; og, osphradial ganglion; os, osphradium; py, pallial cavity; rs, chemoreceptor; sh, shell, wf, water flow.

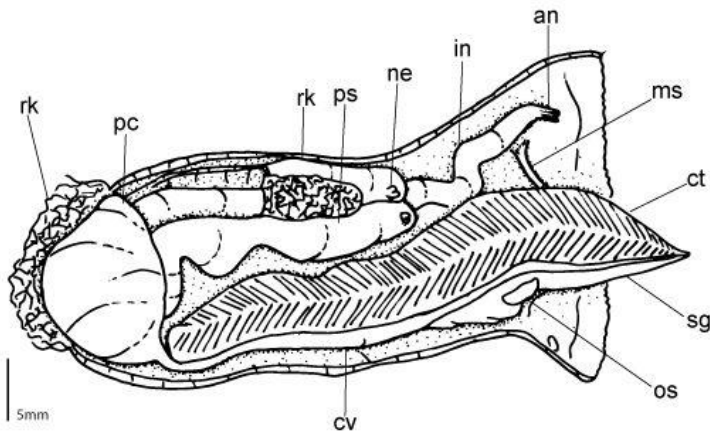
along anterior end of the hemocoel, connecting there with left side of the nerve ring (nr). The osphradial epithelium (ep) is thin (not so thick as represented) and sensorial. It is full of chemoreceptors (rc), other receptors, mucous cells, nervous tissue such as axons (ax) and nerves (on), ciliary connective (ci), etc. The chemoreceptors are the most important, as they do the main organ's function: the olfaction. Determinate molecules present in the water stimulate the receptors, which send to the central nervous system, via osphradial nerve, the message for processing. A sketch of serial section is represented in Fig 1C, in a very simplified pattern, for a more precise representation see Haszprunar (1985a, 1987).

### Button-like osphradium



2-5. *Fissurella clenchi* (MZSP, from São Paulo, Brazil) (L 18 mm); 2, shell, dorsal view; 3, shell, ventral view; 4, specimen extracted from shell, dorsal view; 5, detail of anterior region of gill, ventral-inner view with osphradium weakly dislocated by a forceps, scale= 1 mm. Lettering: gi, gill; mb, mantle border; os, osphradium; pc, pericardium; py, pallial cavity; sm, shell muscle.

The more basal gastropods have the osphradium looking like a small button, located in the base of the gill anterior stalk or rod (Figs. 5, 6: os). The vetigastropods that have a pair of gills, also have a pair of osphradia, one corresponding to each gill (Fig. 4: gi). However, only the most basal vetigastropods have paired gills, other vetigastropods and the other orthogastropods have a single gill, corresponding to the left one. In these cases, the osphradium is also single (Fig. 6).



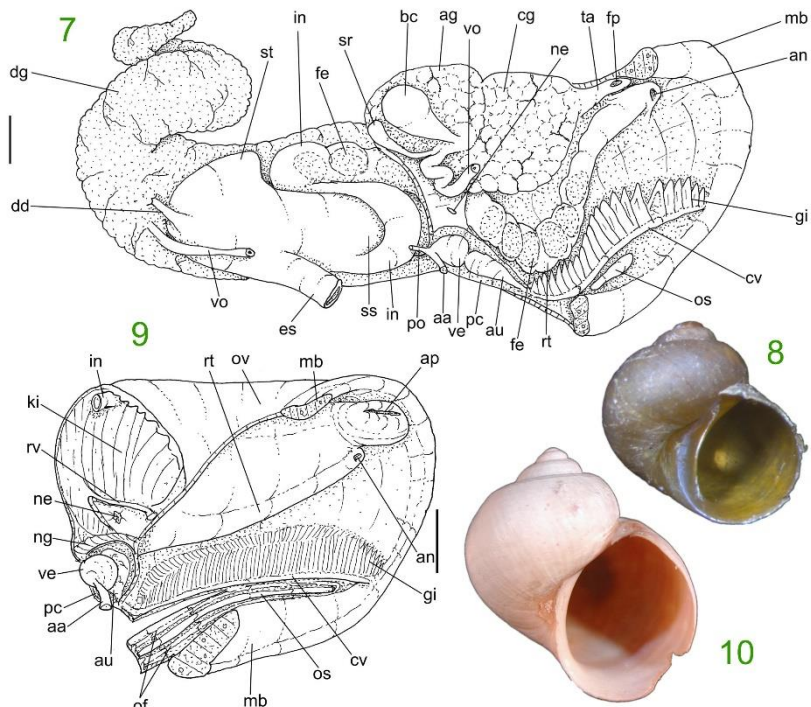
6. *Turbo petholatus* (from Dornellas& Simone, 2020), pallial cavity roof, ventral-inner view. Lettering: an, anus; ct, gill; in, rectum; cv, ctenidial vein; ms, gill suspensory membrane; ne, nephrostome; os, osphradium; pc, pericardium, ps, papillary sac; rk, right kidney; sg, suspensory gill rod.

