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The molluscan pallial cavity

Luiz Ricardo L. Simone

Museu de Zoologia da Universidade de São Paulo
lrsimone@usp.br; lrlsimone@gmail.com
ORCID: 0000-0002-1397-9823

Abstract

The pallial cavity is an important synapomorphy of the Mollusca, permitting delicate structures, as gills, being protected from environment elements and predation. It was modified along the molluscan evolution, being (1) posterior, the plesiomorphic state present currently only in both aplacophoran classes (Caudofoveata and Solenogastres), and in early fossil records on the remaining classes. (2) Circum-pedal, present in the modern Polyplacophora and Monoplacophora. (3) Lateral, as synapomorphy of the Euconchifera (Conchifera excluding the monoplacophorans); it is opened anteriorly and posteriorly in Diasoma (Scaphopoda + Bivalvia), and only anteriorly in Cyrtosoma (Gastropoda + Cephalopoda). Gastropoda further modified to (4) anterior pallial cavity, caused by the torsion. A phylogenetic discussion is also included.

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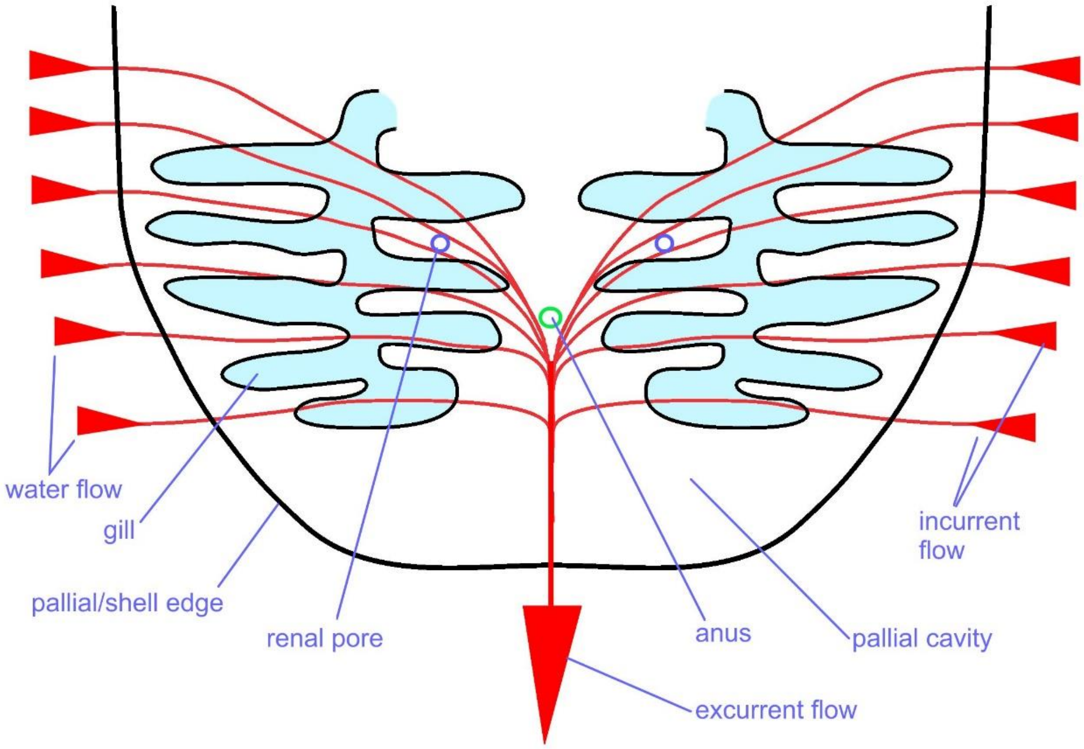
Introduction

The **pallial cavity**, also known as mantle cavity, is one of the synapomorphies of the Phylum Mollusca. As the name says, the structure is a cavity, a hollow region of the animal's body which is mostly circumscribed by the mantle (at least dorsally and laterally). The pallial cavity has an aperture to the environment, in order to permit flow of fluids.

