

The retractor muscles of buccal mass - m2

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Abstract

The pair of retractor muscles of buccal mass, coded m2, are a heterogeneous set of muscles that retract the structure inside the haemocoel. The basal state of m2 originates from the shell and is present in the first molluscan branches, notoriously in the Polyplacophora and Monoplacophora. It disappears in Euconchifera, but reappears independently in several inner branches, this time originating from the haemocoel walls. The pair m2 is synapomorphy of the higher heterobranchs Nudipleura and pulmonates, and in Epiathroidea caenogastropods. This is only the main framework of the m2 molluscan evolution, but a myriad of further modifications, including secondary losses, exist, some few examples are reported.

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Introduction

The molluscan pair of retractor muscles of the buccal mass, collectively codified as “m2,” is a heterogeneous set of muscles, as the name suggests, that retracts the buccal mass inside the body. For that, the pair of muscles naturally must be originated posteriorly in the haemocoelic cavity and must have inserted in any point of the buccal mass, generally in its posterior hemisphere. When the buccal mass is exteriorized, their contraction promotes the retreat of it back to be sheltered inside the body.

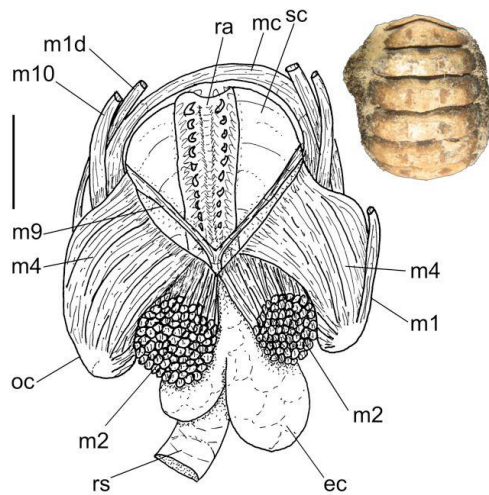
The pair m2 apparently appeared and disappeared several times along the molluscan evolution, and it has a very complex evolutive history. A complete exploration of the evolution and homology comparison amongst the different kinds of m2 is presently impossible both, because some groups vary considerably, and because the present knowledge is far from being complete. A notorious gap is the aplacophorans. Justly these both more basal mollusk branches have their odontophore and buccal mass very modified, difficult to infer homologies. Possibly ontogenetic

investigations in them could bring some light to the question. The buccal mass and odontophore of the 2 aplacophoran classes will be subject of a future Malacopedia issue.

Thus, this paper is focused on Testaria, i.e., Polyplacophora + Conchifera. The plesiomorphic kind of m2 is described, as well as the point in which it disappeared, and, after that, the main kinds of m2 that usually support important branches in the molluscan phylogeny.

1. The plesiomorphic Testaria m2 originated in shell

As referred above, some aplacophorans have retractor muscles of buccal mass, but their structures are too modified to permit clear inferences of homology. Until this subject is clearer, this topic begins in Testaria in this issue, a taxon in which at least 2 first branches have representatives with an interesting m2 pair originating directly from the shell.



1: Odontophore of *Acanthopleura gemmata* as example of m2 connected direct to the shell, dorsal view, scale= 2 mm, and whole specimen (L ~40 mm) (from Jardim et al, 2020). Lettering: ec, esophageal glandular complex; m1-m10, intrinsic-extrinsic odontophore muscles; mc, buccal circular muscle (sphincter); oc, odontophore cartilage; ra, radula; rs, radular sac; sc, subradular cartilage.

It is well known that the last branch of the aculiferans – the Polyplacophora – and the first branch of the conchiferans – the Monoplacophora – have in the anterior region of their shells a pair of scars. This pair is usually called “radular muscles”, which actually are the m2. This pair is usually utilized to determine which is the anterior region of a monoplacophoran fossil, something not so easy, mainly in coiled forms.

