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The caenogastropod brood pouches

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Abstract

A brood pouch immersed in head-foot tissue is a relatively rare incubation strategy in gastropods. Generally, brood pouches can be found next to the female genital structures or in the pallial cavity. Two groups within the Caenogastropoda developed brood pouches independently: the cerithioidean branch Planaxidae-Thiaridae, and the cypraeoidean Pediculariidae. The brood pouch in cerithioideans presents an aperture located in the dorsal-right region of the pallial cavity's floor, just anterior to the female genital aperture; thiarids have a single pouch distended only dorsally, while the planaxids have it double, lying on both sides of the foot. The brood pouch of pediculariids has a ventral aperture on the foot sole and is noticeable as a bulge located in the dorsal region of the foot. Phylogenetic, taxonomic and evolutionary implications of the different aspects of this incubation strategy are discussed herein.

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Introduction

Parental care is a clear evolutionary pathway in almost all molluscan branches. Noticeably, some groups tend to evolve from external fertilization, in which the embryos and young specimens must find a way to survive by themselves, to any kind of embryonic or juvenile protection (Simone, 2011). Typically, in gastropods, the most usual mechanism for brood protection is the egg capsule, which is spawned directly in the environment. These capsules provide some kind of protection in order to improve the chance of offspring survival. Additional strategies are also found in some gastropod groups, such as larval incubation inside the pallial cavity (e.g., columbellids), the maintenance of embryos and young individuals inside any branch of the genital tubes (e.g., some pulmonates like Achathinoidea – Simone, 2018), and the development of brood pouches immersed in head-foot tissues. The Viviparidae, a basal branch of Caenogastropoda, has its name based on the

unusual incubation of young specimens inside the pallial oviduct (Simone, 2004a; Li-Na et al., 2011).

This paper is focused on the brood pouches found in some caenogastropod lineages, discussing their differences, evolution, and phylogenetic and taxonomic significance.

1-3. Shells of representatives of families studied herein: **1**, Planaxidae, *Supplanaxis nucleus*, from Venezuela (L ~17 mm); **2**, Thiaridae, *Melanoides tuberculatus*, from Venezuela (L ~25 mm); **3**, Pediculariidae, Pedicularia tibia, from Brazil (Ceará) (L ~12 mm). Courtesy of Femorale http://www.femorale.com

Three lineages within the Caenogastropoda developed brood pouches inside their head-foot region, apparently removed from the genital system's axis. These then represent the acquisition of a novel structure inside this somatic region. Two of these taxa are apparently related, the Thiaridae (Fig. 2) and the Planaxidae (Fig. 1) (Simone, 2001, 2011). They belong to the same branch in a morphology-based cerithioidean phylogeny (Simone, 2001: 255, fig. 440, node 15) and the presence of a brood pouch with the aperture located on the right side of the head is one of the 6 synapomorphies supporting that node. The other group with a similarly structured brood pouch is Pediculariidae (Fig. 3), a monophyletic family supported by 10 synapomorphies, one of which is the presence of a brood pouch (Simone, 2004b: 174, fig. 531, node 6). More details on the brood pouch of these groups are found below.

