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The odontophore dorsal tensor muscles m4 and m5

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Abstract

The odontophore muscle pairs, designated as m4 and m5, are respectively known as the main and secondary dorsal tensor muscles of the radula. The m4 pair is typically the strongest in the odontophore and is responsible for stretching the radular ribbon within the buccal cavity. Along with the m5 pair, it also plays a role in the internalization of the radular ribbon. Their antagonist is the ventral tensor muscle (m11). The functions and primary variations of the m4-m5 pairs are discussed with examples.

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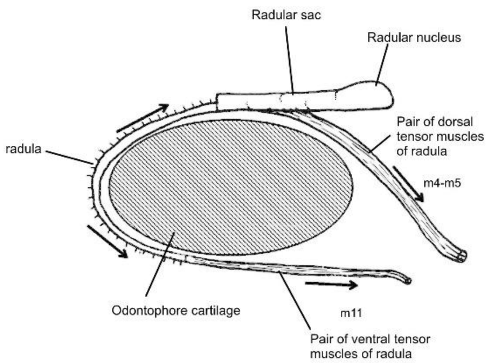
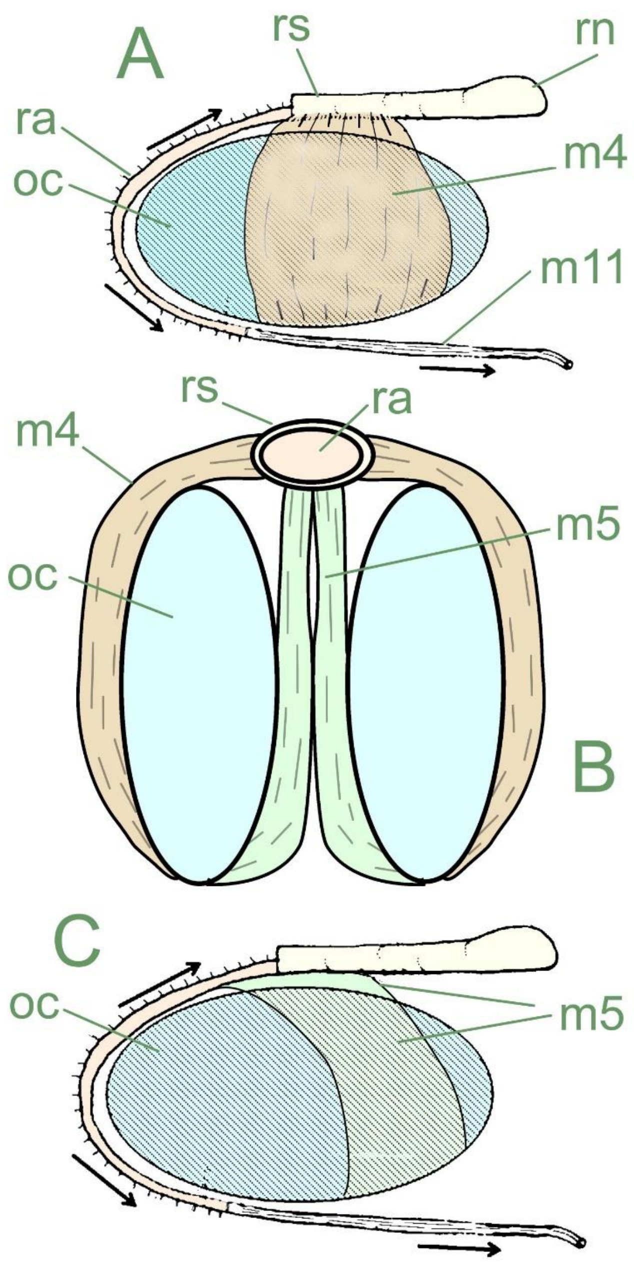
Introduction

The odontophore muscle pair coded as m4 and m5 are referred to as the dorsal tensor muscles of the radula. These muscles are crucial for food scraping and swallowing, making them the most significant and typically the largest muscle pair in the odontophore. Due to their size, they are easily detectable and useful for inferring homologies in comparative analyses. However, their variation is minimal at closer taxonomic levels, limiting their application in comparisons among closely related taxa. Nevertheless, they are highly valuable at higher taxonomic levels.



1: usual schematic representation of radular tensor muscular function. Left view, dorsal muscles showing overly simplified.