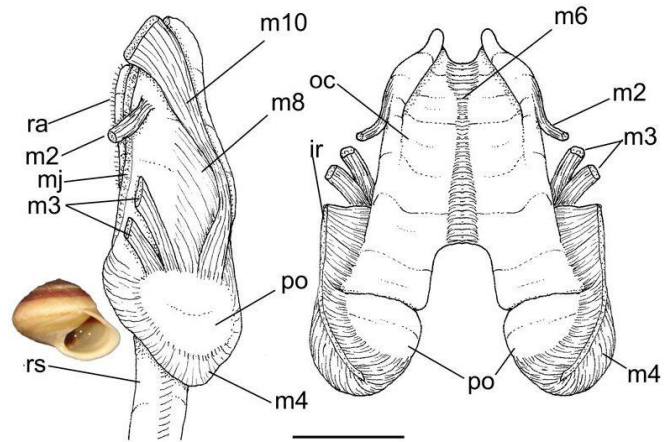
Polyplacophora and Monoplacophora are the 2 first branches of Testaria. The pair m2 of the polyplacophores are powerful in all species in which this structure is known. The origin of these muscles is in the middle region of the lateral sides of the second valves, keeping in them a pair of large scars. No other valve has these scars. The thick pair m2 runs anteriorly a short distance (Fig. 1: m2), and inserts part in median edge of the pair of odontophore cartilages, and part in the adjacent region of radular sac (Jardim et al, 2020: fig. 39). Interestingly, the pair m2 and other larger pairs of muscles (e.g., m4, m5) of the known chitons are composed of several separated small bundles of muscle fibers (Fig. 1).

The pair of m2 of monoplacophorans is relatively weakly known, as most of them are fossils, with m2 inaccessible. The living ones are too minuscule, difficult to study such characters. Thus, all the knowledge is based on *Neopilina galathea*, the big one, thanks to the detailed study by Lemche & Wingstrand (1959). In that study, the authors clearly show a set of muscles in which the main one is named “musculus oralis posterior”, which certainly constitutes the pair m2. The origin is in the shell, joined to “musculus obliquus anterior A” that goes to the foot (their fig. 84).

2. The m2 in the Euconchifera

In Euconchifera, i.e., the non-monoplacophoran Conchifera, the loss of the pair m2 originated from the shell is one of its outstanding synapomorphies (Simone, 2011). From both euconchiferan subdivisions, Diasoma has no trace of m2 in Scaphopoda, while Bivalvia has no buccal mass at all (e.g., Simone, 2009); in Cyrtosoma, the Cephalopoda also there is no trace of m2 in their incredible complex buccal masses, which retraction apparently is promoted by the anterior peribuccal muscles (e.g., Simone, 1997a; Sasaki et al, 2010; Migliavacca & Simone, 2020), and in the 3 basal branches of Gastropoda (sensu Simone, 2011).

Thus, there is no trace of m2 in Patellogastropoda (e.g., Leal & Simone, 1998), in Vetigastropoda (e.g., Dornellas et al., 2020), and in Neritimorpha (e.g., Barroso et al, 2012). There is, however, a pair of muscles called m2, as it has the function of retracting the buccal mass/odontophore inside the haemocoel, in the examined terrestrial neritimorphs Helicinidae (Fig. 2). This is certainly an interesting convergence. A clue of this is given by the insertion of the helicimid m2, very anteriorized in the lateral edge of odontophore cartilages (Fig. 2: m2), instead of being posterior inserted as in the remaining taxa. The origin of this kind of helicimid pair of m2 is in the posterior floor of the haemocoel (Simone, 2018), as any other m2, justifying its denomination.

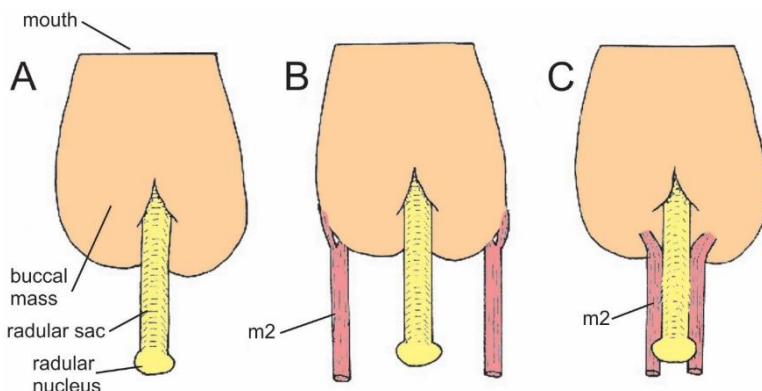


2: Odontophore of *Helicina variabilis*, a terrestrial neritimorph, left a left view, right a dorsal view with radula removed and both cartilages deflected, scale= 1 mm, and whole shell (L ~15 mm) (from Simone, 2018). Lettering: m1-m10, intrinsic-extrinsic odontophore muscles; mj, jaw and peribuccal muscles; oc, anterior odontophore cartilage; po, posterior odontophore cartilage; ra, radula; rs, radular sac.