The localization of the pallial cavity in the body is posterior, but it changed considerably along the molluscan evolution as explored in the present paper, according to the adaptations of the organisms. The main evolutive threads are discussed under a phylogenetic scenario, with a concern to the adaptive implications.



1. Schematic representation of a typical pallial cavity located posterior to the animal's body. Pair of gills and internal epithelium promote water flow (red lines and arrows) by ciliary current, in such excurrent flow carries urine (from renal pores) and feces (from anus).

Despite a cavity looks something strange as a character, its development in the molluscan ancestral permitted an internal arrangement of delicate structures. Protected from the environmental disturbances, the cavity permits the existence of a pair of delicate gills, in such thin walls are functionally better to gas exchange with the environment. A delicate and branching structure like the gills, if located outside, become a snack for predators or opportunists. This problem is minimized within the protection of the mantle, added the adjacent region of the shell. How the water inside the pallial cavity must flow (for air-breading mollusks, a secondary phenomenon, see other future paper), the pair of gills and most of the internal epithelium of the cavity are ciliated. The cilia promote water flow by rhythmic and unidirectional movements. The water comes from the environment, passes through the gill filaments for oxygenation, and is exteriorized carrying the undesired carbon dioxide (Fig. 1). The water flow usually comes from lateral sides, the incurrent flow, and goes towards posterior along the median cavity region (Fig. 1, red lines and arrows), called excurrent flow. This Y-plan of the flow is molded by the design of the pallial cavity.

As the flux of water is relatively continuous, as the ciliary epithelial movement is automatic (the gills cilia continue to move several minutes after the isolation of its filaments), the pallial cavity has an interesting flow capable to carry particles and substances. Therefore, the position of the renal pores and the anus are strategically along the excurrent flow (Fig. 1). The continuous excurrent water flow, thus, is also used to exteriorize the urine and feces away from the animal's body.

In the Figures, the abbreviation "MZSP" indicates samples deposited in the Museu de Zoologia da Universidade de São Paulo malacological collection.