The schematic representation in Fig. 1 illustrates the primary function of the dorsal tensor muscles. As the teeth of the radular ribbon are oriented backwards, the contraction of these muscles



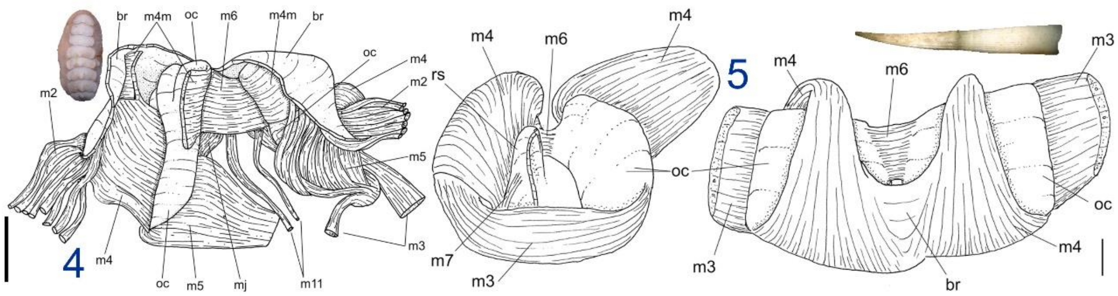
2: Schematic representation of generic m4 and m5 in situ. A, left view, with emphasis on m4; **B**, transverse section in odontophore core; **C**, left view, with emphasis on m5. Lettering: m4, main dorsal tensor muscle of the radula; m5, medial tensor muscle of the radula; m11, ventral tensor muscle of the radula; oc, odontophore cartilage; ra, radula; rn, radular nucleus; rs, radular sac.

moves the radula internally, scraping and transporting food inward. The opposing movement is facilitated by the pair of ventral tensor muscles (m11), which will be discussed in a future issue of Malacopedia. When the m11 pair contracts, the radula returns to its original position, ready to restart the scraping action. Because the radular teeth are turned backwards, they offer little resistance, allowing the m11 pair to be much narrower.

This schematic model, commonly found in textbooks, is actually more complex. The dorsal tensor muscles consist of two pairs (m4 and m5), which are connected to the odontophore cartilages (oc), as illustrated in Fig. 2.

The primary dorsal tensor muscle is the m4 pair. Each muscle typically originates from the anterior edges of the cartilages and their adjacent areas, generally along the outer surfaces of the cartilages. The m4 muscles then continue to encircle both cartilages, covering them externally (Figs. 2A, B: m4). Their insertion points are multiple. They insert along the subradular membrane, mainly in the oral cavity, where the radula is exposed and operational. This insertion helps tension and stretch the radular ribbon in the buccal cavity, enhancing its efficiency. Another insertion is on the radula itself, just posterior to its exposed (buccal) region. In this region, the m4 pair typically inserts into the radular sac (rs) and a connective tissue inside it. This tissue functions as a barrier, preventing food from entering the radular sac and even the haemocoel. This tissue is usually labeled "to" in anatomical drawings, while the m4 insertion on the radula is typically labeled "ir."

The pair of secondary or medial tensor muscles of the radula, coded as m5, typically originate from the cartilages near m4, but on their inner-medial surface. However, in some cases, the m5 pair originates from the posterior surface of m4, or even from both locations. The m5 muscles lie between the two cartilages (Figs. 2B, C), close to the median plane. They insert along the ventral surface of the radula, both in the buccal cavity and slightly posterior to it.



4-5: Examples of dissected odontophores in Polyplacophora and Scaphopoda. **4**, polyplacophore *Hanleya brachyplax*, whole specimen (42 mm), odontophore, dorsal view, both cartilages deflected, most left muscles also deflected, left m4m sectioned longitudinally (from Jardim & Simone, 2010), scale= 2 mm. **5**, scaphopod *Coccodentalium carduus*, shell (74 mm), odontophore, (left) posterior view, radula completely removed, left portion of radular sac shown in situ, right m4 deflect-ed; (right) Same, dorsal view, m3 transversally sectioned, both cartilages deflected (from Simone, 2009), scale= 0.5 mm. Lettering: br, subradular membrane, m2-m7, intrinsic-extrinsic odontophore muscles; oc, odontophore cartilages; rs, radular sac.

