A possible function of the parietal tooth of *Pedipes* (Gastropoda, Pulmonata, Ellobiidae)

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When *Pedipes ovalis* withdraws into its shell, its foot is sequestered between the parietal and the columellar teeth, while the sinus above the parietal tooth encloses the portion of the mantle skirt with the pneumostome. This organization suggests that one function of the long parietal tooth characteristic of the genus is to prevent the snail's foot from blocking the pneumostome.

Key words: gastropod, aperture, pneumostome, functional morphology.

Introduction

Various forms of ribs, ridges and teeth within the shell apertures are widely distributed in both marine and terrestrial snails (Abbott, 1989; Vermeij, 1993). In marine species, the apertural barriers may block the access of potential predators into the shell (Vermeij, 1993). Among terrestrial stylommatophoran snails, apertural formations, including one or more teeth or folds on the parietal wall, are common among members of several speciose families, including the Enidae, Clausilidae, Vertiginidae, Polygyridae, Odontostomidae and the Camaenidae (Abbott, 1989; Pokryszko, 1997). Different functions have been attributed to the apertural formations of stylommatophoran snails (Pokryszko, 1997). Among semi-terrestrial basommatophoran ellobiids, apertural teeth or folds are also present in many genera (Abbott, 1989; Martins, 1996). However, no study of the functional morphology of the ellobiid aperture has recently been published.

The genus *Pedipes* comprises small, semi-terrestrial ellobiid snails with a worldwide distribution (Clench, 1964). The foot of *Pedipes* is divided by a transverse groove into an anterior propodium and a posterior metapodium (fig. 1). The shell aperture is surrounded by two columellar, one prominent parietal and one palatal tooth, sometimes missing (fig. 2). In the very first account of a *Pedipes* species, Adanson (1757) explained the orientation of the parts of the foot in relation to the parietal tooth as follows (in translation): "…when we observe the animal enter and leave its shell many times, we see the two parts [of the foot] returning and passing one on the left and one on the right of the [parietal] tooth, which is extended to almost the interior of the shell." If what Adanson claimed was correct, his claim would imply that when a *Pedipes* withdrew its foot, the parietal tooth separated the propodium from the metapodium and the latter was positioned between the parietal tooth and the lower corner of the palatal wall (when a shell was held

with its apex down as in Adanson's figures). Lowe (1832), however, noted that in *P. afra* an "orifice" occupied "the whole space between the great tooth or fold, and the lower angle of the aperture" (also with the apex down). Therefore, in contrast to Adanson's, Lowe's observation implied that the entire foot was positioned between the parietal tooth and the columella. Here, I present a fresh look at the organization of the body parts of *Pedipes* within the aperture of its shell and argue for a possible function of its parietal tooth.

Material and methods

I collected live *Pedipes* near the high-tide mark on the north shore of Dunedin Causeway to Honeymoon Island in Pinellas County, Florida, USA in April 2009. I identified the snails as *P. ovalis* C.B. Adams, 1849 from their protoconch morphology (Martins, 1996). I watched the snails under a stereo microscope and also took high resolution photographs using an Olympus E-500 camera with a Zuiko 35-mm lens and a 25-mm extension tube.

