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The odontophore horizontal muscle (m6)

Luiz Ricardo L. Simone

Museu de Zoologia da Universidade de São Paulo
lrsimone@usp.br; lrlsimone@gmail.com
OrcID: 0000-0002-1397-9823

Abstract

The horizontal odontophore muscle, designated as m6, is examined in this study. Although its function is not yet fully understood, its anatomical uniqueness makes it a significant structure in comparative morphological studies. The muscle connects the two odontophore cartilages, typically along their ventral margins. It is found in all molluscan classes that possess an odontophore, except for aplacophorans. This work discusses notable variations of the muscle, including duplication, subdivision, positional changes (such as insertion between the cartilages), and even its reduction or complete loss.

Keywords: evolution, phylogeny, taxonomy, morphological modifications.

Introduction

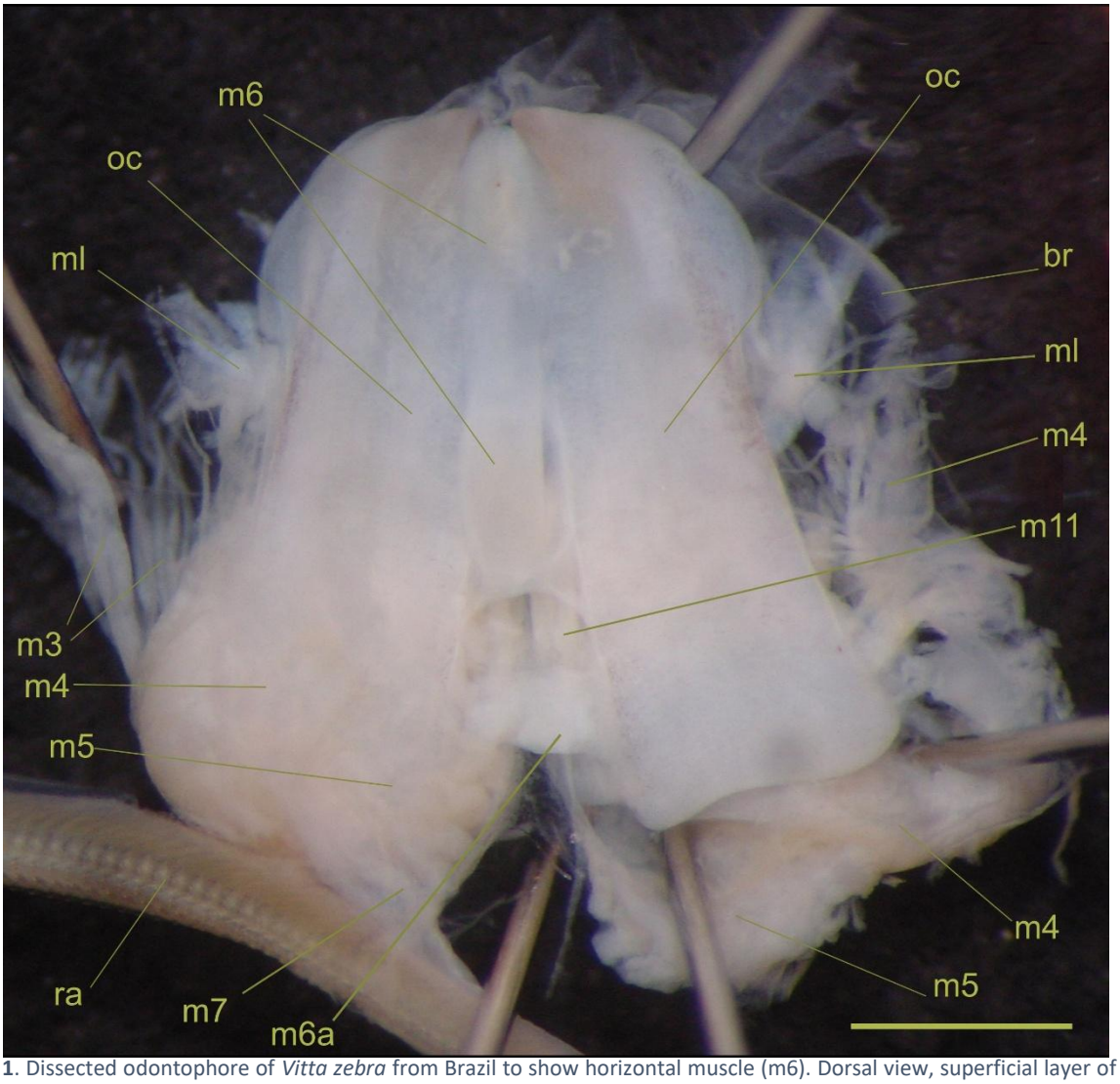
The unpaired horizontal muscle, coded m6, is among the most easily comparable muscles across molluscan taxa. It is single and situated between the two odontophore cartilages and functions to draw them toward each other. The muscle inserts along the ventral edge of each cartilage, with its fibers running transversely, directly connecting one cartilage to the other. Its position and structural characteristics are unique and readily identifiable in all mollusks possessing an odontophore.