As reported above, the button-like kind of osphradium usually is present in herbivore and detritivore snails. They possibly have a limited need for scenting, and, thus, a small structure is sufficient for their biology.

Fig. 6 represents the pallial cavity roof of a single-gill vetigastropod, which is the left side of those with paired pallial structures. Other orthogastropods also have a similar organization as explained below.

### Ridge-like osphradium

The osphradium became elongated, ridge-like in the Caenogastropoda (Fig. 22A). Possibly this feature is a synapomorphy (exclusive character) of them. The insecurity of affirming that is because the three basal-most caenogastropod branches are non-marine taxa. Just the first branch is the terrestrial, air-breathing branch called Cyclophoroidea (Simone, 2004a, 2011). Their pallial cavity is modified to a lung, and gill and osphradium were lost. The second branch, the Ampullarioidea, have their osphradium highly modified (reported below), but its nucleus – the osphradial ganglion, is elongated. A true, easily recognizable ridge-like osphradium starts to be seen in the third branch – the Viviparoidea (Simone, 2004a). Anyway, an essay



7-10. Examples of taxa with ridge-like osphradia; 7, *Potamolithus mirim* (from Simone, 2021), pallial cavity roof and partially uncoiled visceral mass, ventral-inner view, scale= 0.25 mm; 8, same, shell (W 2.6 mm); 9, *Pseudonatica antarctica* (from Simone, 2017), pallial cavity roof, scale= 2 mm; 10, same, shell (W 20.4 mm). Lettering: aa, anterior aorta; ag, albumen gland; an, anus; ap, female aperture; au, auricle; bc, bursa copulatrix; cg, capsule gland; cv, ctenidial vein; de, digestive gland; dd, duct to digestive gland; es, esophagus; fe, fecal pellet; fp, female pore; gi, gill; in, intestine; ki, kidney; mb, mantle border; ne, nephrostome; ng, nephridial gland; of, osphradium satellite folds; os, osphradium; ov, pallial oviduct; pc, pericardium; po, posterior aorta; rt, rectum; rv, renal vessel; sr, seminal receptacle; ss, style sac; st, stomach; ta, genital atrium; ve, ventricle; vo, visceral oviduct.

of an osphradium apparently is present in young cyclophoroideans (Simone, 2004a), and the elongated osphradial nerve of the ampullarioideans, are both strongly indicative for considering the ridge-like osphradium as a Caenogastropoda synapomorphy. Nothing similar is found in other gastropod branches, and all Epiathroidea have ridge-like osphradium or an osphradium clearly derived from it, as discussed below.