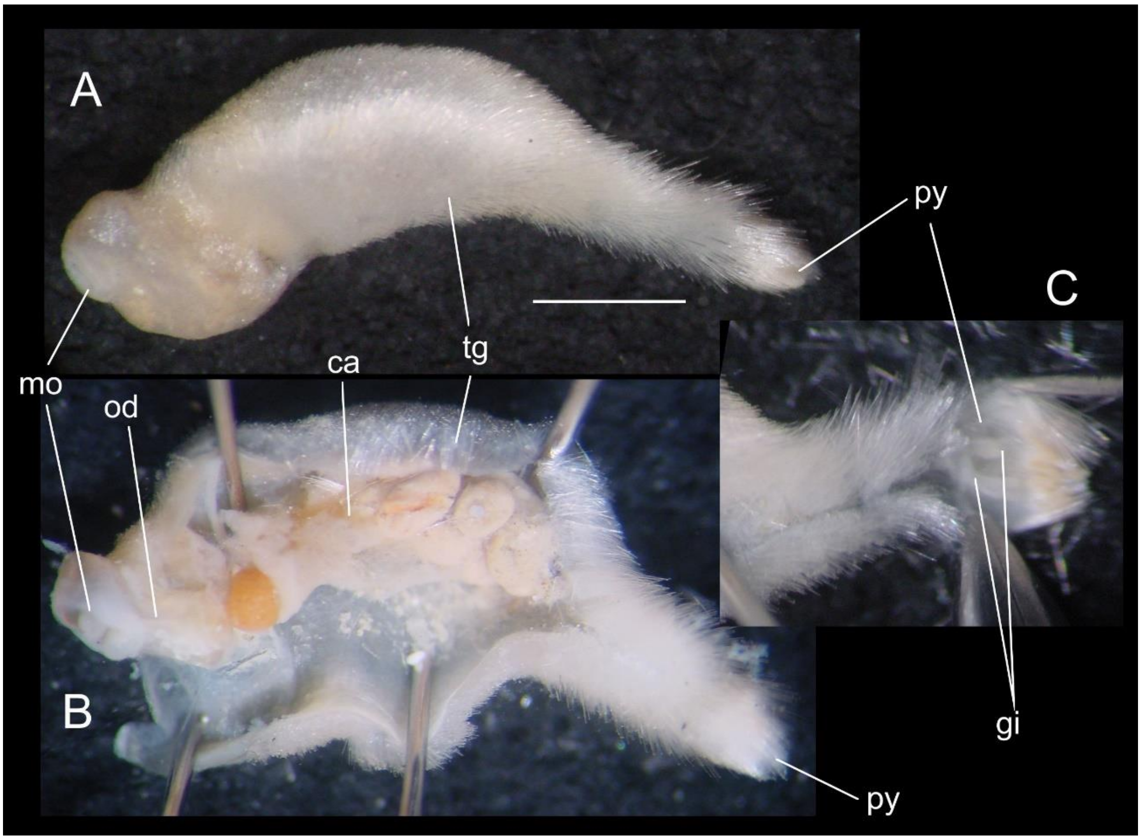
1. Types of pallial cavities

In a taxon as ancient as the mollusks, the course the pallial cavity evolution leads to all imaginable kind of arrangements. The cavity can be huge and the main body's space in some groups (e.g., teredinids), while it completely disappeared in others (e.g., nudibranchs). Therefore, a full exploration of all kinds of pallial arrangements is impracticable. Only the main sort of conformations is discussed herein, with main concern of understanding the main evolution of the mollusks. Several of them will be further explored in future papers dealing specifically on some groups, in these cases only the more basal features are discussed here.

1.1. Posterior pallial cavity

The posterior located pallial cavity is the basal conformation. This has been reinforced as the more basal classes – the aplacophorans Solenogastres and Caudofoveata – have posterior cavities (Fig. 2). The fossil registers also show more basal taxa of each classes having posterior pallial cavities (e.g., monoplacophorans). Additionally, the embryological development of the taxa that have modified pallial cavities, usually have posterior located pallial cavity in early phases.

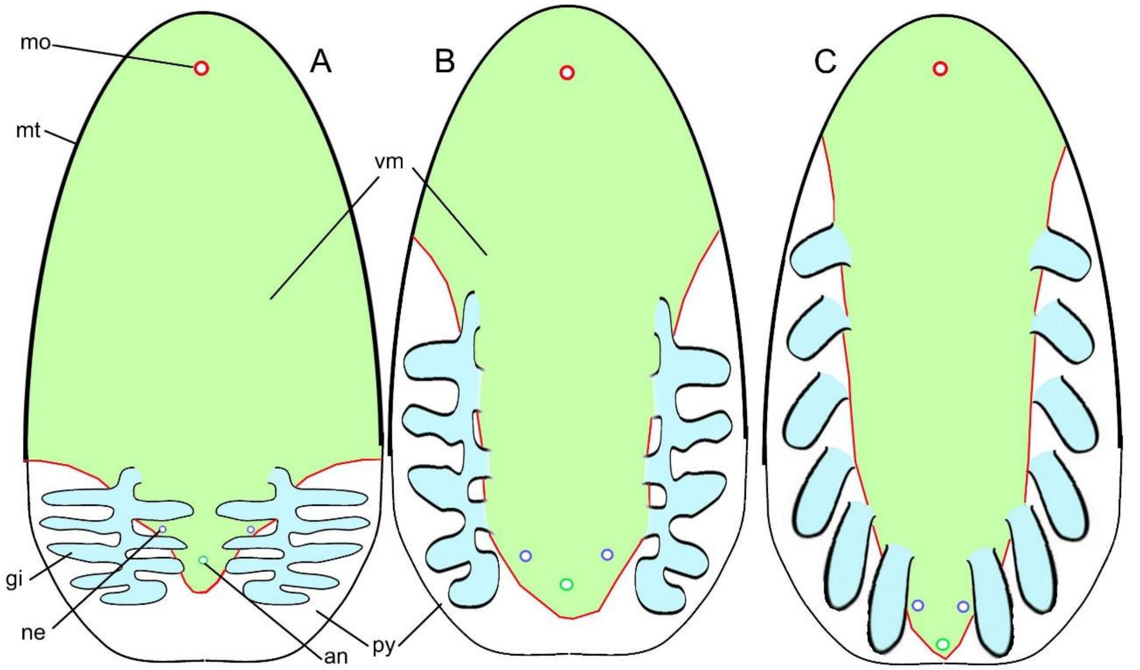
As the name suggests, the localization of the pallial cavity is posterior, i.e., in the posterior end of the body, opposed to the anterior one that bears the mouth.