3. The m2 in the Apogastropoda

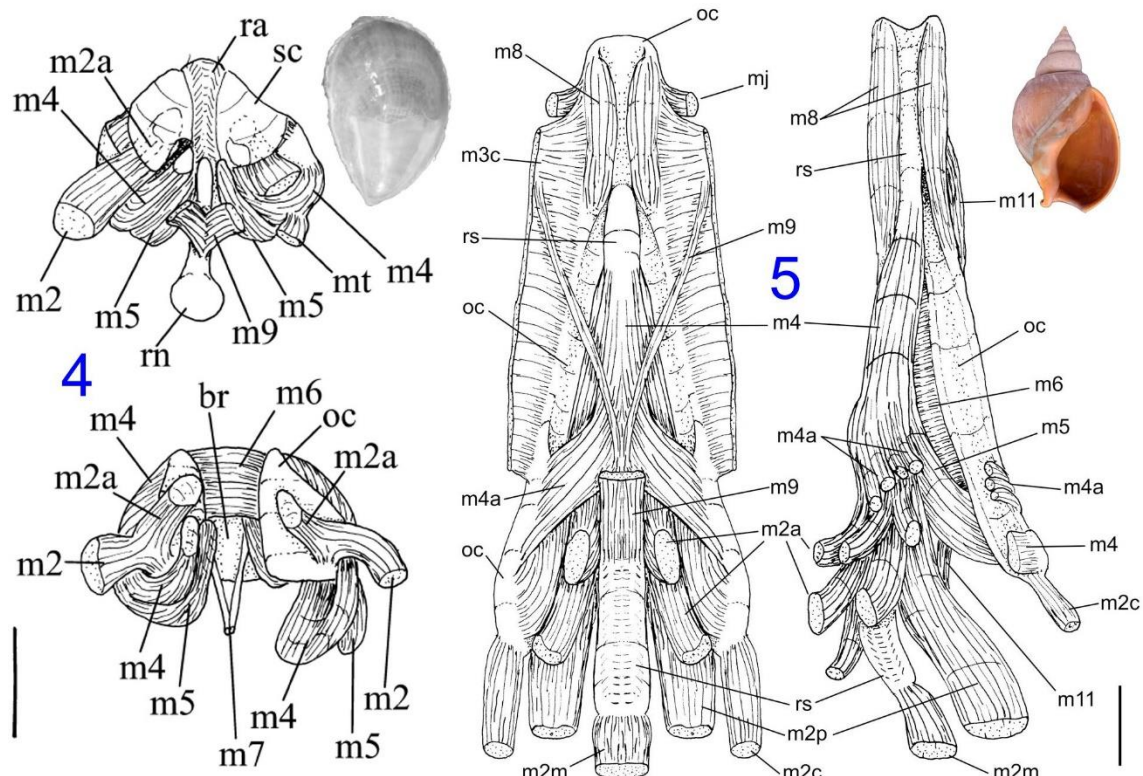
As referred above, the 3 first branches of the gastropod phylogeny (sensu Simone, 2011, endorsed by subsequent papers with morpho-anatomical scope) lack m2. The Apogastropoda, the 4th branch, still remains lacking m2, despite the basal branches of Heterobranchia, as discussed below, are very poorly understood.

On the other hand, inside Caenogastropoda, the reappearing of the pair m2 and its subsequent evolution was explored in the taxon's phylogeny (Simone, 2011), in which figure (that paper fig. 10) is reproduced below. As in remaining basal branches of gastropods, the basal caenogastropods also lack m2 (Fig. 3A). The pair m2 reappears in Epiathroidea in its



3: Scheme of buccal mass in Caenogastropoda, ventral view, mainly showing m2 pair (retractor muscle of buccal mass); A, Condition with m2 wanting; B, m2 laterally and ventrally inserted, found in Epiathroidea; C, m2 inserting closer to median line and, additionally, in radular sac, condition found in Adenogastropoda (from Simone, 2011).

usual insertion in the postero-lateral region of buccal mass/odontophore (Fig. 3B); however, different from the m2 of the basal mollusks, the caenogastropod m2 has not origin in the shell, but so in the posterior regions of the floor or lateral walls of the head-foot's haemocoel. The pair m2 still modifies further in Adenogastropoda, migrating towards medial, becoming closer to the radular sac itself, sometimes even attaching to it (Fig. 3C). The insertion of the m2 can be in the surface of the odontophore, on the external membrane or to the posterior muscles, usually to m4; however, frequently they penetrate deeper and connect to the posterior end of the cartilages. In some taxa there are branches in the m2 connection doing both (superficial and deep) insertions as in Fig 3B. This is interesting taxonomic information and varies considerably amongst the caenogastropods.