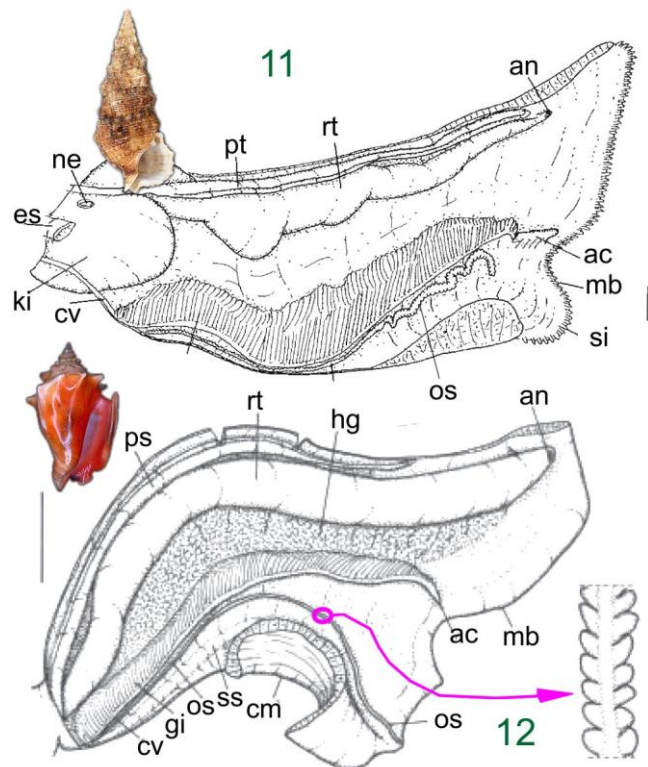
The remaining basal caenogastropod branches preceding the Rhynchogastropoda have typical ridge-like osphradia (Figs. 7-10: os). Even the very minute snails of this group (e.g., Fig. 7: os) have the osphradium slightly elongated, but the elongation is clearer in taxa of larger size (e.g., Fig. 9: os). The osphradial elongation is obviously the first step to increase its surface, and consequently its contact with the environmental water, augmenting its sensibility.

Beyond the simple elongation, two other ways can further increase the osphradial surface. One of them is its additional elongation, producing a zigzag configuration. This happens, e.g., in *Modulus modulus* (Simone, 2001, fig. 302) cerithioidean. The other way is much more common, the increment of the osphradial epithelium, forming folds, leaflets, and filaments. This second model is explored in the osphradium types following.

### Bipectinate ridge-like osphradium

This type of osphradium (Fig. 22D) looks like an ordinary ridge-like, but it possesses a bipectinate conformation if examined closer. The filaments of this kind of osphradium are tiny, but present; usually they are minute folds alternately disposed of in both sides of the osphradial ridge. Two branches of caenogastropods developed the bipectinate ridge-like osphradium: (1) a branch of the Cerithioidea (Fig. 11) and (2) the Strombidae (Fig. 12) (Simone, 2001, 2005). Both are more fully explained below in the phylogeny section.

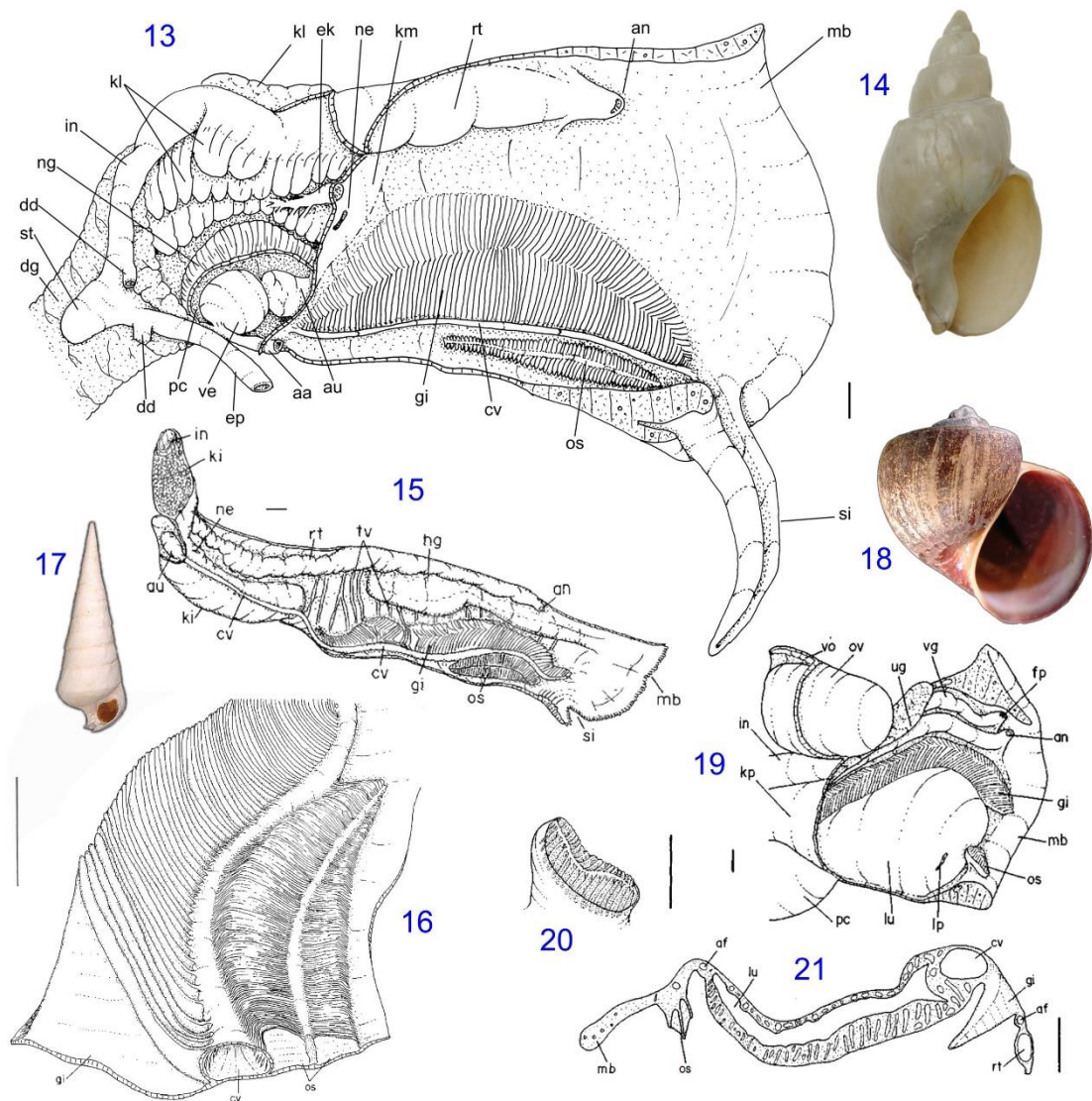
The strombids possibly have the proportionally longest osphradium, as it starts in the posterior end of the enormous gill and ends close to the mantle edge (Fig. 12: os) (Simone, 2005). In the cerithioideans, a typical bipectinate ridge-like osphradium is only found in the larger cerithiids. The minute-sized cerithiids and allied families usually have multilobed osphradium. This certainly is a