2. Brazilian *Claviderma* sp. (MZSP), Caudofoveata, as an example of basal posterior located pallial cavity (py): **A**, hole specimen, left view, scale= 1 mm; **B**, same, mostly opened longitudinally; **C**, same, detail of its posterior region with pallial cavity sectioned longitudinally. Lettering: **ca**, gastric caecum; **gi**, gills; **mo**, mouth; **od**, odontophore; **py**, pallial cavity; **tg**, spicule-bearing integument.

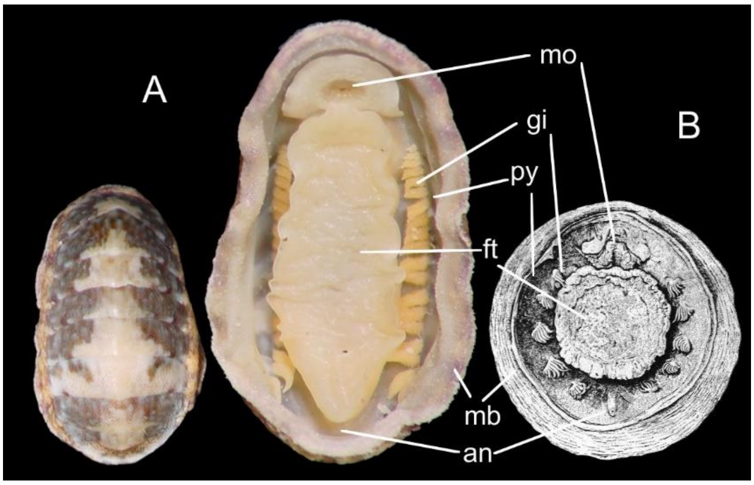
The better example of posterior located pallial cavity is in both aplacophoran classes above mentioned. The Caudofoveata, in particular, have the typical cavity schematized in the Fig. 1, in such the pair of gills and inner epithelium promote the water flow, which secondarily carries the urine and feces. On the other hand, the typical Solenogastres lack gills, but the remaining pallial cavity features are similar; the water flow is, thus, promoted by the inner epithelium alone, and/or some mechanical contraction.

1.2. Circum-pedal pallial cavity



3. Schematic representation of the possible evolution of the circum-pedal pallial cavity, dorsal view. The pallial cavity (py) is represented between the red line (visceral mass edge) and the posterior-lateral black line representing the mantle edge and the shell. **A**, plesiomorphic state with pallial cavity only posterior; **B**, intermediary state with pallial cavity reaching lateral regions and elongation of the gill; **C**, complete circum-pedal pallial cavity. Lettering: **an**, anus; **gi**, gill; **mo**, mouth; **mt**, mantle/shell edge; **ne**, nephrostome; **py**, pallial cavity; **vm**, visceral mass.