The operation of the three pairs of tensor muscles is illustrated in Fig. 3, with the left column representing the initial movement and the right column depicting the scraping and swallowing movement. During the initial movement, when the odontophore contacts the food, both dorsal muscle pairs, m4 and m5, are relaxed, while only the ventral tensor muscle pair, m11, is contracted. The radular rasping occurs when both dorsal tensor muscles, m4 and m5, contract (Fig. 3: right column), causing the ventral muscle, m11, to relax. This movement is repeated as often as necessary, resulting in a sliding motion of the radular ribbon along the anterior surface of the cartilages. As previously explained, since the radular teeth are turned backward (as shown in the left column of Fig. 3), this continuous movement erodes the food, breaks it into smaller particles, and directs the particles down the throat.

This basic schema of tensor muscles is found in all radula-bearing mollusks and is present in their basal branches. However, it has undergone several modifications throughout evolution. Below, some notable modifications are discussed.

In the two basal mollusk branches, Caudofoveata and Solenogastres, the odontophore is also highly modified, and the m4 and m5 pairs are still under analysis. Currently, making any inferences about homology is considered premature. Therefore, this discussion focuses specifically on the Testaria (Polyplacophora + Conchifera). For more general information on the odontophore and surrounding buccal mass, see Simone (2021).

The pairs m4-m5 in Testaria

In Polyplacophora, at least in the species with known odontophore muscles (Fig. 4), the odontophore includes the typical m4 and m5 pairs. Both pairs, especially m4, are notably thick, which is characteristic of herbivores and grazers. This thickening is associated with the extensive radular activity required to compensate for the lower quality of nutrients through greater processing.

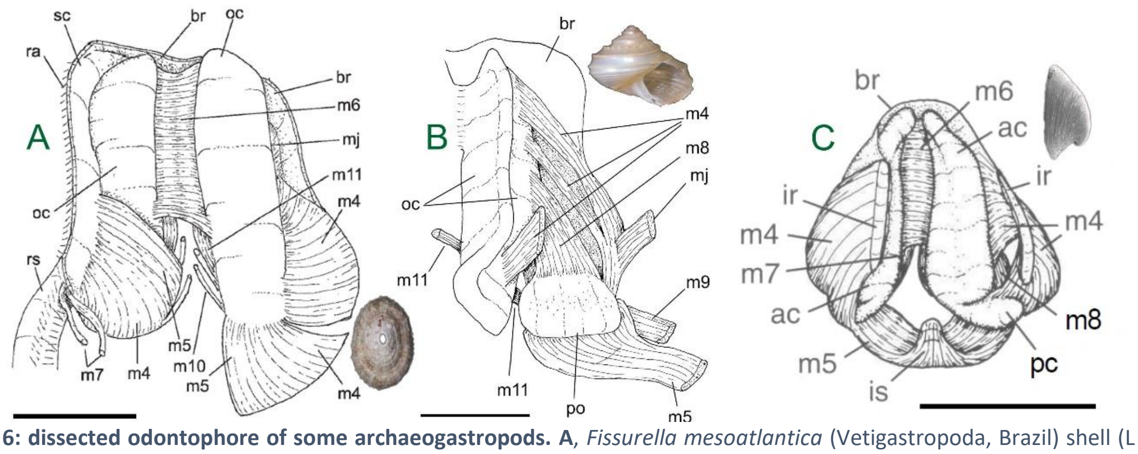
In Scaphopoda (Fig. 5), where odontophore muscles are known in only a few species, the m4 and m5 pairs are fused into a single "m4" pair. As previously reported (Simone, 2009, 2021), the scaphopod odontophore is adapted for crushing rather than scraping prey. Consequently, the combined m4 pair functions more as a holder for the radular ribbon rather than a tensor for its movement. This adaptation is more efficient for crushing. Scaphopods are the only representatives of the Diasoma with an odontophore, as bivalves have completely lost theirs.

In Cyrtosoma, the understanding of odontophore structure is more advanced in gastropods, as discussed below. In Cephalopoda, where the odontophore is further complex and surrounded by an intricate beak musculature, the knowledge remains preliminary. However, it is evident that the m4 and m5 pairs are present at the core of the extensive buccal musculature. These will be discussed in a future issue of Malacopedia.