Although the function of m6 in approximating the cartilages can be readily inferred from its morphology, its actual role in odontophore function remains difficult to interpret. Upon contraction, m6 draws together only the ventral edges of the cartilages, while the dorsal edges remain free, being flanked solely by the paired dorsal radular tensor muscles (m4–m5).

Although m6 remains a functional enigma, it is anatomically valuable, serving as a reliable reference point in the comparative analysis of odontophores across distantly related taxa. It is consistently located ventrally, at the terminal end of the radular ribbon. The muscle is present in nearly

all odontophores, with only a few exceptions, and has been lost in a limited number of taxa, as discussed below.

Generalities of m6



1. Dissected odontophore of *Vitta zebra* from Brazil to show horizontal muscle (m6). Dorsal view, superficial layer of membrane and muscles removed, both cartilages deflected (MZSP 87779). Scale= 1 mm. Lettering: br, subradular membrane; m3, lateral protractor muscles; m4-m5, dorsal radular tensor muscles; m6, horizontal muscle; m6a, additional bundle of horizontal muscle; m7, radular sac muscle; m11, ventral radular tensor muscle; ml, lateral muscle of buccal mass; oc, odontophore cartilage; ra, radular sac.

Fig. 1 shows a relatively typical example of the m6 muscle, which becomes clearly visible during dissection when the odontophore cartilages (oc) are deflected. The structure connecting the two cartilages is the m6. As shown, this horizontal muscle is composed of transverse fibers that link the ventral edges of both cartilages. In most taxa, m6 originates near the anterior margin of the cartilages, while its posterior extent varies by species. Depending on the taxon, it may run the entire length of the ventral edge, terminate near the midpoint, or exhibit intermediate configurations. The proportional length of m6 relative to the length of the cartilages is often consistent within a species, making it a useful taxonomic character. A common feature of m6 is its extension onto the dorsal surface of the cartilages, where it inserts parallel to—but set apart from—their edges, giving the appearance of a ventral covering.

