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The radular sac muscles – m7

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Abstract

The unnamed pair of odontophore muscles coded as m7 is examined. It usually consists of narrow muscles associated with the radular sac, whose function is difficult to interpret. This muscle pair is absent in nearly half of molluscan species and shows considerable variation in its characters, possibly indicating non-homology among different lineages. Nevertheless, pair m7 is useful for comparisons at the species level. An m7 originating from the ventromedial edge of m4 represents a synapomorphy of Caenogastropoda, as does distal fusion of m7, which is a synapomorphy of Peogastropoda.

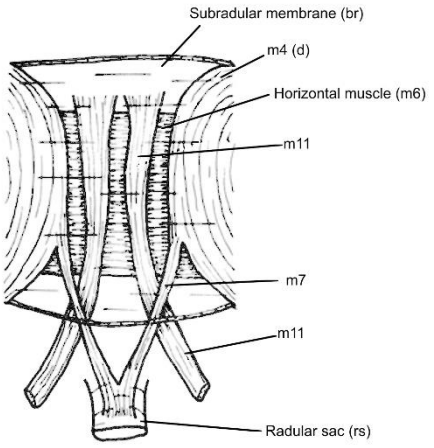
Keywords: odontophore, phylogeny, morphological modifications, anatomy.

Introduction

The pair of muscles associated with the radular sac—coded as m7—constitutes another intrinsic pair of odontophore muscles. Muscle pair m7 is usually narrow and inconspicuous, and its denomination and function are difficult to determine.

Muscle pair m7 is variable at the species level and is therefore useful in comparative analyses such as taxonomy and phylogeny. As it is absent in several taxa and exhibits different attributes in others, the most parsimonious conclusion is that muscle pair m7 is not homologous across all higher taxa in which it occurs.

Despite this lack of homology, any pair of muscles connected to the radular sac is usually denominated "m7".



1. Schematic representation of pair m7 originated from ventral edge of pair m4, detail of odontophore, medial region, dorsal view, with both cartilages deflected and partially separated.

The most common origin of this muscle pair is the odontophore cartilages, either on their inner medial surfaces or on the ventral edges of muscle pair m4 (the main ventral tensor muscles of the radula) (Fig. 1). This narrow muscle pair runs toward the radular sac, in the region preceding the buccal cavity. The muscles penetrate the sac, extend within it for some distance, and each inserts on the inner surface, spreading in a fan-like pattern. However, as shown in the selected examples below, there is considerable variation on this basic scheme. In addition to this more common pattern, other aberrant configurations occur, such as those found in some pulmonates, also illustrated below.

Beyond these general statements, little else can be said about muscle pair m7. A complete survey of all known variations of m7 is impracticable. Therefore, the present account is restricted to the main examples found in several odontophore-bearing taxa, which illustrate the different muscle conformations. As noted above, these variations are primarily of interest at lower taxonomic and phylogenetic levels. However, nearly half of the odontophore-bearing taxa studied lack muscle pair m7, which partly precludes broader phylogenetic or evolutionary inferences.

Pair m7 in Caenogastropoda

The exemplification of muscle pair m7 begins with Caenogastropoda, as this is the only known taxon supported by a character involving this muscle pair. The conformation described above and illustrated in Fig. 1—namely, the origin of m7 on the ventral inner edge of muscle pair m4—is one of the synapomorphies of Caenogastropoda (Simone, 2011: 195) (Figs. 2D, E, G, I). Each muscle originates in the medial region of the m4 edge, attached to the inner dorsal margin of the m4 pair (Figs. 1, 2D, E, G). From there, it runs posteriorly, attached to the subradular membrane. Subsequently, it penetrates the radular sac and inserts on its inner surface a short distance from the radular nucleus.