4-5: Dissected odontophores of modified examples of m2 in Caenogastropoda; **4**, *Crepidula margarita*, Calyptraeidea, above odontophore isolated, ventral view, superficial membrane removed, both sides deflected, insertion of some muscles seen by translucency, below same with radula and subradular membrane removed, both cartilages strongly deflected, right m4 and m5 deflected, scale = 0.5 mm, shell of holotype MZSP 35831 (L ~15 mm) (from Simone, 2006); **5**, *Buccinanops cochlidium*, Buccinoidea, dissected odontophore opened longitudinally along dorsal wall, most muscles expanded in dorsal (left) and right (right) views, scale= 2 mm, shell MZSP (L 83 mm) (from Pastorino & Simone, 2021). Lettering: br, subradular membrane; m1-m11, intrinsic-extrinsic odontophore muscles; mj, jaw and peribuccal muscles; mt transverse muscle; oc, odontophore cartilage; ra, radula; rn, radular nucleus; rs, radular sac; sc, subradular cartilage.

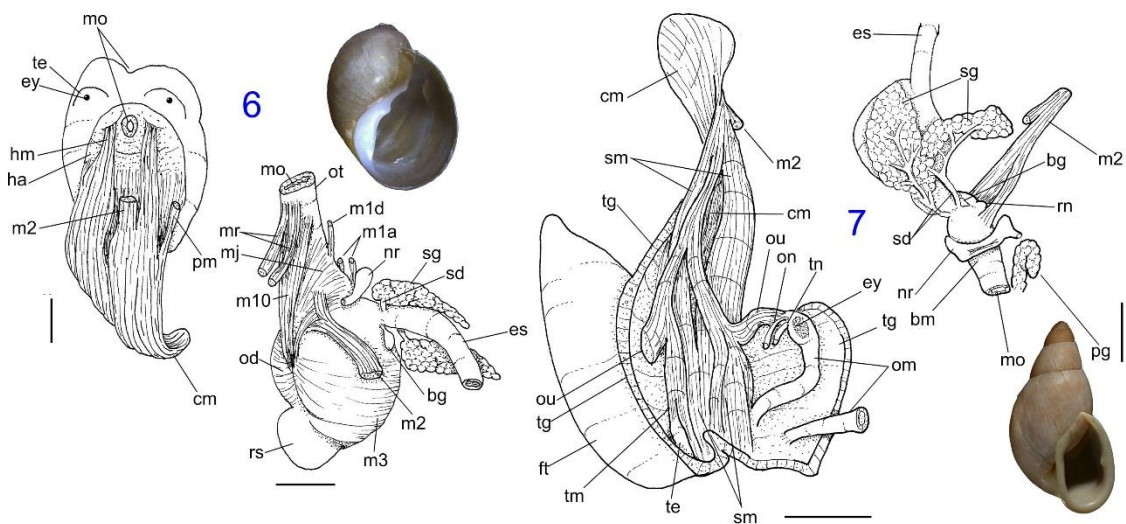
Being a megadiverse taxon, of course the caenogastropod m2 undertook a lot of further modifications, being the above-mentioned scheme only an outline. Impossible is to show all additional modifications that the pair m2 have within Epiathroidea and in Adenogastropoda. This even includes a secondary loss of the m2 as, e.g., in the conoideans. But 2 interesting examples are selected herein. One occurred in the higher Calyptraeidea, studied and discussed elsewhere (Simone, 2002, 2006), in which the pair m2 became inserted more internally in the odontophore cartilages, and, additionally, developed another branch, called m2a, that inserts in the subradular membrane, working as additional dorsal tensor muscle of the radula (Fig. 4). The other selected example comes from the higher neogastropod Buccinoidea (e.g., Simone, 2011, 2021a; Pastorino & Simone, 2021). The buccinoideans have a modified, elongated odontophore, in which pair m2 is usually divided into several pairs (Fig. 5), m2c inserted at the posterior end of the odontophore

cartilage; the m2a and m2p, originating respectively dorsally and ventrally surrounding radular sac; and m2m inserted at tip of radular sac (in radular nucleus). All these m2 run together longitudinally along the ventral wall of the proboscis and, beyond, adjacent ventral wall of haemocoel, up to their origin in this region of the haemocoel. This similar complexity of the pair m2 is also found in other *Rachiglossa* (sensu Simone, 2021a), but the homology of the muscles is not totally understood so far. Even among the Buccinoidea there is a variation that is still under analysis.