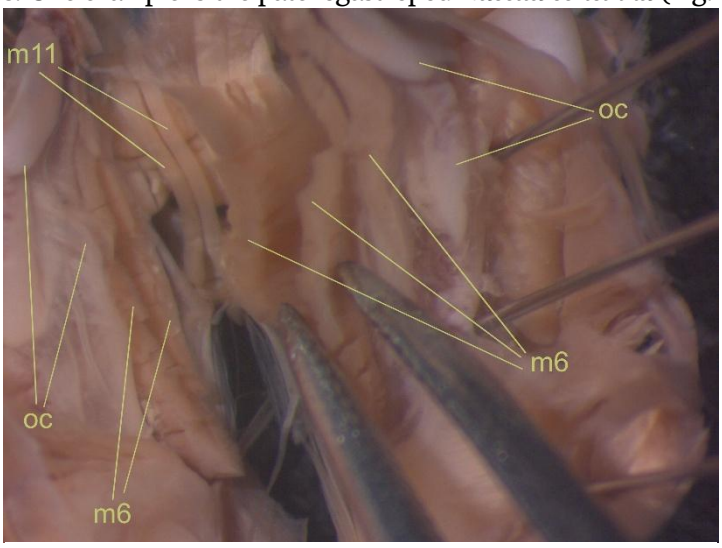
Aside from these general features, there is little to add about m6 beyond its modifications across different molluscan lineages. Several examples of these variations are presented below. Common modifications include its division into two parts, duplication, reduction, or complete loss. These changes have occurred multiple times throughout molluscan evolution and, in some cases, represent defining characteristics of major taxonomic groups, as discussed below.

1. M6 in aplacophorans

As previously discussed (Simone, 2011, 2021: fig. 2), the odontophore in both Caudofoveata and Solenogastres is highly modified, to the extent that establishing homologies between muscles and other structures is challenging. In the species studied to date (unfortunately still unpublished), no structure resembling m6 has been identified. Whether both aplacophoran classes never possessed an m6—making it a potential synapomorphy of Testaria (Polyplacophora + Conchifera)—or whether they originally had an m6 that was subsequently lost or modified remains an open question.

2. Duplication of m6

In a few taxa, a duplication of muscle layers has been observed, giving the appearance of two or more overlapping m6 muscles. One example is the patellogastropod *Nacella concinna* (Fig. 2), which possesses three distinct layers of m6. The two ventral layers are thicker and similar in size, while the dorsal layer is thinner and restricted to the anterior half of the muscle.