The circum-pedal kind of pallial cavity is a relatively shallow groove surrounding lateral and posterior edges of the foot, protected by adjacent edges of the mantle/shell. The water flow is from lateral regions as incurrent stream, passes in the main lateral groove, exiting to the environment in posterior end, on median line. In this region the urinary pores (nephrostomes) and the anus are located. Fig. 3 represents three steps towards a circum-pedal model: Fig. 3A represents the plesiomorphic condition of a fossil animal bearing posterior pallial cavity. The next step (Fig. 3B), the pallial cavity encroaches both sides of the space between foot and mantle edge, the gills become elongated, with outer filaments more developed than the inner ones; and the visceral mass goes further posteriorly. Fig. 3C represents a totally circum-pedal model, in which the pallial cavity surrounds the foot edges

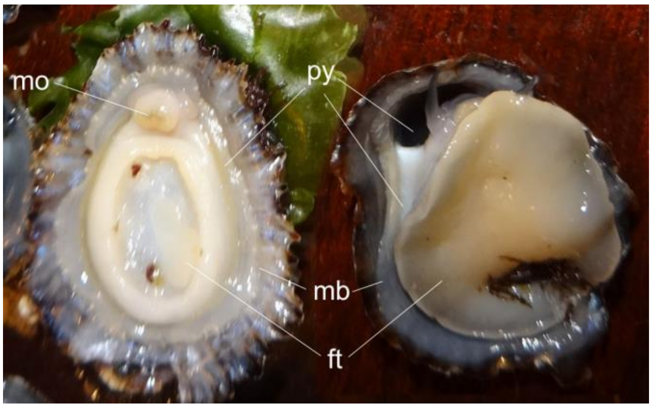


4. Examples of circum-pedal pallial cavities. **A**, *Ischnochiton striolatus*, a polyplacophore (L ~10 mm), dorsal and ventral views (MZSP); **B**, *Neopilina galatheae*, a monoplacophore, ventral view (drawing modified from https://trenton.mcz.harvard.edu/phylum-mollusca) (L ~20 mm). Lettering: **an**, anus; **ft**, foot sole; **gi**, gill; **mo**, mouth; **mb**, mantle/shell edge; **py**, pallial cavity.

almost totally, the gills become only represented by outer filaments apparently originated from pallial roof; the visceral mass is still more posteriorized, approaching the urinary and fecal apertures from posterior edge.

Typical taxa that have circum-pedal pallial cavities are the Recent polyplacophorans (Fig. 4A) and monoplacophorans (Fig. 4B). However, the fossil registers suggest that both groups have primitive branches bearing posterior pallial cavity. The presence of the circum-pedal model in both groups is, thus, a remarkable convergence.

The circum-pedal pallial cavity is a conformation linked to the dorso-ventral flattening of the body, in such the Recent polyplacophorans and monoplacophorans usually have. The pallial cavity surrounding the marginal edges of the body in a flattened animal looks more efficient than a cavity restricted to the posterior end. The analysis of the evolution of these groups reinforces this. Dorso ventrally flattened taxa are also found in several gastropod branches, a process called limpetization (Simone, 2018a); however, because of the anterior positioned pallial cavity (explored below) the pallial cavity of these taxa is only partially encroached laterally, maintaining a deeper anterior region. Amongst the gastropod, an almost purely circum-pedal cavity is found in patelloideans. Despite they have a deeper anterior cavity (Fig. 5-right), which lacks a gill, the cavity extends further lateral region (Fig 5: py), and in several species this space (mainly in Patellidae) is fulfilled by several leaflets of secondary gills.



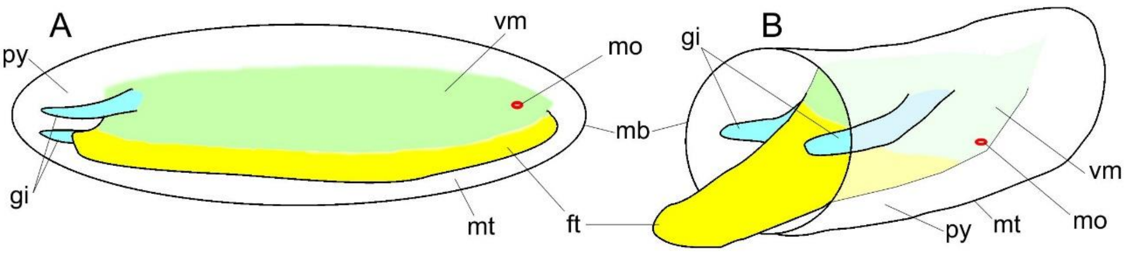
5. Pair of patellids from Azores (MZSP) photographed alive in ventral view; right specimen is trying to turn around, exposing larger right part of its pallial cavity (py). Lettering: **ft**, foot sole; **mo**, mouth; **mb**, mantle edge; **py**, pallial cavity.