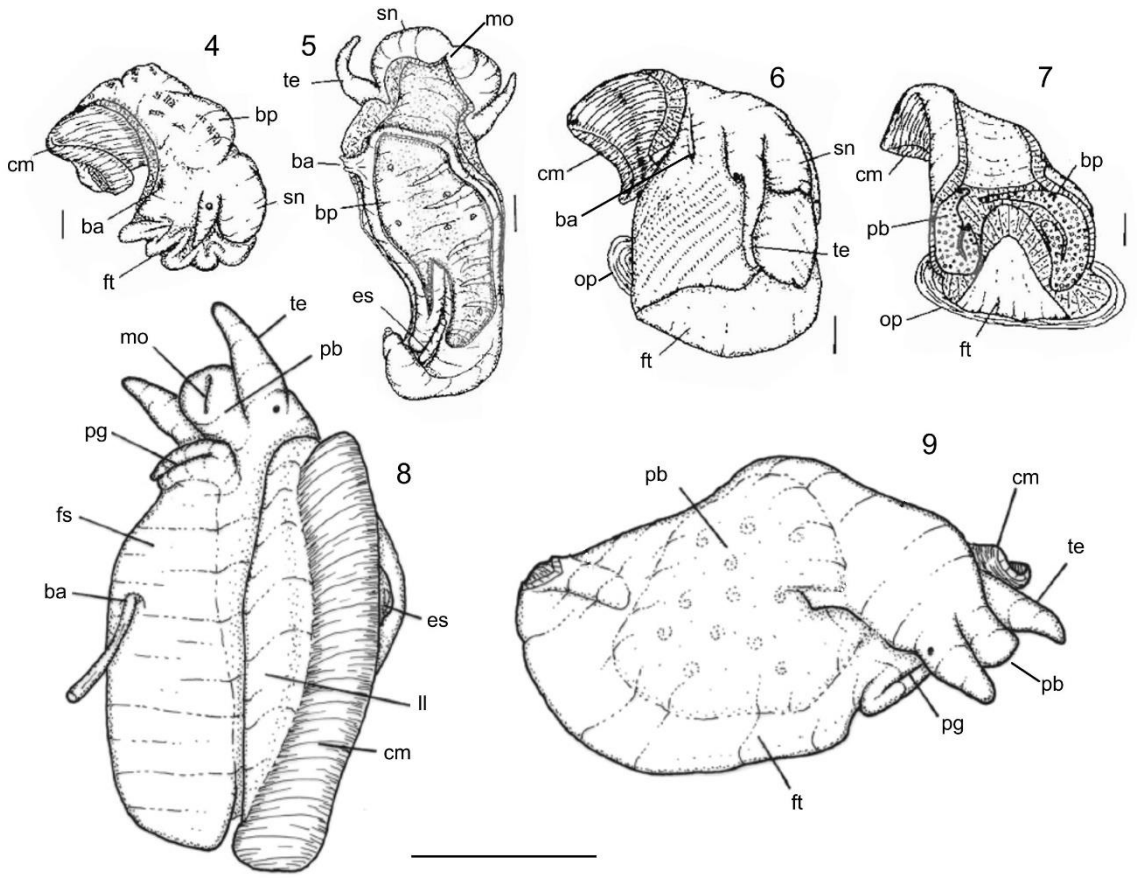
Cerithioidean brood pouches

As mentioned above, two cerithioidean families developed brood pouches immersed in the head-foot tissues – the Thiaridae and the Planaxidae. Beyond that, their brood pouches have in common an aperture located on the right side of the head, close to the base of the right cephalic tentacle (Figs. 4, 6: ba). Beyond their equivalent apertures, there are no further structural similarities. In thiarids, the brood pouch lies to the left and expands abruptly forming a hump behind the head, protruding into the floor of the pallial cavity (Figs. 4-5, 10-11: bp). Inside the brood pouch, several young specimens can be found, generally in different stages of development. In *Aylacostoma*, for example, about a dozen specimens can be found simultaneously inside the brood pouch; hoverer; in *Melanoides*, hundreds of specimens often shelter inside the pouch (Simone, 2001). In live mature individuals, young specimens can be observed finding their way out of the brood pouch through its aperture, and they begin to crawl just afterward.

Planaxid brood pouches have two branches connected to the common aperture (Figs. 6-7: bp, 12-13). The right branch runs ventrally just below its aperture. The left branch initially runs dorsally towards the animal's left side, gradually expanding and lying ventrally (Figs. 12-13, darker side). Both branches of the brood pouch are bent internally in the ventral region (Fig. 7). Hundreds of young specimens are usually found inside planaxids during dissection (Simone, 2001), in the brood pouch that expands on both sides of the foot, precluding its retraction inside the shell. These young specimens are usually in the same stage of development. The location of the brood pouch aperture is somewhat close to the female genital system's aperture. In some species, a short furrow

in the pallial floor connects both structures. So, it is possible to infer that the embryos are transported from the female aperture to the brood pouch via ciliary current.