11-12. Examples of bipectinate ridge-like osphradia; pallial cavity roof, ventral-inner view, with example of a species' shell; **11**, *Cerithium atratum* (from Simone, 2001), Cerithioidea, scale= 1 mm, shell= 30 mm; **12**, *Strombus pugilis* (from Simone, 2005), Stromboidea, with a detail of indicated region of the osphradium, scale= 10 mm, shell= 50 mm. Lettering: ac, anterior gill fold; an, anus; cm, columellar muscle; cv, ctenidial vein; es, esophagus; gi, gill; hg, hypobranchial gland; mb, mantle border; ne, nephrostome; os, osphradium; ps-pt, prostate; rt, rectum; si, siphonal region; ss, style sac.

consequence of the miniaturization (Simone, 2001, 2011).

### Bipectinate elliptical osphradium



**13-21.** Examples of elliptical bipectinate osphradia; pallial cavity roof, ventral-inner view, with example of a species' shell and some details; **13**, *Buccinanops cochlidium* (from Pastorino & Simone, 2021), Buccinoidea, anterior end of dissected visceral mass also shown, scale= 5 mm; **14**, same, shell= 77 mm (ZMUC); **15**, *Campanile symbolicum* (from Simone, 2001), Cerithioidea, scale= 10 mm; **16**, same, transverse section of posterior level of osphradium and adjacent structures, ventral view, scale= 1 mm; **17**, same, shell= 60 mm (courtesy Femorale); **18**, *Pomacea scalaris* (from Simone, 2004a), Ampullarioidea, shell= 30 mm (MZSP 29590); **19**, same, pallial cavity roof, scale= 2 mm; **20**, same, detail of osphradium, scale= 2 mm; **21**, same, transverse section in middle of pallial cavity roof, scale= 2 mm. Lettering: aa, anterior aorta; af, afferent gill vessel; an, anus; au, auricle; cm, columellar muscle; cv, ctenidial vein; dd, duct to digestive gland; dg, digestive gland; ek, efferent renal vessel; ep, posterior esophagus; fp, female pore; gi, gill; hg, hypobranchial gland; in, intestine; ne, nephrostome; ng, nephridial gland; os, osphradium; ov, pallial oviduct; pc, pericardium; rt, rectum; si, siphon or siphonal region; ss, style sac; st, stomach; tv, transverse pallial vessels; ug, urinary gutter; ve, ventricle; vg, vaginal duct; vo, visceral oviduct.