3. The m2 in the Heterobranchia

As referred above, the evolution and inferences of homology of the buccal mass/odontophore muscles in the Heterobranchia is not as well understood as in remaining gastropod branches. There is a reasonable quantity of Eupulmonata studied, however, in the basal heterobranch groups, the gap of knowledge still precludes wide conclusions. The pair m2 has not been found in Mathildoidea-Architectonicoidea (e.g., Haszprunar, 1985a, b; Bieler, 1988); in the minute forms Rissoelloidea, Omalogyroidea, Orbitestelloidea, etc. (e.g., Simone, 1995, 1997b; Simone & Zelaya, 2004); Aplysioidea (e.g., Cunha & Simone, 2018); Cephalaspidea and Sacoglossa (e.g., Galvão, 2018). However, pair m2 are found in higher heterobranchs, like Nudibranchia (e.g., Lima & Simone, 2015, 2018a, b), Hygrophila (e.g., Simone, 2021b) and Eupulmonata (e.g., Simone, 2022a).

Interestingly, the m2 pair of the formerly pulmonates (*Hygrophila* and Eupulmonata) recovered the primitive condition of being connected to the shell. The pair m2 are inserted in the postero-ventral surface of the odontophore, it runs directly posteriorly (Figs. 6-7, right images), and its posterior region mixes with posterior region of the columellar muscle (Figs. 6-7, left images), in its final portion attaches to the shell. Different from the primitive condition, which has