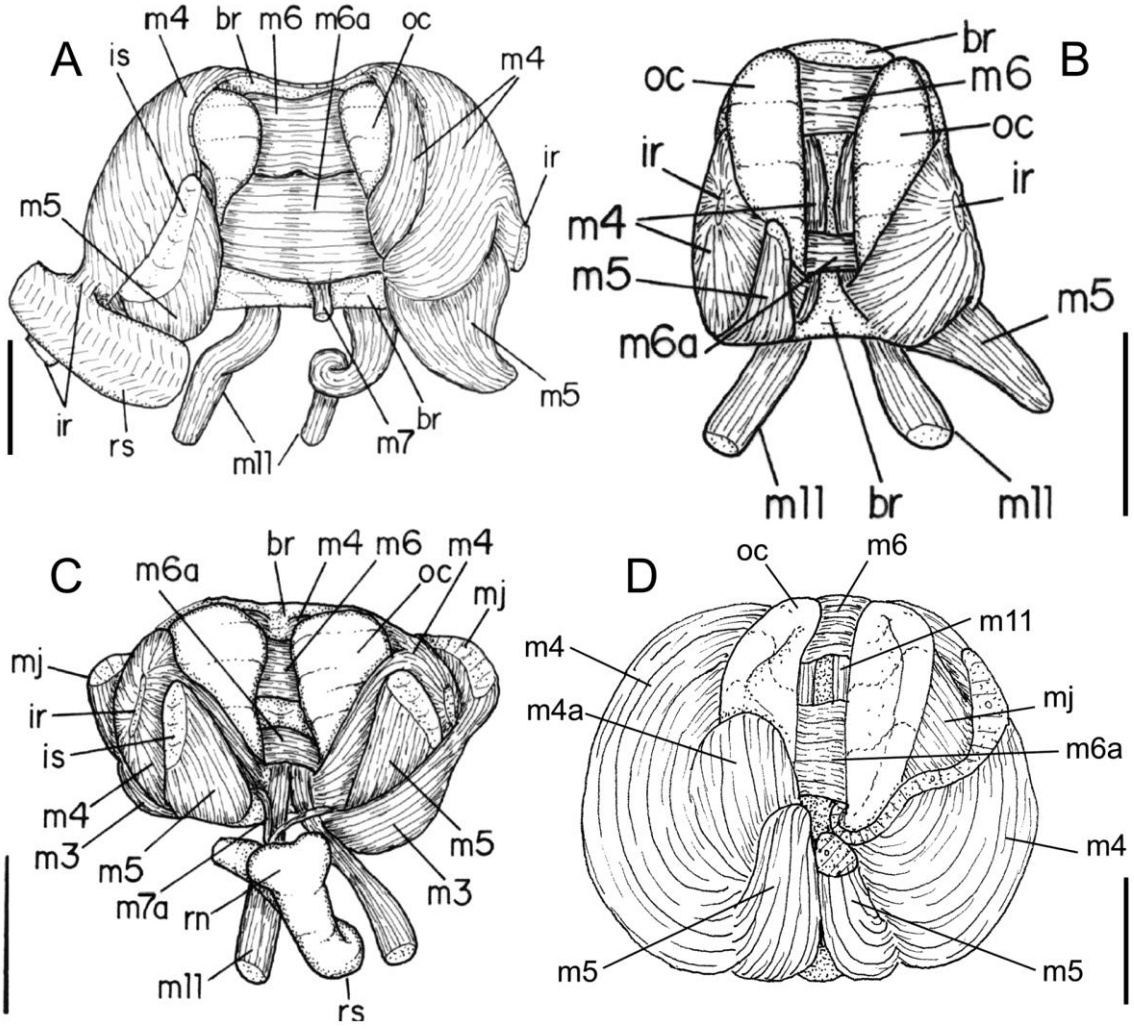


2. Dissected odontophore of *Nacella concinna* from Antarctica to show duplicated horizontal muscle (m6) actually in 3 layers. Dorsal view, superficial layer of membrane and muscles removed, both cartilages deflected, m6 sectioned longitudinally and both halves slightly separated from each other (MZSP). Forceps end = 1 mm. Lettering: m6, horizontal muscle, oc, odontophore cartilage.

The multiplication of muscle layers is not simply related to an increase in the overall thickness of m6, as very thick m6 muscles have been observed in several taxa that consist of a single, dense layer. The presence of multiple layers appears to be an independent phenomenon with distinct functional and taxonomic significance. However, there is currently no clear evidence linking m6 duplication to specific taxonomic or phylogenetic patterns. This is partly because the internal morphology of patellogastropods remains poorly understood, and no phenotype-based phylogenies have yet been developed for their internal branches. Other patellogastropods studied for odontophore characters (e.g., *Propilidium curcumin* Leal & Simone, 1998) possess a single-layered m6, though their extremely small size may obscure detection of any layering.

3. Division of m6

Unlike the duplication or multiplication of m6, the division refers to the transverse separation of the muscle along its longitudinal axis. In this condition, both components lie in the same plane rather than being superimposed.