The elliptical bipectinate osphradium (Fig. 22B, C, E) is actually the commonest kind. It is a synapomorphy of the Rhynchogastropoda and an important structure for the taxon's recognition.

It usually consists of an elongated osphradial ganglion, parallel to the left edge of the gill, surrounded by alternately disposed filaments. As these filaments are wider in the middle, tapering off at both ends, the overall shape is elliptical.

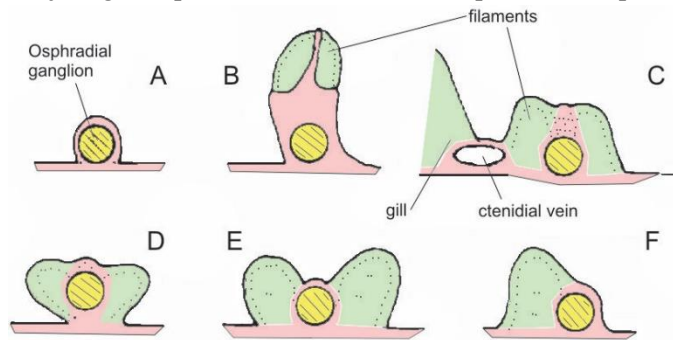
The development of a bipectinate osphradium only occurred in the Caenogastropoda. The elliptical model, however, evolved independently three times. One of them is in Ampullarioidea (Figs. 18-21, 22B), the first branch of the Hydrogastropoda. The other is in *Campanile* (Campanilidae – Cerithioidea) (Figs. 15-17, 22C). The third is the most widespread and is the above-mentioned synapomorphy of Rhynchogastropoda (Figs. 13, 22E), a large taxon that bears the higher mesogastropods and all neogastropods (Simone, 2011).

Despite being considered in a single category – elliptical bipectinate osphradium, the three kinds of osphradia have interesting differences, being other indicative of independent origins.

The ampullarioidean type of elliptical bipectinate osphradium (Figs. 18-21: os, 22B) is located on a basal integumentary stalk, which is relatively flexible, and usually has a low fold flanking externally the filaments. Interestingly, the ampullarioideans have the osphradium located in front of the lung (lu), a separated sac with its own pneumostome (lp), relatively away from the gill (gi).

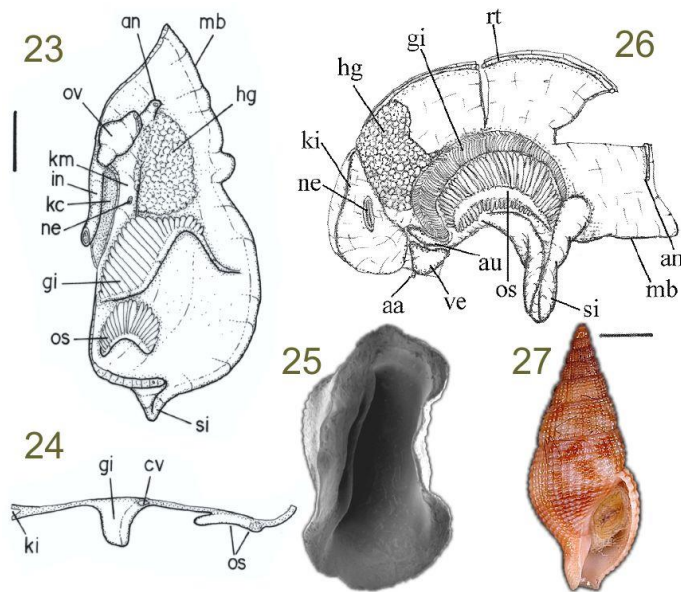
The *Campanile* type (Figs. 15-17, 22C) is the single that has the right filaments also connected to the ctenidial vein, apparently being also irrigated by it (Simone, 2004a, 2011) (Fig. 16). This type of osphradium possibly was found in all Campanilidae, however, the taxon is almost entirely extinct, mostly known by fossil shells. The studied *Campanile symbolicum*, from Australia, is the single living species. In all remaining aspects, the campanilid osphradium is similar to those of rhynchogastropods, as commented below.

