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The unnamed odontophore muscles m3 and m9

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Abstract

The odontophore muscles coded m3 and m9 are usually difficult to name. Their occurrence is splayed in the molluscan phylogeny in different localizations, functions, and constitutions. For this reason, they are more useful in comparative studies in levels close to species, rather than higher taxonomic levels, as they are not homologous. Several interesting examples are given, particularly in gastropods and scaphopods.

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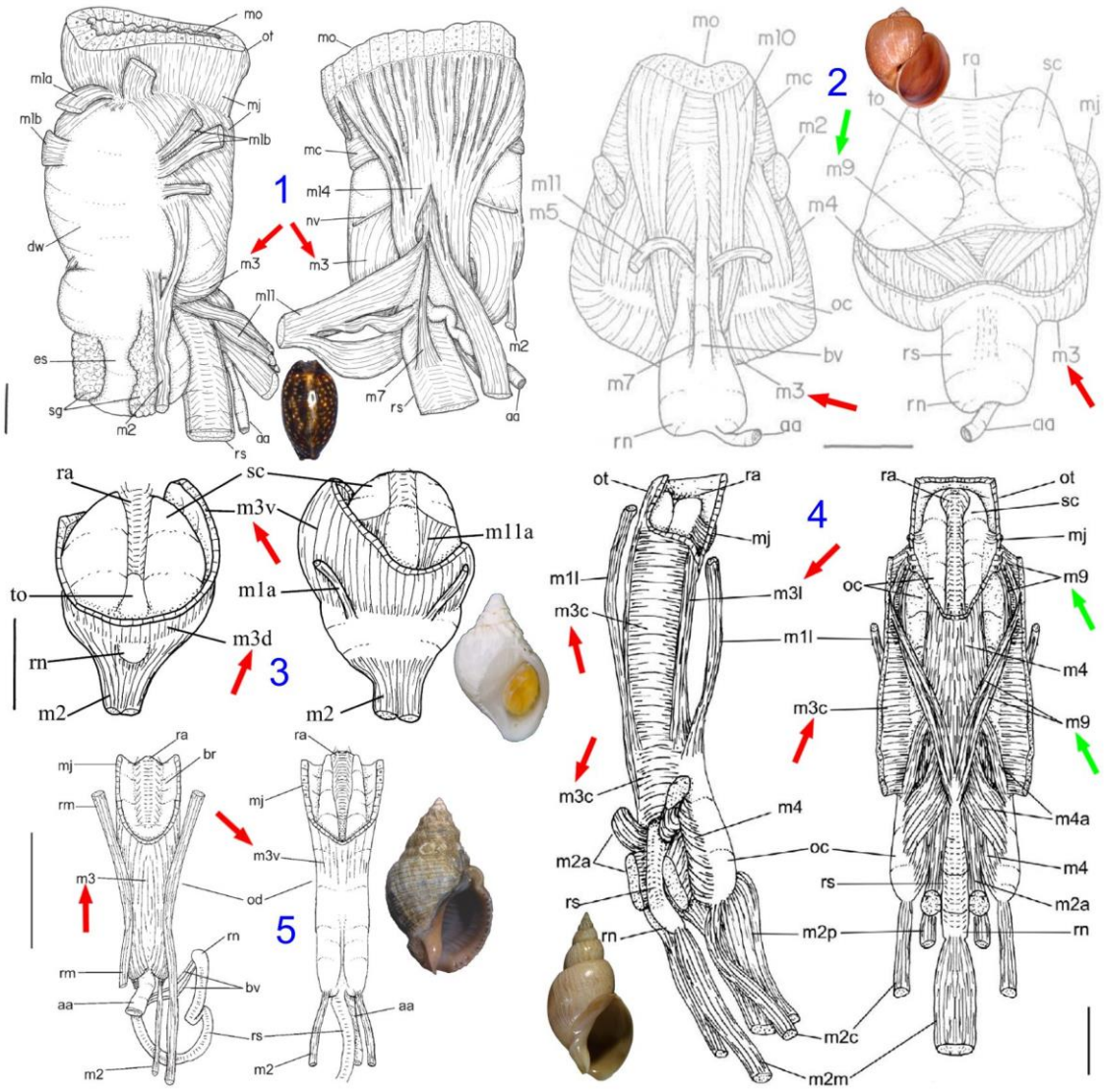
Introduction

The odontophore muscles coded m3 and m9, usually, but not always, paired, are intrinsic muscles of enigmatic function, and, thus, difficult to name. They are interspecifically very variable, and, for that, very useful for taxonomic and phylogenetic studies in levels close to species. They are, on the other hand, and for this, of little use for comparative studies in higher taxonomic levels.