In Gastropoda, the m4 and m5 pairs have undergone various modifications, ranging from significant increases in size to complete disappearance, and from fusion with each other to total separation. In some groups, they have also subdivided into additional muscles. Examples of these variations are discussed below. In the extensive phylogeny of Gastropoda, which primarily focuses on caenogastropods (Simone, 2011), 15 characters (345 to 359, pp. 252-253) are related to the m4 and m5 pairs.

In the four most basal branches of Gastropoda (Patellogastropoda, Cocculiniformia, Vetigastropoda, and Neritimorpha), the odontophore typically features two pairs of cartilages: a larger anterior pair and a smaller posterior pair (Fig. 6: oc-ac, po-pc). The arrangement of muscles is more complex in these basal groups, incorporating approximator muscles (m8) and other muscles. In these taxa, the m5 pair usually originates from the posterior cartilages (Fig. 6), while the m4 pair is characterized by multiple branches, with various origins and insertions (Fig. 6B) depending on the taxon. Within this archaeogastropod grade, some taxa exhibit a simplification of the m4 and m5 pairs. For example, in known fissurellids, distinguishing between m4 and m5 is challenging, with m5 being a posterior-medial continuation of m4 (Fig. 6A), and the m4 pair itself forming a single broad bundle. Some cocculiniforms lack posterior odontophore cartilages, while others have them partially fused with the anterior ones (Fig. 6C: pc), resulting in the m4 pair having two branches.