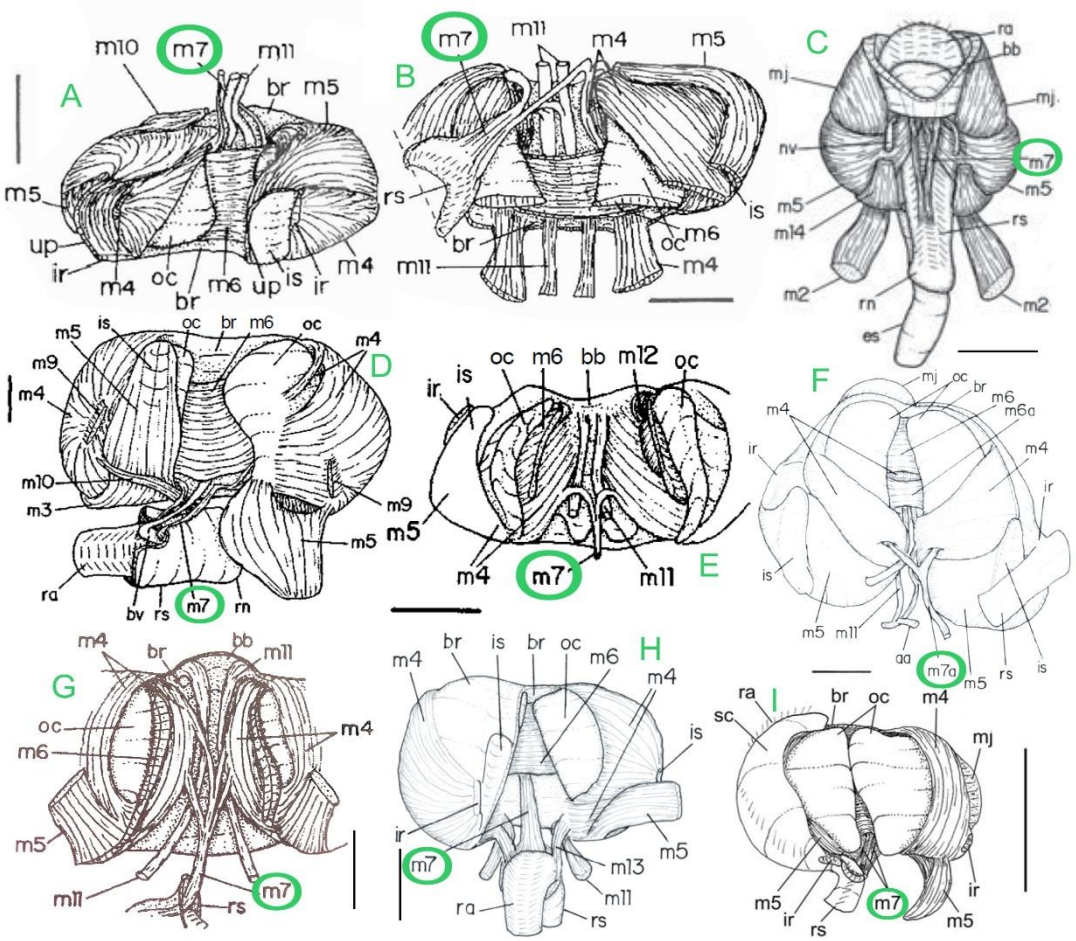
In Peogastropoda (Simone, 2011, 2024b), an additional synapomorphy occurs: the two m7 muscles fuse and present a single, fan-shaped insertion (e.g., Simone, 2004b, fig. 400) (Fig. 2H).

Naturally, this basic plan exhibits a wide range of variations among caenogastropod lineages, including complete reduction of muscle pair m7, as observed, for example, in Cypraeidae (Simone, 2004b). In some cerithioideans, such as pachychilids, muscle pair m7 is extremely narrow and runs parallel to muscle m11 until it pierces the radular sac (Simone, 2001) (Fig. 2A). Other cerithioideans exhibit an additional origin from muscle m11, as in modulids (Simone, 2001) (Fig. 2B).

In some calyptraeoideans, muscle pair m7 runs directly toward the radular sac and may function as an additional dorsal tensor of the radula (Simone, 2002) (Fig. 2C). In certain cypraeoideans, such as ovulids, muscle pair m7 pierces the bases of muscle pair m4, passing through them for a short distance after their origin (Simone, 2004b) (Fig. 2F). In some stromboideans, such as strombids, muscle pair m7 is relatively robust and exhibits multiple origins along the edge of muscle pair m4 (Simone, 2005) (Fig. 2G).