Cypraeoidean brood pouches

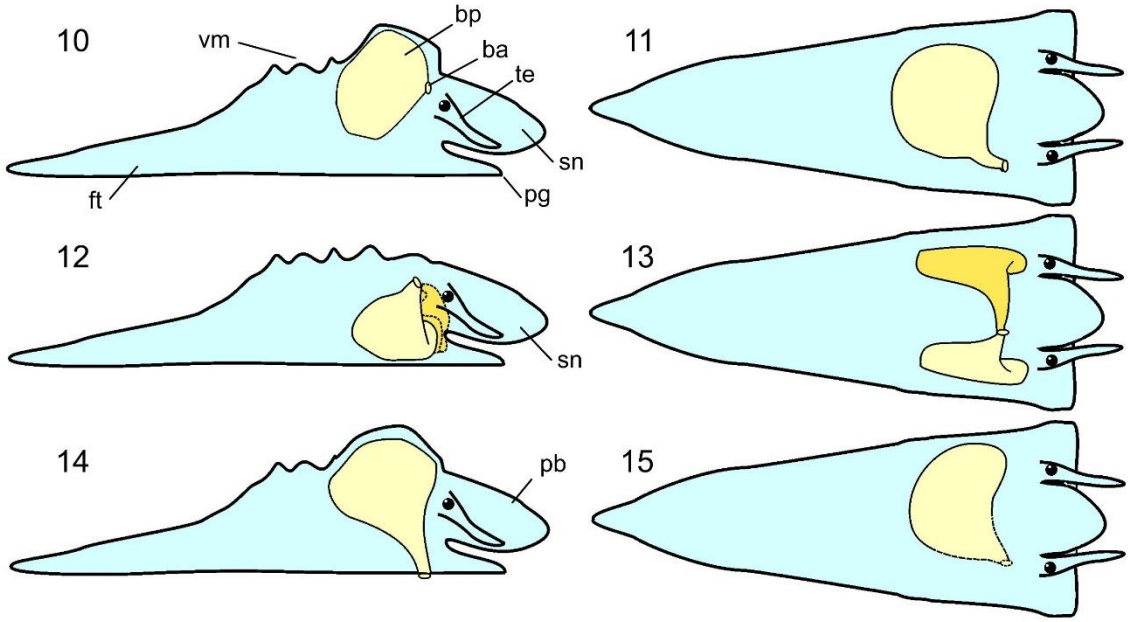


4-9. Anatomical drawings from examples of studied material. **4**, thiarid *Melanoides tuberculatus*, head-foot, lateral-right view, some young specimens seen by translucency inside the brood pouch; **5**, same, ventral view, foot and columellar muscle removed, most haemocoelic organs removed except for the brood pouch, opened longitudinally with young specimens inside removed; **6**, female of planaxid *Supplanaxis nucleus*, head-foot, lateral-right view; **7**, same, posterior region of foot after frontal section in its middle region; **8**, female of pediculariid *Pedicularia* sp, head-foot lateral-left view, small portion of mucus exiting from brood pouch aperture; **9**, same, dorsal-right view, brood pouch seen by translucency. Scales= 1 mm. (4-7 from Simone, 2001; 8-9 from Simone, 2004). Lettering: ba, brood pouch aperture; bp, brood pouch; cm, columellar muscle; es, esophagus; fs, foot sole; ft, foot; ll, left mantle lobe; mo, mouth; op, operculum; pb, proboscis; pg, pedal gland furrow; sn, snout; te, cephalic tentacle.

As mentioned before, the Pediculariidae have a well-developed brood pouch (Figs. 8-9: bp, 14-15). In some aspects, it is similar to that of the cerithioideans in being immersed in the head-foot tissue, and in bulging in a region posterior-right to the head (Fig. 9: bp), forming a dorsal hump in the mature females. However, differently from cerithioideans, the pediculariid brood pouch has its aperture located in the foot sole (Fig. 8: ba), slightly dislocated to the right, from the middle to the anterior region of the foot sole (Simone, 2004b). A few dozens of young specimens can be usually found inside pediculariid brood pouches, apparently in the same stage of development.

Evolution of the caenogastropod brood pouches

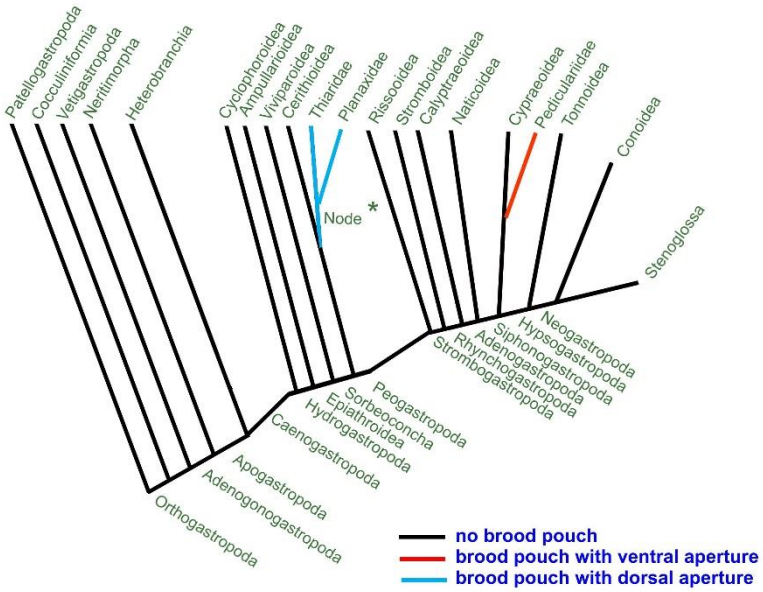
Almost nothing can be inferred about the evolution of the brood pouches of the three taxa mentioned above. None of these structures are present among their close relatives, and there is no trace of these structures in males. Possibly, as the anatomical attributes of related taxa are revealed, this evolutionary scenario will be further elucidated.