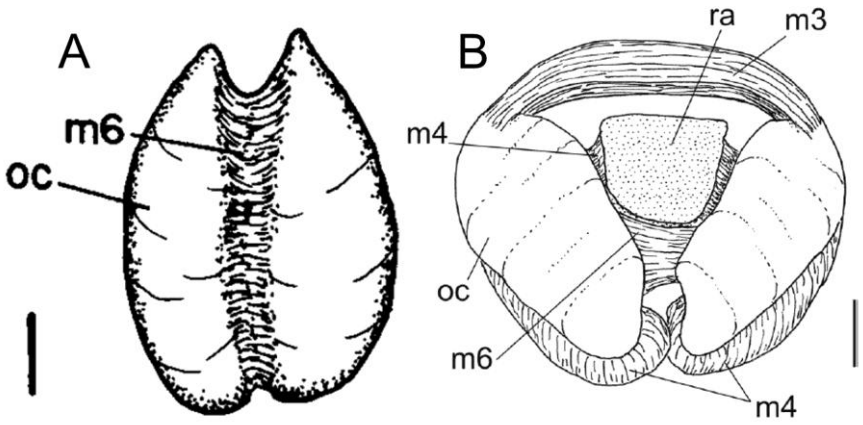
3. Examples of divided m6 in some families of Cypraeoidea (a synapomorphy). All odontophores with superficial layer of muscles and membranes removed, radula removed, both cartilages deflected, dorsal view. **A**, *Lamellaria branca* (Lamellariidae), scale= 1 mm; **B**, *Pedicularia sp.* (Pediculariidae), scale= 0.25 mm; **C**, *Calpurnus verrucosus* (Ovulidae), radular sac deflected downwards, scale= 2 mm (these 3 from Simone, 2004); **D**, *Macrocypraea mammoth* (Cypraeidae), scale 5 mm (from Simone & Cavallari, 2020). Lettering: br, subradular cartilage; ir, insertion of m4 in tissue on radular ribbon; is, insertion of m5 in subradular cartilage; m3, transverse superficial muscle; m4, main dorsal tensor muscle of radula; m5, secondary dorsal tensor muscle of radula; m6, horizontal muscle; m6a, posterior component of m6; m7, radular sac muscle; m11 ventral tensor muscle of radula; mj, jaw and peribuccal muscles; oc, odontophore cartilage; rn, radular nucleus; rs, radular sac.

This particular modification of m6 occurs in a few taxa, but it stands out as a remarkable synapomorphy of the Cypraeoidea, a significant superfamily within Caenogastropoda (Simone, 2004, 2011). For reasons that remain unclear from a morphological perspective, lamellariids and their allies are currently classified separately from Cypraeoidea, within the superfamily Velutinoidea (MolluscaBase, 2025). However, a monophyletic Cypraeoidea—including Velutinoidea as its basal branch—is strongly supported by no fewer than 41 synapomorphies (Simone, 2004, 2011), including the m6 division highlighted here (Fig. 3). Lamellariids exhibit a divided m6 (Fig. 3A), with both components positioned closely together, whereas members of other families—such as pediculariids (Fig. 3B), ovulids (Fig. 3C), and cypraeids (Fig. 3D)—display the two components slightly more separated.

Division of m6 is also observed in other taxa unrelated to cypraeoideans, representing interesting cases of convergence. One example is the neritimorph *Vitta zebra*, previously discussed (Fig. 6A) (Barroso et al., 2012). However, due to the limited current understanding of neritimorph morphology, the taxonomic and phylogenetic significance of this m6 division remains unclear. At least one other neritimorph, the terrestrial *Helicina variabilis* (Helicinidae – Simone, 2018), lacks a divided m6.