Special care is required to avoid confusing muscle pair m7, which is usually very narrow, with the radular vessel(s) supplying the radular sac, particularly the radular nucleus. Radular vessels are never observed running inside the radular sac; instead, they lie externally. A well-developed radular vessel is frequently present in gastropods, attached to the tip of the radular nucleus. This

vessel is typically detached from the buccal mass and can be readily observed as originating from the buccal blood sinus.



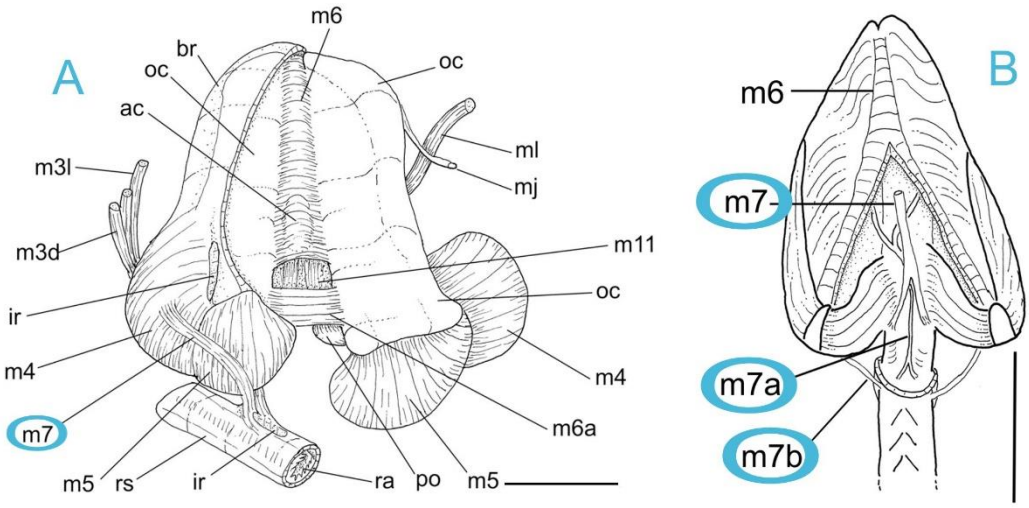
2. **Examples of pair of muscles of the radular sac – m7 – in Caenogastropoda**. All are drawings of dissected odontophores, dorsal views, first layer of structures removed, both cartilages deflected, radular sac removed of deflected. **A**, *Doryssa macapa* (Cerithioidea) (from Simone, 2001), scale= 1 mm; **B**, *Modulus modulus* (Cerithioidea) (from Simone, 2001), scale= 0.5 mm; **C**, *Trochita trochiformis* (Calyptraeoidea) (from Simone, 2002), scale= 1 mm; **D**, *Pomacea crosseana* (Ampullarioidea) (from Simone, 2004a), scale= 1 mm; **E**, *Viviparus acerosus* (Viviparoidea) (from Simone, 2004a), scale= 1 mm; **F**, *Cyphoma signatum* (Cypraeoidea) (from Simone, 2004b), scale= 1 mm; **G**, *Strombus pugilis* (Stromboidea) (from Simone, 2005), scale= 2 mm; **H**, *Niveria pediculus* (Triviidae) (from Simone, 2004b), scale= 1 mm; **I**, *Laevilacunaria antarctica* (Littorinidae) (from Simone, 2017), scale= 1 mm. Lettering: aa, anterior aorta; bb, sublingual organ; br, subradular membrane; bv, blood vessel; es, esophagus; ir, insertion of m4 in subradular membrane; is, insertion of m5 in subradular membrane; m1-m14, intrinsic and extrinsic odontophore muscles; mj, jaws and peribuccal muscles; nv, nerve; oc, odontophore cartilage; ra, radula; rn, radular nucleus; rs, radular sac; sc, subradular cartilage; up, connection between both m5.

Pair m7 in archaeogastropod grade

In archaeogastropod-grade taxa, muscles associated with the radular sac are present and have been coded as m7. However, as noted above, the likelihood that these muscles are homologous across all such taxa is remote. In marine Neritimorpha, for example, a robust m7 pair is present, but it originates from the outer surface of muscle pair m4 (Barroso et al., 2012) (Fig. 3A). In contrast, no structure comparable to m7 has so far been identified in terrestrial neritimorphs.