In Neritimorpha, all examined forms—both marine (e.g., Barroso et al., 2012) and

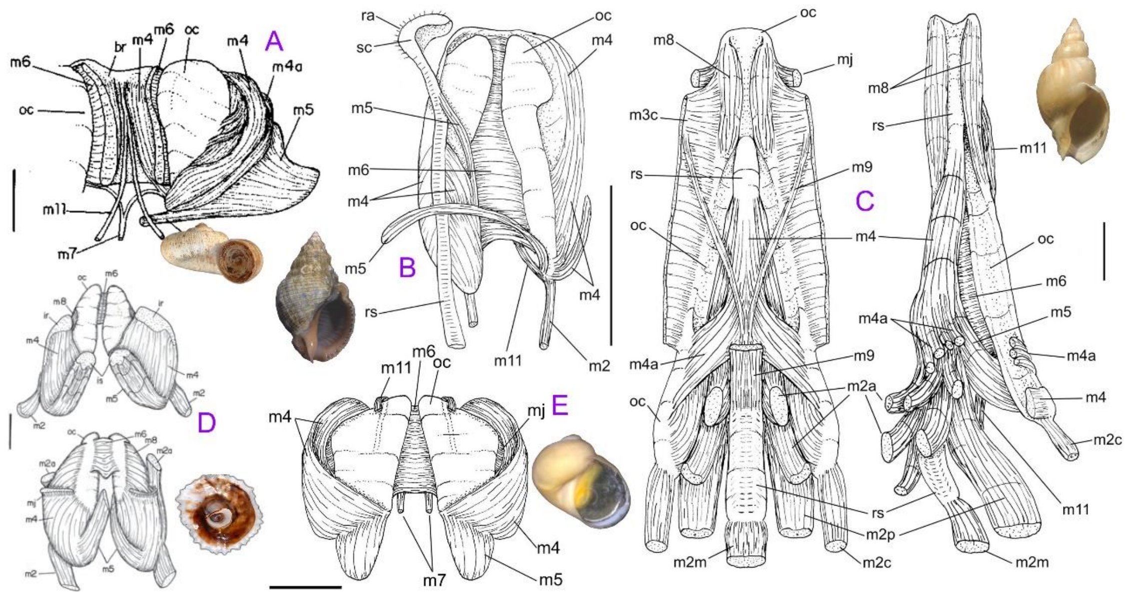


6: dissected odontophore of some archaeogastropods. A, *Fissurella mesoatlantica* (Vetigastropoda, Brazil) shell (L 14 mm), odontophore in dorsal view, both cartilages deflected, subradular membrane sectioned longitudinally, radular sac and ribbon deflected to left with intrinsic muscles attached to them, right muscles deflected (from Simone, 2008, scale= 1mm); **B**, *Margarites imperialis* (Vetigastropoda, Brazil) shell (L 10 mm), detail of odontophore in its right side with anterior cartilage deflected upwards, separating from posterior cartilage to show intrinsic muscles origins and insertions (scale= 1 mm); **C**, *Copulabyssia riosi* (Cocculiniformia, Brazil), shell (L 3 mm), odontophore in dorsal view, radular ribbon and radula sac extracted, most of muscles and cartilages deflected to expose inner surfaces, right-side structures more deflected than those on left side (from Leal & Simone, 2000; scale= 0.5 mm). Lettering: ac, anterior cartilage; br, subradular membrane; ir, insertion of m4 in radula; is, insertion of m5 in radula; m4-m11, intrinsic-extrinsic odontophore muscles; mj, jaw-peribuccal muscle; oc, anterior odontophore cartilage; po, posterior cartilage; ra, radula; rs, radular sac.

terrestrial (e.g., Simone, 2018)—exhibit both pairs of cartilages, with the m4 pair having a broader posterior region (Fig. 7). The m5 pair is narrow and located posteriorly. The m4 pair consists of a single bundle each, but a large approximator muscle (m8) is present.

In Apogastropoda (Heterobranchia + Caenogastropoda), which is the next branch after the archaeogastropod grade, the m4 and m5 pairs generally follow the basic model described above. However, these pairs have been highly modified across different branches within both groups, making it impractical to cover all variations. Nonetheless, some notable examples are discussed below.

The pairs m4-m5 in Caenogastropoda



8: Dissected odontophore of some Caenogastropoda. A, *Neocyclotus prominulus* (Cyclophoroidea, Brazil), shell (15 mm), half odontophore with m6 sectioned longitudinally, only middle and right structures shown, m4 partially separated from cartilage, scale= 0.5 mm (from Simone, 2004); B, *Thaisella guatemalteca* (Neogastropoda, Guatemala), shell (29 mm), odontophore in dorsal view, superficial layer of muscles and membrane removed, both cartilages deflected, radular sac removed to left, right muscles deflected to show cartilage (oc), left muscles still connected to radula, scale= 1 mm (from Simone 2017a); C, *Buccinanops cochlidium* (Neogastropoda, Argentina), shell (64 mm), odontophore left: dorsal view, some more superficial muscles partially removed; right: right-slightly dorsal view, more dorsal muscles deflected to show more internal structures, scale= 2 mm (from Pastorino & Simone, 2021); D, *Crucibulum* auricula (Calyptraeoidea, Caribbean), shell (20 mm), odontophore above: dorsal view, only more internal muscles exposed cartilages partially deflected; below: same, ventral view, scale= 0.5 mm (from Simone, 2002); E, *Laevilacunaria antarctica* (Rissooidea, Antarctica), shell (7 mm), odontophore with radular structures removed, most structures deflected to show cartilages, scale= 0.5 mm (from Simone, 2017b). Lettering: ac, anterior cartilage; br, subradular membrane; ir, insertion of m4 in radula; is, insertion of m5 in radula; m4-m11, intrinsic-extrinsic odontophore muscles; mj, jaw-peribuccal muscle; oc, anterior odontophore cartilage; po, posterior cartilage; ra, radula; rs, radular sac.

As reported in previous studies (e.g., Ponder et al., 2007; Simone, 2011, 2021), the caenogastropod odontophore no longer exhibits the back-and-forth movement of the radula, where the radular ribbon slides across the odontophore cartilages. Instead, the caenogastropod radula barely makes contact with the cartilages, being primarily separated from them by the m4 and m5 pairs and other structures. In these gastropods, the m4 pair mainly functions to stretch the radula within the buccal cavity rather than to move it. The scraping action is thus performed by the odontophore itself, using a blotting-paper-like movement. Consequently, the ventral pair of tensor muscles (m11) is typically reduced and may even be atrophied in caenogastropods.

The caenogastropod m4 pair appears to be the result of the fusion of several muscle pairs present in the odontophore of the archaeogastropod grade branches. One of these is the approximator muscle pair (Fig. 6: m8). As a result, the m4 pair in the first two caenogastropod branches is often composed of two or more layers (Fig. 8A: m4, m4a). In the Epiathroidea (Viviparoidea + Sorbeoconcha), the m4 pair has evolved into a single bulk as a synapomorphy (Figs. 8D, E).