The flattened, limpet or limpet-like forms, are usually developed as an adaptation to high energetic environments, e.g., high waves; the less the animal must detach the shell edges from the substratum, the better. A circum-pedal kind of pallial cavity looks the better one, as the incurrent (lateral) and excurrent (posterior) flows are far separated, and a narrow gap can attend their functional needs.

1.3. Lateral pallial cavity

The here called lateral pallial cavity is an outstanding synapomorphy of the Euconchifera, the conchiferan branch after its Monoplacophora first branch(es). Both higher conchiferan branches – the Diasoma (Bivalvia + Scaphopoda), and the Cyrtosoma (Gastropoda + Cephalopoda) – have it, or evolved from taxa that modified the pallial cavity from it.

Fig. 6 shows schematically the generic features of a posterior-positioned pallial cavity (Fig. 6A). As reported above, this type is mainly found in both basal aplacophoran classes, but is also found in basal fossil taxa of all remaining classes, dated from the early Paleozoic. The pallial structures, mainly the pair of gills (gi), are located in posterior end of the animal's body, opposite do the anterior region marked by the mouth (mo).



6. Schematic representations of generic conformation of pallial cavities; **A**, a mollusk with posterior pallial cavity, right-slightly ventral view; **B**, a mollusk with lateral pallial cavity, right-slightly posterior view (some portions seen as if the mantle/shell were transparent). Lettering: **ft**, foot; **gi**, gill; **mo**, mouth; **mb**, mantle edge; **mt**, mantle/shell; **py**, pallial cavity; **vm**, visceral mass.

The so-called lateral pallial cavity is schematized, in generical terms, in Fig. 6B. The formerly posterior positioned pallial cavity evolved to a deeper conformation, surrounding the lateral surfaces of the foot (ft) and visceral mass (vm). The mouth (mo) also modified to a more posterior and ventral position. In this type of pallial cavity, the main parts of the animal's body stay shielded inside an ample cavity provided by the mantle.

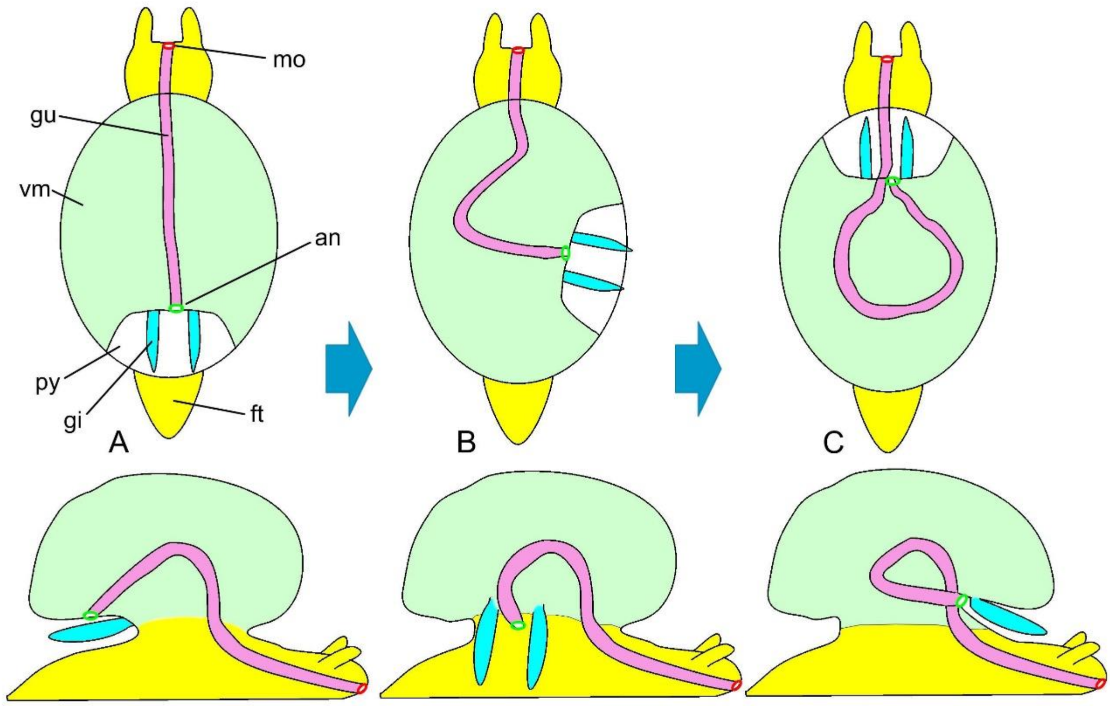
As the four non-monoplacophoran conchiferan classes, the Euconchifera, represent most of the molluscan diversity, this described basal model of pallial cavity suffered all kinds of modifications. The main treads will be explored in future papers, specific to each class. In over-all, the Diasoma (Scaphopoda + Bivalvia) have typical lateral pallial cavities, they are exclusive in having the foot directed anteriorly, adapted to dig in unconsolidated sediment, and an aperture of the cavity extending anteriorly. These features and 13 others that support, at least in morphological terms, the formal taxon Diasoma, are explained elsewhere (Simone, 2009).