In Vetigastropoda, a wide range of m7 conformations is observed, some of which are illustrated by Dornellas et al. (2020, fig. 13a–l). Differences in muscle pair m7 among vetigastropods are useful for comparative analyses, including phylogenetic and taxonomic studies. One example

is provided by calliostomatids, which possess three successive and differently positioned m7 pairs (Dornellas & Simone, 2013) (Fig. 3B).



3. **Examples of pair of muscles of the radular sac – m7 – in some archaeogastropod branches**. All are drawings of dissected odontophores, dorsal views, first layer of structures removed, both cartilages deflected, radular sac removed of deflected. All are drawings of dissected odontophores, dorsal views, first layer of structures removed, both cartilages deflected, radular sac removed of deflected. **A**, *Vitta zebra* (Neritimorpha, Neritidae) (from Barroso et al, 2012), scale= 1 mm; **B**, *Calliostoma adspersum* (Vetigastropoda, Calliostomatidae) (from Dornellas & Simone, 2013) scale= 2 mm. Lettering: ac, accessory cartilage immersed in m6; br, subradular membrane; ir, insertion of m4 in subradular membrane; m1-m9, intrinsic and extrinsic odontophore muscles; mj, jaws and peribuccal muscles; ml, lateral muscle of buccal mass; oc, odontophore cartilage; po, posterior odontophore cartilage; ra, radula; rs, radular sac.

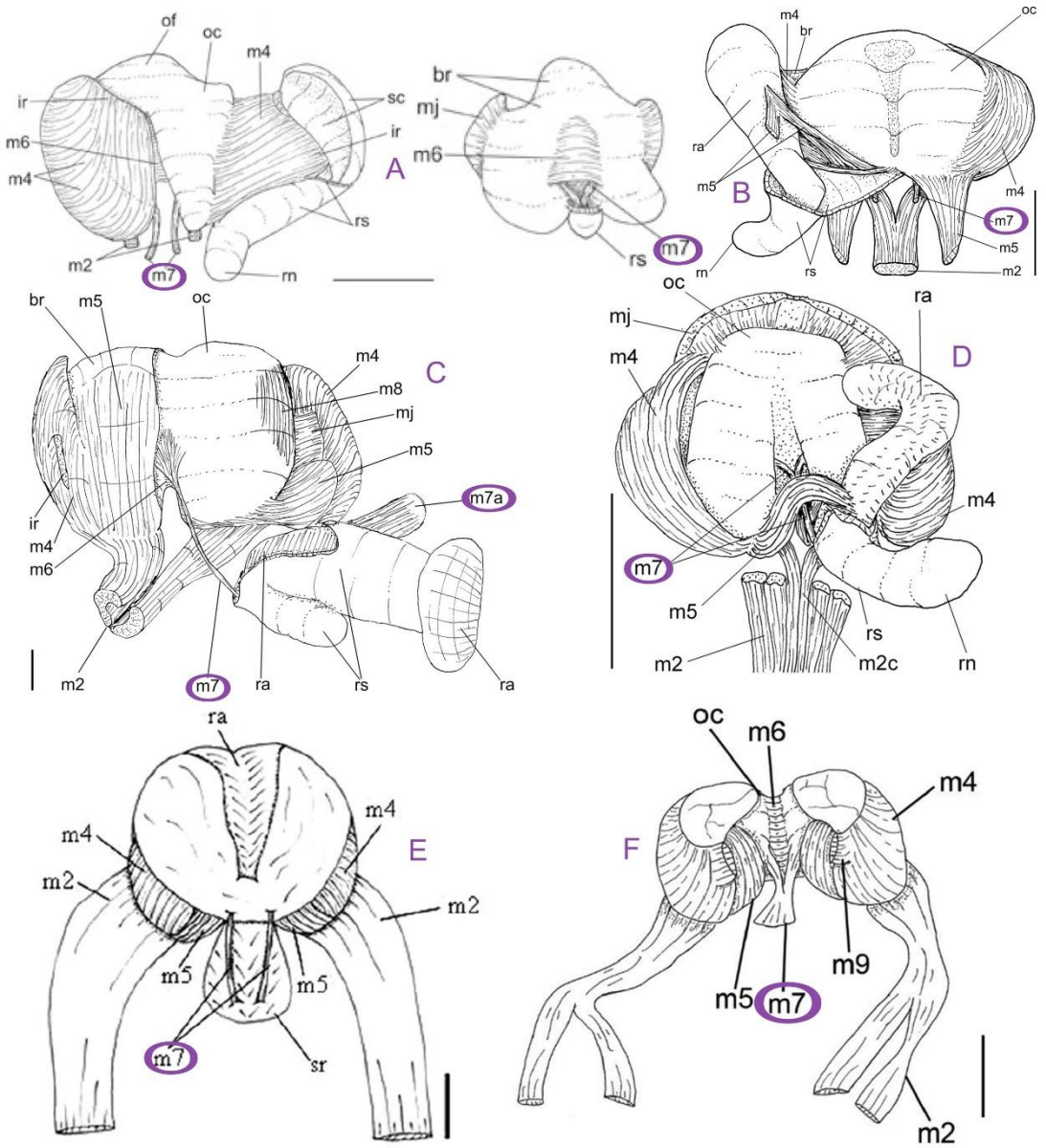
No structure comparable to muscle pair m7 has so far been found in Patellogastropoda or Cocculiniformia, although the number of species studied from this perspective remains relatively small.