The Rhynchogastropoda kind (Figs. 13, 14, 22E), as referred above the most widespread, has an elongated central osphradial ganglion flanked by alternate high filaments. This conformation simulates a bipectinate gill-like structure and sometimes is confused with gills by students. In some snails with small size, the gill is smaller than the osphradium. Thus, possibly, a function in the blood oxygenation is not an undiscarded function of the osphradium. The typical rhynchogastropod bipectinate osphradium runs parallel to the gill's left edge, flanking the ctenidial vein (cv), but is not connected to it. Being a feature of such a huge taxon, several kinds of osphradial modifications happened in rhynchogastropod evolution. Some of them are discussed below, including the monopectinate condition, the trifid design, and even the reversion to ridge-like type in two rhynchogastropod branches.



22. Schematic representation of a transverse section of a middle region of main types of osphradia; A, Ridge-like, simple; B, Bipectinate on a stalk (restricted to ampullarioideans); C, Bipectinate, with right filaments connected to ctenidial vein (exclusive of *Campanile*); D, Ridge-like, narrowly bipectinate (found in strombids and some cerithioideans); E, Bipectinate with elliptical outline (of higher Rhynchogastropoda); F, Monopectinate (common in miniaturized forms). Colors: orange= integument; green= filaments; yellow= ganglion.

## Partial or totally monopectinate osphradium



23-27. Examples of total or partial monopectinate osphradia; pallial cavity roof, ventral-inner view, with example of a species' shell and some details; **23**, *Pedicularia* sp. (from Simone, 2004b), scale= 0.5 mm; **24**, sale, transverse section in middle level of osphradium; **25**, shell UNSM 857666, L= 7 mm; **26**, *Amphissa acuminata* (from Simone & Leme, 2001), scale= 1 mm; **27**, shell (courtesy Femorale), L= 13 mm. Lettering: aa, anterior aorta; an, anus; au, auricle; cv, ctenidial vein; gi, gill; hg, hypobranchial gland; in, intestine; ki, kidney; kc, kidney lobe; km, kidney membrane; mb, mantle border; ne, nephrostome; os, osphradium; ov, pallial oviduct; rt, rectum, si, siphon or siphonal region; ve, ventricle.

metric, highly asymmetric, and monopectinate osphradia is a single evolutionary pathway linked to the miniaturization process. This is an empirical observation as larger species tend to have symmetric osphradium, and smaller ones highly asymmetric or even monopectinate one. The reasons for this evolutionary connection are not totally clear, but possibly the left filaments disturb the flow of water in the left pallial cavity side in miniaturized forms.

## Additional osphradial adaptations

### Satellite folds

Some snails that have ridge-like osphradium additionally developed a satellite pair of glandular folds (Fig. 9: of), or a fold that surrounds it completely (e.g., *Bittium varium* – Simone, 2001: fig. 335) (Simone, 2011). Glandular folds adjacent to any pallial structure attend an extra necessity of mucus. Some examples are the own hypobranchial gland (several Figs.: hg) (Simone, 2011) and of the endostyle of filter-feeding snails (e.g., turritellids – Simone 2001; calyptraeids – Simone, 2002; viviparids - Simone, 2004a). Possibly osphradial satellite folds are an additional method for improving the organ's function, as it constantly cleans it.

### Trifid osphradium

Another interesting osphradial morphological modification appeared in a branch of the Cypraeoidea (Simone, 2004b: node 12; Simone, 2011: node 129). The ordinary elliptical bipectinate osphradium became trifid. Possibly, the axis parallel to the gill, located at the right side, may be the

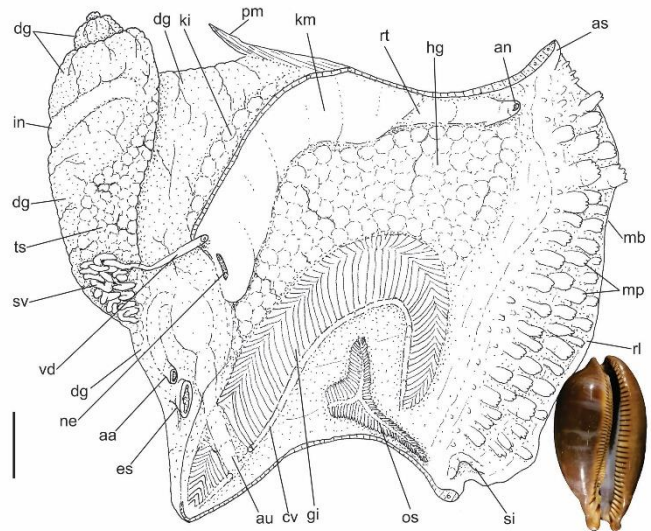
As referred above, the total or partial monopectinate condition of the osphradium (Figs. 22F, 23-27) is derived from the symmetric or weakly asymmetric one. As monopectinate osphradia are usually found in minute species, the condition may be part of the miniaturization process.