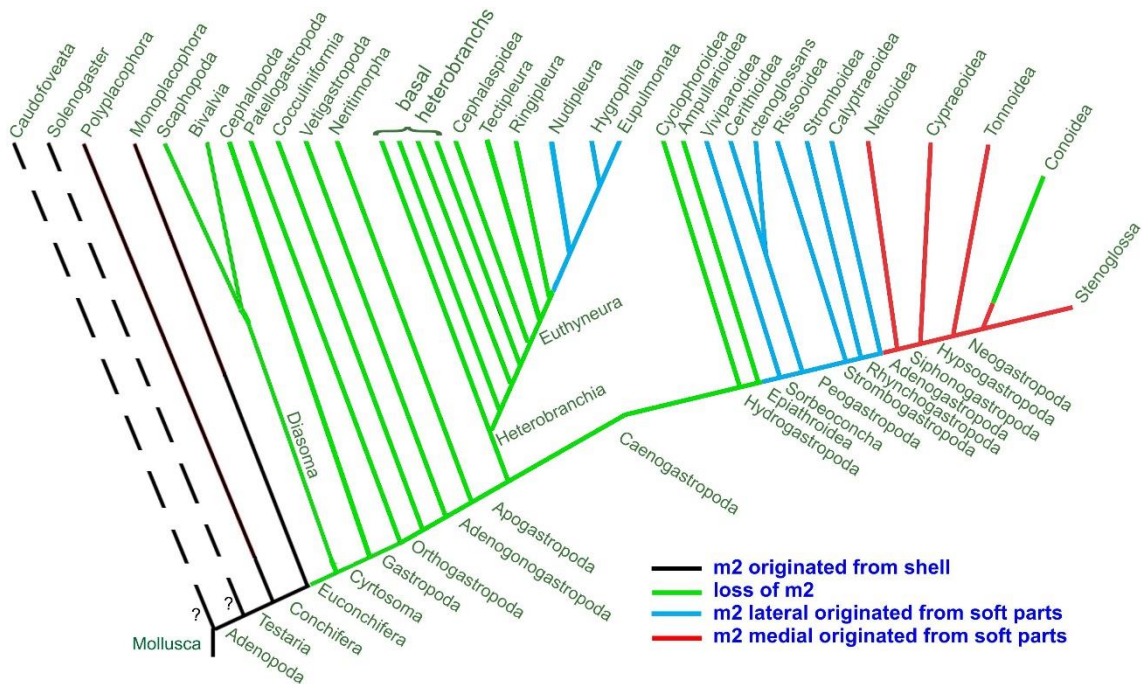


6-7: Dissected head-feet and odontophores of pulmonates; **6**, *Chilina megastoma*, Hygrophila, Chiliniidae, left head-foot, dorsal view, dorsal integument and inner structures removed, right foregut left-slightly ventral view, scales = 1 mm, shell MZSP 151286 (L ~10 mm) (from Simone, 2021b); **7**, *Catracca uhlei*, Eupulmonata, Strophocheilidae, left head-foot, dorsal-right view, dorsal integument and inner structures removed, right foregut left view, scales= 5 mm, shell holotype MZSP 151900 (L 44 mm) (from Simone, 2022). Lettering: bg, buccal ganglion; bm, buccal mass; cm, columellar muscle; es, esophagus; ey, eye; ft, foot; ha, haemocoel; hm, head retractor muscle; m1-m10, intrinsic-extrinsic odontophore muscles; mj, jaw and peribuccal muscles; mo, mouth; mr, retractor muscles of buccal mass; nr, nerve ring; od, odontophore; om, ommatophore; on, ocular nerve; ot, oral tube; ou, ommatophore muscle; pm, penial muscle; rn, radular nucleus; rs, radular sac; sd, salivary duct; sg, salivary gland; sm, secondary cephalic muscles; sg, salivary gland; te, cephalic tentacle; tm, tentacular muscle; tn, tentacular nerve; tg, integument.

the m2 attached to the shell hoof, the pulmonates' m2 has it attached to the columella, joined to the columellar muscle.

The pair m2 in higher heterobranchs like nudibranchs and pulmonates is notoriously a reappearance, a convergence, a novelty of this heterobranch branch. However, the m2 relation with columella cannot be presently checked in the shell-less nudibranchs, except after a possible ontogenetic study. Both, in nudibranchs and hygrophilans so far examined, the pair m2 has a somewhat anterior insertion in the odontophore (Fig. 6), being lateral, separated from each other. While in eupulmonates, the pair m2 is almost a single wide medial bundle that usually surrounds the radular sac, generally extending up to lateral regions of the odontophore (Fig. 7), being very thick in some groups (e.g., Strophocheilidae – Simone & Leme, 1998).

4. Phylogenetic inferences of the pair m2



8: Unpretentious phylogenetic cladogram of Mollusca based on morphological characters, mostly extracted from Simone (2011 and subsequent papers) and, secondarily, MolluscaBase (2023), indicating, with colors, the main type of retractor muscle of buccal mass – pair m2 – basing some nodes as indicated.

The main types of pair m2 above described support branches in the phylogeny of the Mollusca, represented in Fig. 8. Of course, it does not represent particularities and further modifications found in some subgroups, which are beyond the scope of this paper. The pair m2 originated directly from the shell can be regarded as the basal model, and is present in the first branches. This model is surely present in Monoplacophora and Monoplacophora (black color), and its presence in the 2 first branches – Caudofoveata and Solenogastres – is still doubtful both, because they do not have shell, and their buccal mass are too modified to permit inferences, at least in the known species. This is the reason for the question marks and for the dashed lines in their representations.

The loss of the pair m2 happened in the Euconchifera, being one of its synapomorphies. Of course, their buccal mass has some capacity of extrusion and retraction, but the retraction is promoted, as referred above, by other muscles, such as peribuccal muscles or secondary jugal muscles

– m1 (Simone, 2022b). They are different from m2 in being more anteriorized both, in their origins and insertions. The loss of the m2 is represented by the green color in Fig 8.

The pair m2 reappear as convergences in 2 gastropod branches, in Epiathroidea and in higher heterobranchs. Despite the caenogastropod and heterobranch kind of m2 differ in several details, they are represented with the same color blue in Fig. 8. Also, even though the eupulmonates have their m2 pair originated from the shell, actually they are inserted along the columellar muscle, and the structure as a whole is inserted in the shell's columella.

As also reported above, the pair m2 has undertaken a lot of modifications along the gastropod evolution, impossible to detail here. Anyway, at least 2 modifications are reported in Fig. 8: the approximation of the pair m2 to the medial line occurred in the Adenogastropoda (red line), and the secondary loss of it in most (not all) Conoidea (green line again).

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