Pair m7 in Heterobranchia

Heterobranchs represent another group in which odontophore morphology remains poorly studied. In marine taxa, such as sea slugs and other groups with reduced shells, odontophore features are only beginning to be documented. To date, only a few heterobranch species have been shown to possess muscle pair m7, which usually originates directly from the odontophore cartilages.

An example is provided by doridids, which have a very narrow pair of muscles attached to the radular sac (Lime & Simone, 2015) (Fig. 4E). Another example occurs in discodoridids, in which muscle pair m7 is more robust and the two muscles fuse shortly after their origin (Lima & Simone, 2018) (Fig. 4F).

Eupulmonata include a relatively larger number of species for which odontophore features are known, and most of them lack muscle pair m7. In those taxa that do possess it, the origin is likewise from the medial region of the odontophore cartilages. In solaropsids, muscle pair m7 originates from the inner medial edge of the odontophore cartilages (Simone, 2010) (Fig. 4A). A similar condition occurs in odontostomids such as *Anthinus*, although in this case the origin is on the dorsal surface of the cartilages (Simone, 2022a) (Fig. 4B). In both cases, the two m7 muscles run separately along the radular sac.



4. **Examples of pair of muscles of the radular sac – m7 – in different Heterobranchia**. All are drawings of dissected odontophores, dorsal views, first layer of structures removed, both cartilages deflected, radular sac removed of deflected. **A**, *Olympus nimbus* (Eupulmonata, Solaropsidae) (from Simone, 2010), scale= 1 mm; **B**, *Anthinus synchondrus* (Eupulmonata, Odontostomidae) (from Simone, 2022a), scale= 2 mm; **C**, *Kora corallina* (Eupulmonata, Bulimulidae) (from Simone, 2024a), scale= 1 mm; **D**, *Lavajatus moroi* (Eupulmonata, Achatinidae) (from Simone, 2018), scale= 1 mm; **E**, *Doris januarii* (Nudibranchia, Dorididae) (from Lima & Simone, 2015), scale= 1 mm; **F**, *Platydoris angustipes* (Nudibranchia, Discodorididae) (from Lima & Simone, 2018), scale= 1 mm. Lettering: br, subradular membrane; ir, insertion of m4 in subradular membrane; m1-m9, intrinsic and extrinsic odontophore muscles; mj, jaws and peribuccal muscles; oc, odontophore cartilage; of, odontophore cartilage fusion; ra, radula; rn, radular nucleus; rs, radular sac; sc, subradular cartilage.