Some taxa, e.g., some columbellids and turritiforms, have the osphradium highly asymmetric, with left filaments very reduced and even missing in the anterior region (Fig. 26: os) (Simone & Leme, 2001). Other taxa, e.g. pediculariids, have species both, with this high asymmetry, and species with total monopectinate osphradial condition (Simone, 2004b) (Fig. 23: os).

It is not difficult to deduce that the symmetric, weakly asymmetric,



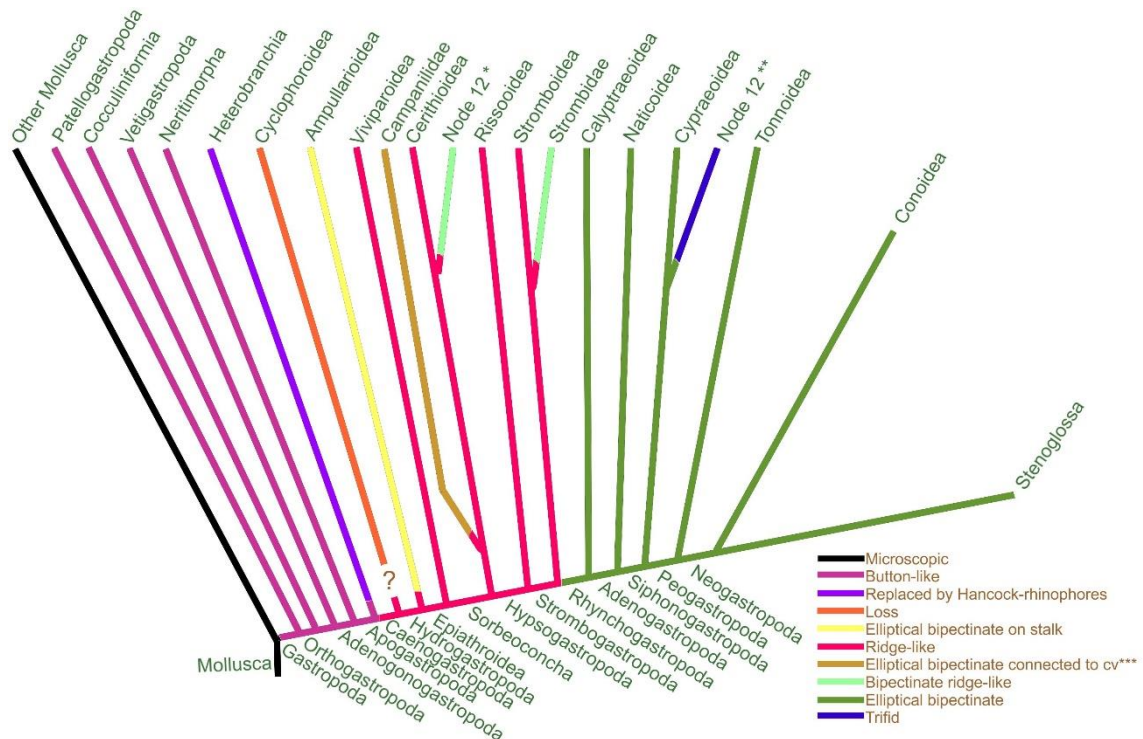
homolog portion of the elliptical bipectinate osphradium of the remaining rhynchogastropods. The new acquisition was the additional left axis, which barely points to the siphon (Fig. 28: os). The cypraeoidean trifold bipectinate osphradium has been referred like “tripectinate”, this name does not look adequate. This cypraeoidean new osphradial conformation looks a result of founding effect, which appeared in the ancestor of the Cypraeidae-Ovulidae branch, and was maintained in all its descendants.