The Cyrtosoma (Gastropoda + Cephalopoda), on the other hand, have their pallial cavity as a deep blind-sac, and the foot directed ventrally. The Cyrtosoma is supported by 14 synapomorphies (Simone, 2011). As referred above, the characters of the pallial cavity of both classes will be explored in future papers. The cephalopods, for instance, have the exclusivity of a highly contractile muscular mantle, used for jet-propulsion. The anterior-positioned gastropod pallial cavity is briefly explained below.

1.4. Anterior pallial cavity

An outstanding synapomorphy of the class Gastropoda is the torsion. This means a rotation of ~180° of the posterior body axis, in order to the pallial cavity and its internal structures become anterior positioned (Fig. 7). The somatic movement schematized in Fig. 7 is found in the typical gastropod embryology. In early development, the gastropod pallial cavity is posterior (Fig. 7A); it becomes anterior by an anticlockwise (in dorsal view) turn (Fig. 7C). The intermediary step (Fig. 7B) is theoretical, as it is not found in any fossil, neither in a gastropod embryo, as the torsion is relatively quick.

The reasons, recompenses and consequences of the gastropod torsion are questions long debated in the molluscan literature, in such abstract and references are found elsewhere (Simone, 2011, 2018b). However, the anterior positioned pallial cavity also causes an anterior positioned anus and renal pores. The evolutionary history of the gastropods is rich in solutions for avoiding the auto-pollution, fascinating issue that will be explored in future papers, which include the further modifications for air breathing.



7. Schematic representations of the gastropod torsion, superior row in dorsal view, inferior row in right view; **A**, monoplacophoran-like ancestor with posterior pallial cavity; **B**, intermediary step with right positioned pallial cavity (anticlockwise rotation); **C**, final gastropod model with anterior located pallial cavity. These movements are found in typical gastropod embryogenesis. Lettering: **an**, anus; **ft**, foot; **gi**, gill; **gu**, gut; **mo**, mouth; **mb**, mantle edge; **mt**, mantle/shell; **py**, pallial cavity; **vm**, visceral mass.