Usually, those called m3 are more superficial, more commonly modifications and specializations of the membrane that surrounds the odontophore or buccal mass, which becomes muscular or develops a muscular region. While the called m9 are more internal. Both, m3 and m9, start and end, i.e., originate and insert in the own odontophore/buccal mass.

Their function is hard to interpret by only analyzing their topology and direction of fibers. They usually are tensors, compressors, shorteners, approximators, or something like that, usually located in some weird region in which another closely related species has no muscle.

This makes us conclude that all kinds of m3 and m9 found along mollusk phylogeny are not homologous, except for those belonging to closer related branches. Thus, this paper is mostly

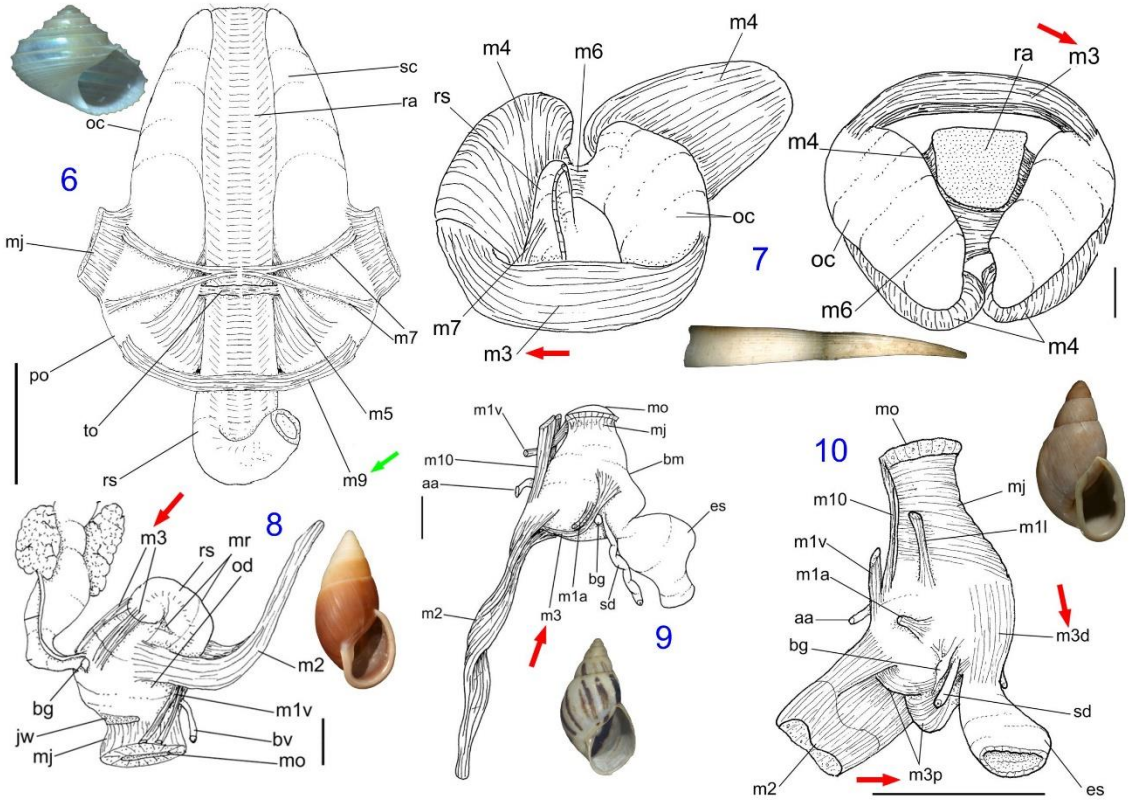


1- 5: Examples of muscles m3 and m9. 1, cypraeoidean *Macrocypraea zebra*, buccal mass, dorsal and ventral views, scale= 2 mm (from Simone 2004a), shell (L ~70 mm); **2**, ampullarioidean *Pomacea crosseana*, odontophore, ventral and dorsal views, scale= 2 mm, shell (L~55 mm) (from Simone, 2004b); **3**, stenoglossan *Benthobia atafona*, odontophore, dorsal and ventral views, scale= 0.25 mm, shell holotype (L 8 mm) (From Simone 2003); **4**, stenoglossan *Buccinanops cochlidium*, odontophore, dorsal-right and dorsal views, scale= 2 mm, shell MZSP (L ~72 mm) (from Pastorino & Simone, 2021); **5**, stenoglossan *Thaisella guatemalteca*, odontophore, ventral and dorsal views, scale= 1 mm, shell holotype (L ~29 mm) (from Simone, 2017). Shell 1, courtesy Femorale.com. Red arrows indicating m3, green arrows indicating m9. Lettering: aa, anterior aorta; br, subradular membrane; bv, blood vessel; es, esophagus; mc, circular muscle – sphincter; m1-14, odontophore intrinsic-extrinsic muscles; mj, jaw and peribuccal muscles; mo, mouth; nv, nerve; ot, oral tube; ra, radula; rm, proboscis retractor muscle; rn, radular nucleus; rs, radular sac; sc, subradular cartilage; sg, salivary gland; to, tissue on radular sac.