4. M6 located between the cartilages

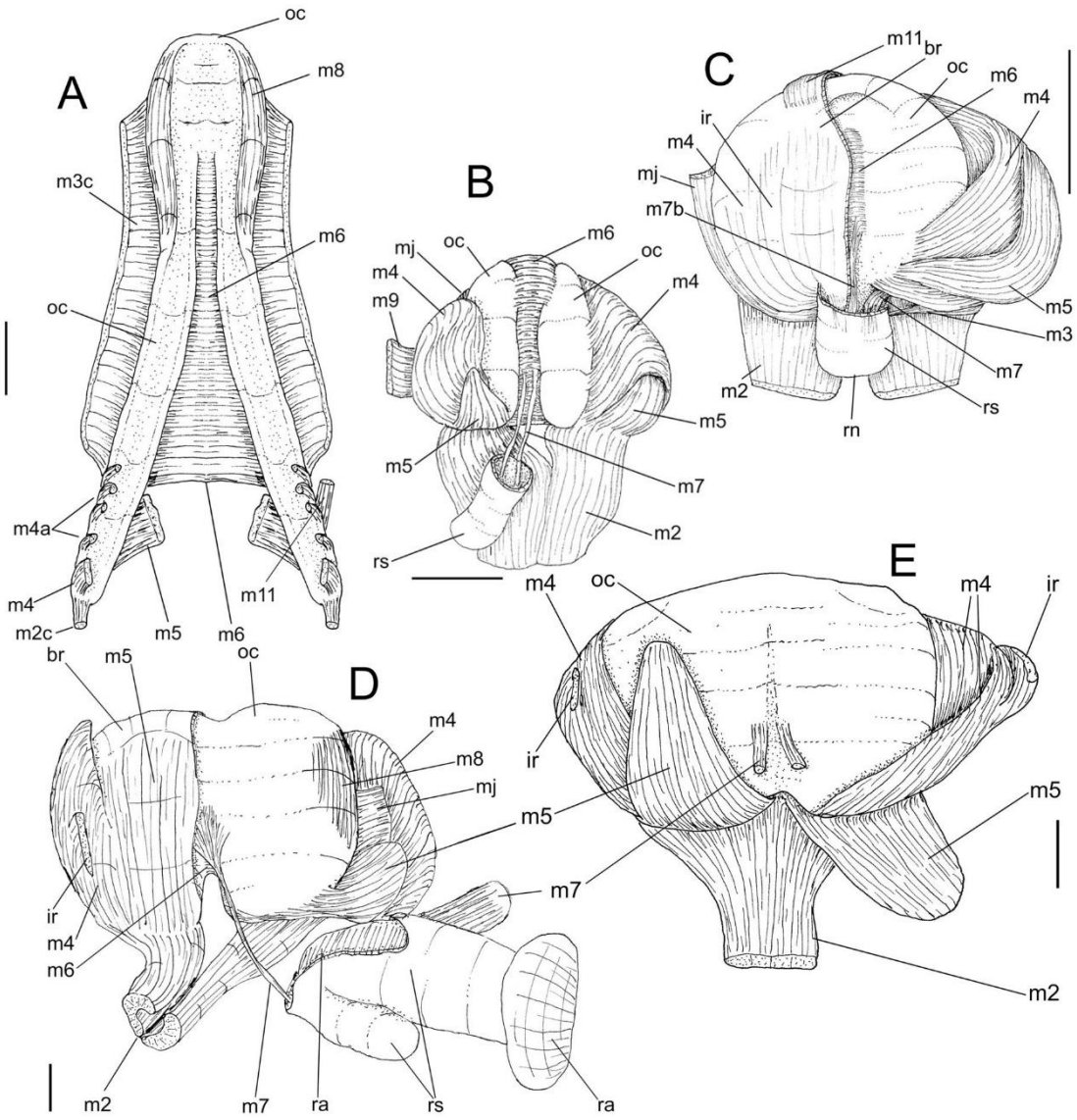
In some taxa, m6 is positioned between the cartilages rather than outside them. In these cases, its insertion occurs on the inner surfaces of both cartilages, rather than on their outer surfaces (Fig. 4). This arrangement has been considered the ancestral condition for Mollusca (e.g., Haszprunar, 1988), although it has not been observed in polyplacophorans (e.g., Jardim & Simone, 2010). In aplacophorans, as noted above, the odontophore is so highly modified that m6 cannot be individually identified, making it difficult to infer the muscle's original configuration in either aplacophoran class. Among Conchifera, no detailed information is available regarding the intrinsic muscles of the odontophore in the anatomically best-known monoplacophoran, *Neopilina galatheae* (Lemche & Wingstrand, 1959). In fact, the configuration where m6 is located between the cartilages has only been observed in miniaturized patellogastropods, such as Propilidium curumim (Lepetidae) (Fig. 4) (Leal & Simone, 1998). Larger patellogastropods do not exhibit this condition (Fig. 2).