10-15. Schematic representations of isolated head-foot of families studied herein, left in right view, right in dorsal view. Brood pouch (yellow) as in situ seen if the animal was transparent. Not to scale, approximate proportions preserved. **10-11**, a thiarid (*Aylacostoma ci*); **12-13**, a planaxid (*Supplanaxis nucleus*), left branch of brood pouch represented slightly darker; **14-15**, a pediculariid (*Pedicularia* sp.). Lettering: be, brood pouch aperture; bp, brood pouch; pb, proboscis; pg, region of pedal gland furrow; sn, snout; te, cephalic tentacle; vm, visceral mass (removed).

In the planaxids and thiarids, a possible origin of the brood pouch lies in the increase of a concavity located in the pallial floor behind the female genital aperture, in order to protect the offspring until they are further developed.

Nevertheless, how the brood pouch evolved with an aperture in the foot sole in pediculariids is still a mystery. A possible evolutionary scenario is the development of a higher concavity originated from the cement gland. The cement gland is usually located in the middle of the anterior level of the foot sole and is apparently a synapomorphy of the Hypsogastropoda (tonnoideans + neogastropods) (Simone, 2011: 217) (Fig. 16). However, a pre-gland can appear in the Siphonogastropoda, a branch before hypsogastropods that includes Cypraeoidea (Fig. 16).



16. Gastropod phylogeny, mostly based on Simone (2011), showing the position of brood-pouch bearing taxa as shown in color key. Node *= 34 (by Simone, 2011), or 15 (by Simone, 2001).

As represented in Fig. 16, the brood pouch has two independent evolutionary origins: in cerithioideans, with a dorsal aperture, and in the cypraeoideans with a ventral aperture. Both have been proved to be synapomorphies of, respectively, a branch uniting planaxids and thiarids [node 15 by Simone (2001), and 34 by Simone (2011)] inside Cerithioidea; and pediculariids [node 6 by Simone (2004b), and 123 by Simone (2011)] inside Cypraeoidea.

Discussion

As remarked above, the caenogastropod brood pouches evolved independently in two branches, each one with a different aperture. Besides, nothing similar can be found in the known close relatives, not even in the males, which precludes further inferences. Even so, it is rather common in molluscan evolution for an important structure to appear in a given lineage while its close relatives present nothing similar.

Additional cerithioideans have been described as bearing a brood pouch, e.g., *Tanganyicia rufofilosa*, a Paludomidae (Strong & Glaubrecht, 2001). It was described as having a brood pouch similar to those of the thiarids, which suggests a closer relationship between paludomids and thiarids, rather than planaxids; or that *Tanganyicia* could actually be a thiarid. This possibility, i.e., that some brood pouch-bearing species supposedly belonging to other cerithioideans families might actually belong to Thiaridae can be analyzed, like, e.g., *Brotia laodelectata* Köhler, 2007, a supposed Pachychilidae.

Another important question arises from analyzing gastropod brood pouches: how do the young specimens breathe and feed inside them? Despite the lack of physiological experiments and observations, the breathing may possibly be provided via simple diffusion through the nuchal integument. This may explain why the brood pouch of both groups is superficial in females, so much so that the young specimens can be seen by translucence. The youth feeding inside the brood pouch is slightly harder to explain, but, apparently, they do feed (not only on vitellus), as in some groups (like thiarids) the specimens are born with 4-5 teleoconch whorls. Possibly, the feeding may be provided by an alimentary mucus secreted by the brood pouch's inner epithelium. The presence of this mucus is easily observed during dissection.

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