dedicated to show examples, without any phylogenetic implication or functional explanation, once these depend on more detailed context or additional, unavailable knowledge.

Examples of m3

In Cypraeoidea, the pair m3 is a thin layer immersed in the postero-ventral membrane evolving odontophore. It becomes a particularly thick, well-developed pair in the branch uniting ovulids-cypraeids (Fig. 1), as a pair of posterior muscular cover, even given support to the insertion of the pair m2 (Simone, 2004a). A similar m3 occurs in ampullarioideans, basal caenogastropods

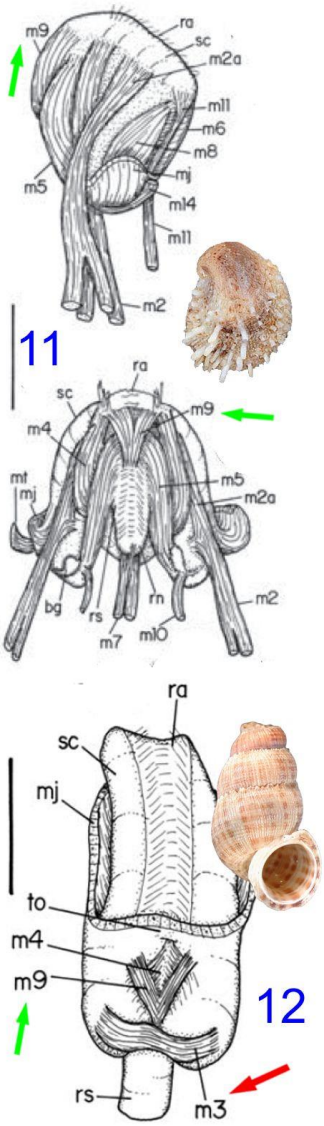


6-10: Examples of muscles m3 and m9. 6, trochoidean *Margarites imperialis*, odontophore, dorsal view, scale= 1 mm (from Simone & Dornellas, submitted), shell MZSP (W ~10 mm); **7**, scaphopod *Coccodentalium carduus*, odontophore posterior and anterior views, shell MZSP 32977 (L 74 mm) (from Simone, 2009); **8**, eupulmonate bulimulid *Kora corallina*, buccal mass, left view, scale= 2 mm, shell holotype (L ~43 mm) (inedited); **9**, eupulmonate bulimulid *Drymaeus currais*, buccal mass, left view, scale= 2 mm, shell holotype (L ~30 mm) (from Simone et al, 2020); **10**, eupulmonate strophocheilid *Catracca uhlei*, buccal mass, left view, scale= 5 mm, shell holotype (L ~44 mm) (from Simone, 2022). Red arrows indicating m3, green arrows indicating m9. Lettering: aa, anterior aorta; bg, buccal ganglion; bm, buccal mass; bv, blood vessel; es, esophagus; m1-10, odontophore intrinsic-extrinsic muscles; mj, jaw and peribuccal muscles; mo, mouth; mr, muscular cover; oc, odontophore cartilage; po, posterior odontophore cartilage; ra, radula; rs, radular sac; sc, subradular cartilage; sd, salivary duct; to, tissue on radular sac.