### Phylogenetic inferences

Mainly based on the phylogenetic arrangement by Simone (2011), the evolution of the osphradium can be represented as in Fig. 29. The Button-like model appears as a synapomorphy of the Gastropoda, as a specialization of the microscopic model of other mollusks. The button-like osphradium (Figs. 2-6) is

28. Example of trifold bipectinate osphradium in *Macrocypraea mammoth* (from Simone & Cavallari, 2020); pallial cavity roof, ventral-inner view and coiled visceral mass, with example of a species' shell (holotype MZSP 137544, L 133 mm); Lettering: aa, anterior aorta; an, anus; as, anal siphon; au, auricle; cv, ctenidial vein; dg, digestive gland; gi, gill; hg, hypobranchial gland; in, intestine; ki, kidney; km, kidney membrane; mb, mantle border; mp, mantle papillae; ne, nephrostome; os, osphradium; pm, pallial muscle; rt, rectum; si, siphon; sv, seminal vesicle; ts, testicle; vd, vas deferens.



29. Morphology-based Mollusca phylogeny, focusing Gastropoda, mostly based on Simone (2011), showing different types of osphradia as indicated by the colors (see text for details). The survey is not exhaustive. ? in Cyclophoroidea mean a suggestion, as osphradium is only found in early development looking like ridge-like; \*by Simone, 2001; \*\* by Simone, 2004b; \*\*\*= ctenidial vein.

present in all of 4 basal branches, at least in the representatives that bear gill(s). The patellids (Patellogastropoda), for example, lost the ordinary gills, which were replaced by secondary gills apparently lacking osphradium (Simone, 2011).

The Heterobranchia have lost the osphradium, replaced by the Hancock organ or the rhizophore as olfactory structures. As the phylogeny of the Heterobranchia is not totally clear, there is no sure at which point they lost the structure. The more basal ones that still possess (apparent primary) gill, such as, e.g., *Cyclothyca pacei* (Amathinidae), *Cylindrobulla* (Cylindrobullidae) (personal observation, papers still unpublished), etc., have no signal of macroscopic osphradium. On the other hand, a large, right-positioned, strange osphradium was detected in *Tuba valkyrie* (Mathildidae) (Haszprunar, 1985b: fig 1: os). The homology of this mathindid osphradium with the ordinary prosobranch one is still debatable.

The typical ridge-like osphradium is here suggested to be a Caenogastropoda new acquisition, i.e., a synapomorphy (Figs. 7-10). As reported above, the doubt is because of the loss in the first branch (Cyclophoroidea, adapted for air-breathing) and its modification to stalked elliptical bipectinate osphradium in the second branch (Ampullarioidea). The suggestion is based on the presence of a ridge-like structure that looks at the osphradium in early cyclophoroideans development, and the elongated osphradial ganglion of ampullarioideans (Simone, 2004a, 2011 and references therein).

Along with the caenogastropod evolution, the ridge-like osphradium modified further. In Ampullarioidea the osphradium became bipectinate, placed on a stalk (Figs. 18-21). Within the Cerithioidea, two branches diverged: the Campanilidae with an osphradium highly bipectinate, but with right filaments connected to ctenidial vein (Figs. 15-17); and in a branch (node 12 by Simone, 2001) including cerithiids, which has ridge-like bipectinate osphradium (Fig. 11). Convergently, the same kind of osphradium is found in a branch of the Stromboidea – the strombids (Fig. 12) (Simone, 2005).

The Rhynchogastropoda have as one of their synapomorphies the elliptical bipectinate osphradium (Figs. 13-14), which is a very widespread model, presented in diverse groups like the neogastropods. Despite in having an obvious advantage in increasing the olfactory surface, the bipectinate condition is not restricted to carnivore-predatory branches, as it is present in the calyptraeideans and cypraeideans, which are not typically predators. The bipectinate condition was reverted to ridge-like osphradium in Hipponicidae (Calyptraeidea) and in *Amauropsis* (Naticoidae) (Simone, 2002, 2011).

To avoid excess information in the cladogram of the Fig. 29, the above-mentioned reversion from elliptical bipectinate osphradium to ridge-like osphradium, as well as the partial-total monopectinate condition and the presence of satellite glandular folds (discussed above) are not reported, as these conditions occur in several small, terminal branches (see Simone, 2011).

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