In the mesogastropod grade within the Epiathroidea, the morphology of the m4 and m5 pairs remains relatively conservative. However, their relationship with each other, particularly their origins, varies considerably. In some taxa, the m5 pair originates from the posterior surface of the m4 (Fig. 8E), while in others, both pairs originate directly from the posterior end of the odontophore cartilages (Fig. 8D). There are taxa where the m4 and m5 pairs are distinctly separate, whereas in others, they are fused or continuous, making it difficult to discern their borders.

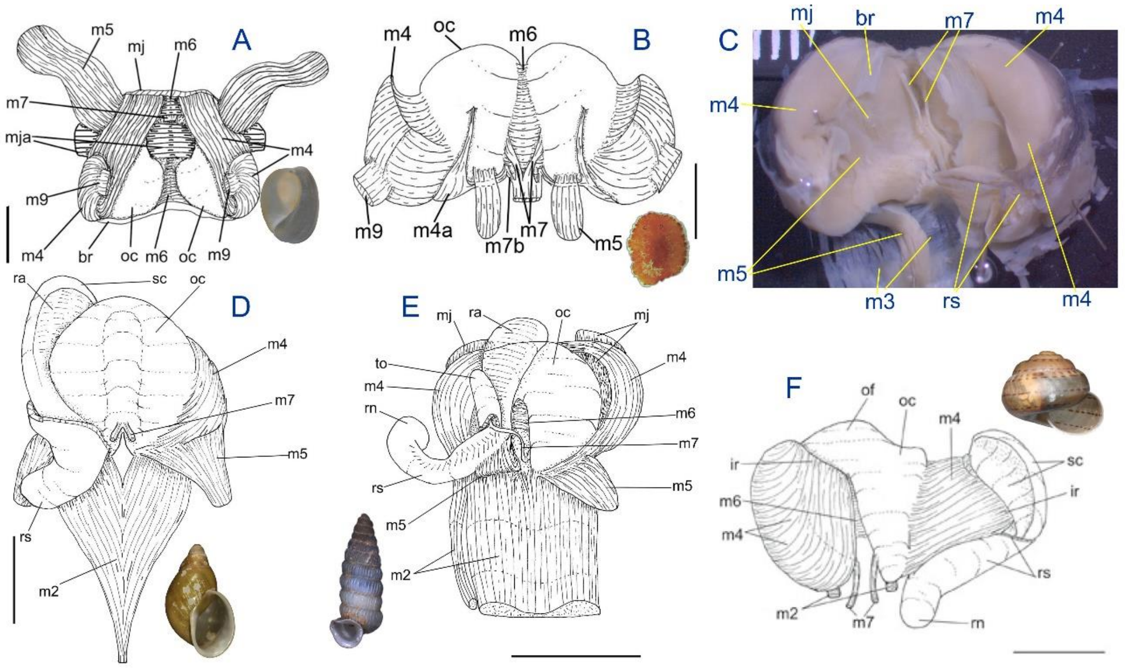
As previously reported (e.g., Simone, 2011, 2021), the movement of the radular ribbon sliding across the odontophore cartilages is restored in Neogastropoda, which is important for their predatory behavior. Consequently, neogastropods have regained a strong ventral tensor muscle of the radula (m11) (Figs. 8B, C), which was lost or significantly reduced in their mesogastropod ancestors. In neogastropods, the m11 pair is somewhat different, being attached to the posterior odontophore cartilages rather than the buccal musculature, as seen in the more basal gastropods (although several exceptions will be discussed in a future issue of Malacopedia on m11). It is plausible that the neogastropod m11 pair is derived from a ventral branch of the m4 pair itself. While the lateral and dorsal branches of m4 have retained their role as dorsal tensors, the ventral branch appears to have shifted function and become a ventral tensor. Ontogenetic or developmental studies could provide further insight into this transition.

The typical neogastropod odontophore is notably elongated (Figs. 8B, C). Its cartilages are narrow and long; in more basal forms, the cartilages are separated from each other (Fig. 8B: oc), whereas anterior fusion becomes common in more advanced branches (Fig. 8C). The tensor muscles—m4, m5, and m11—are usually narrow and long, originating from the posterior end of the cartilages. The m4 pair, as usual, is the most robust and forms a substantial muscular mass surrounding the radular sac in the region preceding the buccal cavity. In some advanced neogastropods, particularly volutoideans and buccinoideans (Fig. 8C), the odontophore is incredibly complex. These taxa have additional muscle pairs and subdivisions of the usual muscles, especially the m4 pair (Fig. 8C), compared to more basal neogastropods (Fig. 8B) and mesogastropods (Figs. 8A, D, E). In these advanced forms, the m4 and m5 pairs originate from different sides of the posterior end of the cartilages.