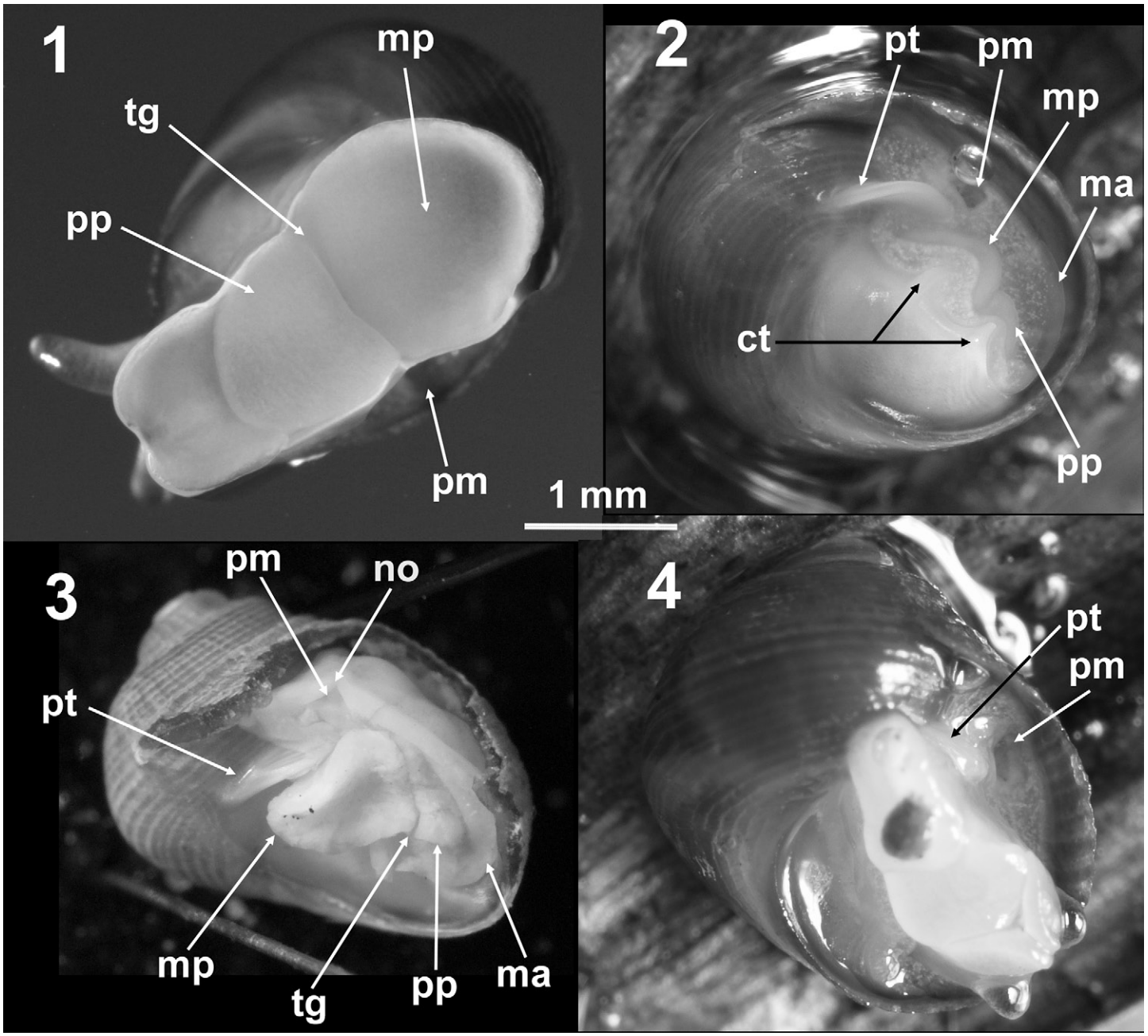
Results and discussion

When *P. ovalis* is partially withdrawn into its shell, the mantle skirt circumscribes the inner surface of the aperture while enveloping the foot, which is sequestered in its entirety between the parietal and the columellar teeth (figs 2-3). In this position, the transverse groove is compressed and the back half of the metapodium is positioned inside the canal between the parietal and the upper columellar teeth (fig. 2), while the space between the parietal tooth and the palatal wall encloses the portion of the mantle skirt with the pneumostome (figs 2-4). These observations discount Adanson's (1757) claim that the parietal tooth separates the propodium from the metapodium, but are in agreement with Lowe's (1832) observations. It is of historical interest to note that Lowe (1832) was trying to determine if *P. afra* was a pulmonate snail and although he seems to have realized the "orifice" he saw had a respiratory function, he instead relied on the equivocal results of his sea water-immersion experiments and grouped *P. afra* with the gill-bearing "Pectinibranchia".

The positioning of the pneumostome in a sinus walled by the parietal tooth strongly implies that a function of the latter is to prevent the foot from smothering the pneumostome, especially when the snail is withdrawn into its shell. The photographs often show the metapodium propped against the parietal tooth, but never extending over it towards the pneumostome (figs 3-4). Unlike most other ellobiids, *Pedipes* species do not resorb the inner whorls of their shells (Martins, 1996). In the specimens of *P. ovalis* I examined, the parietal tooth extended approximately a quarter whorl into the shell and its height did not diminish almost till the beginning of the tooth. Therefore, the parietal tooth can prevent the metapodium from covering or squeezing the pneumostome even when the snail is withdrawn as deep as a quarter whorl away from the aperture.

In addition, the palatal rim of the peristome of *P. ovalis* has a shallow notch corresponding to the location of a notch in the mantle skirt above the pneumostome (fig. 3). The alignment of these notches when a snail is out of its shell probably further ensures the unobstructed access of the pneumostome to air.

Numerous functions have been proposed for the apertural barriers of pulmonate snails (for a review, see Pokryszko, 1997). These include the lessening of water loss (Tillier, 1989), the blocking of the entry of and the strengthening of the aperture against small predators (for example, Gittenberger, 1996), the positioning of the shell during locomotion in ellobiids (Martins, 1996) and the protection of the pneumostome in several families of stylommatophorans (Suvorov, 2002). The available evidence indicates that pulmonates descended from an operculated ancestor (for a review, see Gittenberger, 1996). The apertural barriers probably evolved in response to simultaneous multiple selective pressures and have retained multiple functions. The evolution of the apertural barriers is likely to have occurred concurrently with the diminishing of the operculum and the modification of the mantle cavity into a lung with a pneumostome. If the parietal tooth of the non-stylommatophoran *Pedipes* is homologous with the corresponding tooth in the shell apertures of many stylommatophorans, this will indicate that the proposed function of the parietal tooth to facilitate breathing has been conserved during the evolution of pulmonates.



Figs **1-4**. *Pedipes ovalis*. **1**, crawling on a glass plate tilted at a 60° angle above the horizontal; **2**, in its shell with the foot enveloped within the mantle and sequestered between the parietal and columellar teeth. These specimens had no palatal tooth. **3**, preserved specimen with the palatal wall removed showing the respective positions of various parts; **4**, emerging from its shell. Abbreviations: ct, columellar teeth; ma, mantle; mp, metapodium; no, notch in the mantle skirt; pt, parietal tooth; pm, pneumostome; pp, propodium; tg, transverse groove.

Acknowledgements

This paper is dedicated to the memory of my wife Nicole. I thank Barry Roth and Geerat J. Vermeij for reviewing earlier drafts of the manuscript.

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