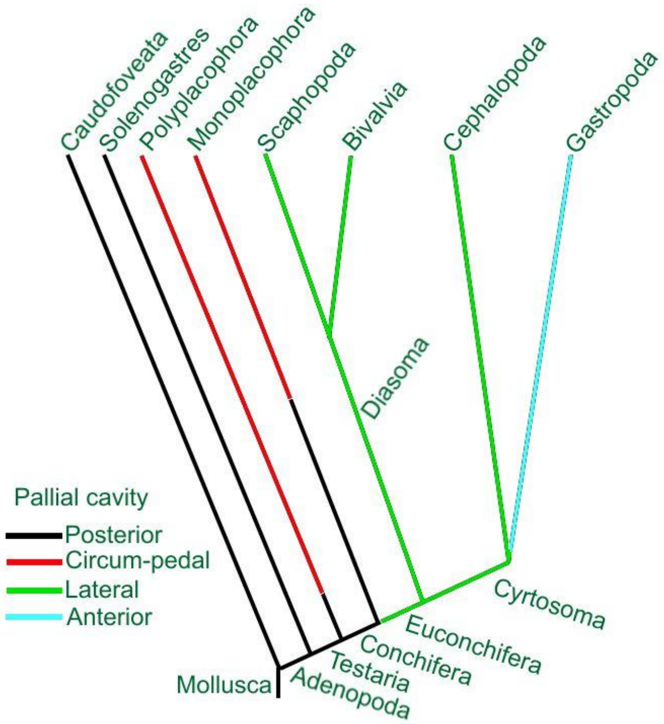
All gastropods have a twisted body conformation, including the opisthobranchs, which has been interpreted as having a detorsion. This issue is also debated elsewhere (Simone, 2011, 2018b: 18). Though, the anterior pallial cavity derived from the lateral type (item 1.3) is clearer in Orthogastropoda, i.e., the gastropod branches allocated after the two basal ones – Patellogastropoda and Cocculiniformia (Simone, 2011) – as they have deeper shell cavity (Simone, 2018a).

1.5. Loss of the pallial cavity

Despite the pallial cavity has, as explored above, several important physiological and adaptative advantages, some few branches evolved to the loss of it. The loss is noteworthy in some gastropod branches that suffered the limacization degree 2 process (Simone, 2018b: 15), in such the animal becomes a complete slug. Good examples are the marine nudibranchs and the terrestrial systellommatophorans. Beyond the limacization, adaptations to parasitism also caused loss of pallial cavity, an example is the eulimid endoparasite *Entoconcha* (Warén, 1983).

2. Phylogenetic implications

The phylogenetic arrangement that makes more sense in morphological terms is represented in the Fig. 8. The posterior pallial cavity (black lines) is the more basal type, demonstrated by the fossil records. Only both aplacophoran classes – Caudofoveata and Solenogastres – have it in Recent. In the remaining molluscan classes, the posterior pallial cavity is only found in the more basal branches, from the early Paleozoic. This is the reason for a black line is represented in the base of their branches. The circum-pedal pallial cavity appears in the modern polyplacophorans



8. Morphology-based Mollusca phylogeny, mostly based on Simone (2009, 2011), showing different types of pallial cavities as indicated by the colors (see text for details). The survey is not exhaustive.

and monoplacophorans, regarded as a convergence resulted by dorso-ventral flattened conformation. As discussed above, some gastropod limpet taxa also have a circum-pedal-like pallial cavity, but they are not classified like that in the cladogram because they still remain a deep anterior cavity (Fig. 5). This is important, anyway, to demonstrate that the dorso-ventral flattening causes circum-pedal invasion of the pallial cavity, as some patellids have secondary gills in circum-pedal area.

The Euconchifera have the lateral pallial cavity as basal synapomorphy (green). Of course, this cavity conformation is derived from the posterior one (Fig. 6), present only in early evolutive phase of these four classes, possibly in Cambrian. The Diasoma (Scaphopoda + Bivalvia) have a typical lateral pallial cavity, but they are exclusive in having the cavity with aperture in both sides (anterior and posterior – scaphopods and basal bivalve branch – Simone, 2009) and even ventral (remaining bivalves). The Cyrtosoma, on the other hand, have the pallial cavity opened only anteriorly, being a deep blind sac. The Gastropoda further modified this conformation by the torsion (Fig. 7). It is important to emphasize that the idiosyncrasies of each these euconchiferans, e.g., the muscular mantle of cephalopods, the torsion consequences and air breathing of gastropods, etc., will be matters of future papers.

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