(Fig. 2), in which the pair m3 forms a strong dorso-ventral muscular cover (Simone, 2004b). Another caenogastropod example is the transverse m3 of annulariids (Fig. 12), located in the postero-ventral region of odontophore, preceding radular sac base (Simone, 200b).

An interesting evolution of m3, but usually unpaired, occurs in stenoglossan neogastropods. The m3 muscles are usually relatively thick muscular covers, which make us think about the toothpaste phenomenon, as they look to have the function of compressing the odontophore or buccal mass for any enigmatic reason. They are present in basal stenoglossan, like benthobiids (Simone, 2003) (Fig. 3), and muricids (e.g., Simone, 2017; Souza & Simone, 2019) (Fig. 5), as well as in more advanced ones, like buccinoideans, as in *Buccinanops* (Pastorino & Simone, 2021) (Fig. 4). Stenoglossan neogastropods usually have more than one kind of m3, some with transverse, others with longitudinal fibers, in their very complex odontophores.

In Eupulmonata, a myriad of m3 conformations exists. They usually are derived from the posterior membrane that surrounds the posterior region of the odontophore and the esophageal insertion (Figs. 8-10). In some cases, the m3 is a single cover (Fig. 10: m3d), while in other cases it is a pair that somehow helps in holding the radular sac (Figs. 8-9: m3; 10: 13p). These are only some examples.



11-12: Examples of muscles m3 and m9. 11, calyptraeoidean *Bostrycapulus odytes*, odontophore, left and ventral views, scale= 1 mm (from Simone, 2002), shell courtesy Femorale (L ~16 mm); **12**, rissooidean *Annularia* sp, odontophore, dorsal view, scale= 1 mm, shell MZSP 28266 (L ~8 mm) (from Simone, 2004b). Red arrows indicating m3, green arrows indicating m9. Lettering: see previous Figures.

In Scaphopoda, the only living Diasoma that has an odontophore, the structure is highly modified. It is adapted for crushing the prey, usually minute foraminifers, instead of having the scraping function as the remaining mollusks. In all so far studied scaphopods, the m3 is part of a gizzard-like odontophore, together with the pair of cartilages and the m6 (Fig. 7), being thick and strong (Simone, 2009). When this ring-like structure contracts, it smashes that inside. The unpaired m3 working as a m6 accessory, is an outstanding scaphopod synapomorphy.

Examples of m9

In vetigastropods, some trochoideans like margaritids and calliostomatids have an interesting transverse m9 located in the posterior end of odontophore (Fig. 6) (Dornellas et al, 2020).

Advanced stenoglossan neogastropods, like Buccinoidea and Volutoidea, have pairs of m9 that apparently are additional dorsal tensors of the radula (Fig 4) (e.g., Pastorino & Simone, 2021). Despite in being dorsal, they apparently are auxiliary of the ventral tensors (m11). Interestingly, the same characteristic is found, as a convergence, in some more basal caenogastropods. In calyptraeids, for example (Simone, 2002) the pair of m9 is allocated from radular sac to subradular membrane (Fig. 11). Something very similar happens annulariids (Fig. 12), although located slightly more posteriorly (Simone, 2004b). While in ampullariids, the pair of m9 connects the radular sac with the anterior region of the subradular cartilages (Fig. 2: sc). The function is something very difficult to interpret.

Discussion

As reported above, all the odontophore muscles coded m3 and m9 are not homologous, except for those found in close related species. For this reason, the m3 and m9 muscles have limited use for phylogenetic analyses (Simone, 2011), but they are very useful in alpha-taxonomy. They, when present, can help in distinguishing close related species that sometimes are very similar in the remaining aspects.

The codification m3 or m9 is not absolute. Sometimes this codification could be switched in a second future look, as well as some coded "mt", which supposedly means transverse muscle in the odontophore, should be named m3 or m9. An example is the mt of calyptraeoideans (Simone, 2002), it should be better named as m9. The same can be inferred about the scaphopod m3, as it is more internal, it also should be better named as m9. It is never too late to get all this right, or at least to show the reason for treating both muscles in this article.

It is not inconvenient to inform that there are many other kinds of m3 and m9 in gastropods that were not reported here. This paper, repeating, has only the intention of showing examples, to show how variable both muscles are, and how difficult it really is to interpret their function without additional functional investigation that, as far as known, was never performed.

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