The pairs m4-m5 in Heterobranchia

As previously reported (Simone, 2011, 2021), the evolution of odontophore muscles in heterobranchs is not as well understood as in the prosobranchs discussed above. In the top branch, Eupulmonata, a substantial number of species have well-documented odontophore and buccal mass structures, which are remarkably similar to the basal plan described earlier (Figs. 9D-F). However, there is a significant gap in our knowledge regarding the more basal heterobranch branches and nudibranchs. Very few taxa have detailed anatomical information on their buccal mass, and some taxa have data available only for the radula.

Even someone well-versed in odontophore anatomy can be surprised by the diversity



9: Dissected odontophore of some Heterobranchia. A, *Haminoea marray* (Cephalaspidea), shell (20 mm), dontophore in dorsal view, m4 and m5 deflected to expose cartilages, scale= 0.5 mm (from Galvão et al, 2024); B, *Platydoris guarani* (Nudibranchia), whole specimen (25 mm), odontophore in dorsal view, with folded down muscles, scale= 2 mm (from Lima & Simone, 2018); C, *Aplysia depilans* (Aplysiida), odontophore in dorsal view, both halves deflected, left muscles expanded (scale in mm); D, *Anthinus vailanti* (Eupulmonata, Odontostomidae), shell (29 mm), odontophore in dorsal view, superficial layer of muscles and structures removed, most muscles deflected, radular ribbon deflected to left, scale= 2 mm (from Simone, 2022a). E, *Habeas lekolus* (Eupulmonata, Urocoptidae), shell (7 mm), odontophore in dorsal view, radula deflected to left, right muscles deflected to right, scale= 0.5 mm (from Simone, 2022b); F, *Olympus nimbus* (Eupulmonata, Solaropsidae), shell (16 mm), odontophore in dorsal view, radula removed and deflected to right still connected to m4, left muscles as in situ; radula seen in profile, scale= 1 mm (from Simone, 2010). Lettering: ac, anterior cartilage; br, subradular membrane; ir, insertion of m4 in radula; is, insertion of m5 in radula; m2-m9, intrinsic-extrinsic odontophore muscles; mj, jaw-peribuccal muscle; oc, anterior odontophore cartilage; po, posterior cartilage; ra, radula; rs, radular sac; rn, radular nucleus; sc, subradular cartilage; to, tissue on radula preceding buccal cavity.

found in non-pulmonate heterobranchs. Some species exhibit extraordinary pre-buccal adaptations, such as bivalve-like jaws, expansive chambers, alien-like tentacles, or broom-like jaws or radulas. These structures, often associated with the odontophore muscles, significantly deviate from the typical buccal mass configuration. Figure 9 displays odontophores with more typical conformations.

As examples of anatomical oddities, some cephalaspideans have a prominent muscular rod passing through the anterior region of the odontophore, displacing adjacent muscles (Fig. 9A: mja). In contrast, some doridacean nudibranchs feature unusual m4 branches that penetrate the middle region of the odontophore cartilages and emerge on the other side (Fig. 9B: m4a). The aplysiomorphs studied so far (Fig. 9C) exhibit a near absence of odontophore cartilages, which are reduced to a tape-like structure, giving the appearance that muscles originate from other muscles. Despite these variations, the m4 and m5 pairs in aplysiomorphs appear relatively ordinary (Figs. 9A-C), with the m5 pair originating directly from the posterior region of the cartilages (Figs. 9A, B).

A different situation is observed in eupulmonate heterobranchs, which, as mentioned earlier, typically have a relatively regular odontophore. The common feature among them is that both odontophore cartilages are fused along the ventral-medial edge (Figs. 9D-F: oc), with varying degrees of fusion extending from the anterior region. Typically, the m5 pair originates from the surface of the m4 pair (Figs. 9D, E). In some taxa, the m5 pair is incorporated into the m4 pair (Fig.

9F), forming a single, unified bulk.

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