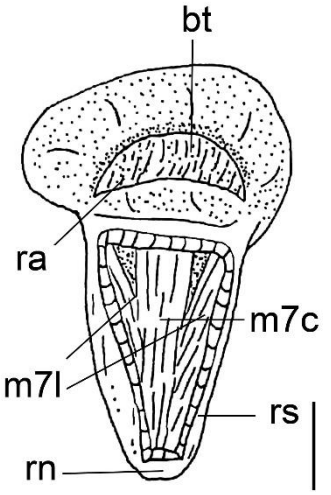
A different configuration of muscle pair m7 occurs in bulimulids such as *Kora* (Simone, 2024a), in which the origin is single, located in the region between both odontophore cartilages at the posterior end of their fusion (Fig. 4C). From this point, the two muscles run fused along their entire length. A similar configuration is found in the achatinid *Lavajatus* (Simone, 2018); however, in this taxon, muscle pair m7 is initially separated at its origin and fuses after a short distance (Fig. 4D).

Among eupulmonates, a special case is found in megalobulimines (Odontostomidae). These large-sized snails have the radular sac completely filled with muscular tissue, also coded as

m7. The radula itself lies at the periphery of these muscles, flanking their ventral and lateral surfaces (Silva & Simone, 2022). Examination of this musculature reveals a broad central bundle (Fig. 5: m7c) flanked by a pair of lateral oblique bundles (Fig. 5: m7l).

Analysis of these muscles indicates that they connect the region of the radular nucleus to the septum that precedes the exposed (functional) portion of the radula within the buccal cavity. This septum is a rigid structure termed the "hardened region of radular tissue preceding the buccal region" (Fig. 5: bt). As muscle function is limited to contraction, the functional role of this highly modified megalobulimine m7 remains unclear.

To date, all studied megalobulimines exhibit this type of m7 musculature within the radular sac. This character is absent in closely related taxa, such as *Catracca* (Simone, 2022a). It therefore possibly represents an additional synapomorphy of the subfamily.



5. **Isolated radular sac of *Megalobulimus oblongus*** (Eupulmonata, Odontostomidae) opened longitudinally, dorsal view (from Silva & Simone, 2022), scale= 5 mm. Lettering: bt, hardened region of radular tissue preceding buccal region; m7, muscles inside radular sac; ra, radula; rn, radular nucleus; rs, radular sac.

Pair m7 in other classes

Beyond Gastropoda, odontophore characters are even less explored, and proportionally few taxa have their odontophore morphology documented. Within the aculiferan grade, a muscle pair coded as m7 has been identified in Caudofoveata that retain a relatively typical odontophore, as most caudofoveates show a highly modified condition bearing only a pair of hook-like teeth. *Claviderma virium*, for example, possesses a relatively strong m7 pair connecting the proximal end of the radula to the radular nucleus (Fig. 6B), possibly functioning as auxiliary ventral tensor muscles.

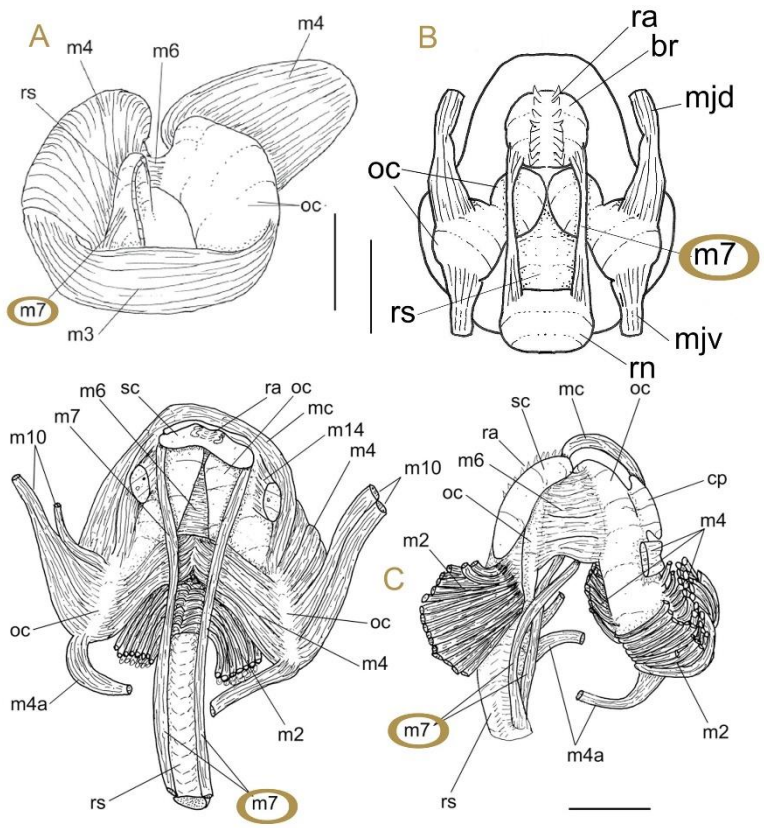
In *Acanthopleura gemmata* (Polyplacophora), a strong m7 pair is also present, with features similar to those observed in *Claviderma*. The muscles originate at the proximal end of the radular ribbon, run along the radular sac, and insert close to the radular nucleus (Jardim et al., 2009) (Fig. 6C). This aculiferan configuration may represent the basic plan for muscle pair m7 in Mollusca, although this hypothesis is still under analysis.

Within Conchifera, three additional classes possess an odontophore. In Monoplacophora, odontophore anatomy has been described (Lemche & Wingstrand, 1959); however, because different methodological protocols were used, interpretation of the musculature is difficult. In *Neopilina galatheae*, at least, a muscle pair extends from the proximal end of the radula to the ventral wall of the haemocoel and was termed *musculus radulae longus ventralis*, which likely corresponds to muscle pair m11 (ventral tensor muscles of the radula; Simone, 2011).

This muscle pair bears two branches connected to the radular sac (Lemche & Wingstrand, 1959: fig. 82), described as "retractors of the radular sac," which could be coded as m7. However, no comparable configuration has been identified in any other mollusk studied to date.

In the cephalopods studied to date, the radular sac is completely embedded within the powerful muscular complex that constitutes the buccal mass. Under these conditions, identification of a distinct muscle pair m7 has not been possible.

In Scaphopoda, at least within Dentaliida, a muscle pair m7 has been identified. In *Coccodentalium caduum*, for example, it is longitudinally arranged on both sides of the dorsal surface of the short radular sac (Simone, 2009) (Fig. 6A).



6. **Examples of pair of muscles of the radular sac – m7 – in different classes.** All are drawings of dissected odontophores, dorsal views, first layer of structures removed, both cartilages deflected, radular sac removed of deflected. **A**, *Coccodentalium caduum* (Scaphopoda) (from Simone, 2009), scale= 0.5 mm; **B**, *Claviderma virium* (Caudofoveata) (original), scale= 0.5 mm; **C**, *Acanthopleura gemmata* (Polyplacophora) (dorsal and ventral views) (from Jardim et al., 2009), scale= 2 mm. Lettering: br, subradular membrane; cp, cartilage appendix; m1-m14, intrinsic and extrinsic odontophore muscles; mc, circular muscle (sphincter); mj, jaws and peribuccal muscles; oc, odontophore cartilage; ra, radula; rn, radular nucleus; rs, radular sac.

Discussion

As discussed above, except in a few higher taxa (e.g., Caenogastropoda and Peogastropoda), muscle pair m7 is primarily informative at the species level, owing to its high degree of variation. For this reason, together with muscle pair m1, it represents one of the most useful odontophore characters for distinguishing species.

The hypothesis that the basic pattern of muscle pair m7 corresponds to an auxiliary ventral tensor of the radula, as observed in the aculiferans examined so far, remains under investigation. Nevertheless, as discussed above, the wide diversity of m7 configurations observed across different molluscan lineages clearly indicates that these muscles are not homologous.

This essay on muscle pair m7 is the seventh in a series devoted to odontophore structures, a neglected but important component in comparative biology. The previous contributions in this series addressed: (1) general aspects of the buccal mass (Simone, 2021); (2) muscle pair m1 (jugal muscles) (Simone, 2022b); (3) muscle pair m2 (retractor muscle of the buccal mass) (Simone, 2023a); (4) muscle pairs m3 and m9 (Simone, 2023b); (5) muscle pairs m4 and m5 (dorsal tensor muscles of the radula) (Simone, 2024c); and (6) muscle m6 (horizontal muscle) (Simone, 2025).

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