4. Examples of m6 located between cartilages. Both odontophores with superficial layer of muscles and membranes removed, radula removed. **A**, *Propilidium curumim* (Lepetidae, Patellogastropoda), isolated cartilages with only m6 preserved, dorsal view, scale= 0.1 mm (from Leal & Simone, 1998); **B**, *Coccodentalium carduus* (Dentaliidae, Scaphopoda), radular sac sectioned in middle, anterior view, scale= 0.5 mm (from Simone 2009). Lettering: m3, transverse muscle; m4, main dorsal tensor muscle of radula; m6, horizontal muscle; oc, odontophore cartilage; ra, radular sac.

Another group in which m6 is found between the cartilages is the Scaphopoda (Fig. 4B) (Simone, 2009). In scaphopods, the odontophore is modified for crushing prey rather than for scraping. Here, m6 functions in conjunction with m3—an exclusive scaphopod muscle—forming a structure that acts somewhat like a gizzard to crush prey (Fig. 4B). As a result, m6 has been repositioned to a more internal location, likely for functional reasons.

5. Reduction and loss of m6



5. Examples of reduced or atrophy of m6. Odontophore with superficial layer of muscles and membranes removed, both cartilages deflected, radular sac removed or deflected downwards, dorsal view. **A**, *Buccinanops cochlidium* (Neogastropoda Buccinoidea), scale= 2 mm (from Pastorino & Simone, 2021); **B**, *Bulimulus sula* (Eupulmonata, Orthalicoidea), scale= 1 mm (from Simone & Amaral, 2018); **C**, *Sanniostracus carnavalescus* (Eupulmonata, Orthalicoidea), scale= 1 mm (from Simone & Salvador, 2016); **D**; *Kora corallina* (Eupulmonata, Orthalicoidea), scale= 1 mm; **E**, *Koltrora pyrostoma* (Eupulmonata, Orthalicoidea), scale= 1 mm (both from Simone, 2024). Lettering: br, subradular cartilage; ir, insertion of m4 in tissue on radular ribbon; m2, retractor muscle of buccal mass; m3, transverse superficial muscle; m4, main dorsal tensor muscle of radula; m5, secondary dorsal tensor muscle of radula; m6, horizontal muscle; m7, radular sac muscle; m8, shortening muscle; m9, internal transverse muscle; m11 ventral tensor muscle of radula; mj, jaw and peribuccal muscles; oc, odontophore cartilage; ra, radula, rn, radular nucleus; rs, radular sac.

The reduction or even complete atrophy (loss) of the horizontal muscle (m6) is consistently associated with the additional phenomenon of fusion of the odontophore cartilages (Fig. 5). Typically, the odontophore cartilages form a pair of elliptical to elongated, flattened structures (Simone, 2021). In various taxa, these cartilages exhibit different degrees of fusion, ranging from minimal contact to complete union. Although the odontophore cartilages will be addressed in a future *Malacopedia* issue, it is relevant here to note that fusion always begins at the anterior end of the cartilages and progresses along their ventral edge—precisely where m6 is located.

It is reasonable to interpret that when the cartilages are fused along their ventral edge, the functional role of m6 becomes reduced—or even obsolete. Consequently, the reduction or complete loss of m6 is a predictable outcome.

Fusion of the odontophore cartilages is observed in several branches of Neogastropoda (Caenogastropoda) (Fig. 5A), including, for example, Volutoidea and Buccinoidea. In these taxa, m6 is typically thin and restricted to the region posterior to the fused area (Fig. 5A: m6), with its size decreasing in proportion to the extent of the cartilage fusion.

Odontophore cartilages are also frequently fused in land snails (Eupulmonata) (Figs. 5B–E). In the superfamily Orthalicoidea, for example, there is a range of conditions: some species have completely separated cartilages (Fig. 5B), while others show complete fusion, accompanied by total loss of m6 (Fig. 5E). Intermediate conditions are also present, such as species with a low degree of cartilage fusion and a well-developed m6 (Fig. 5C), and species with more extensive fusion and a vestigial, barely discernible m6 (Fig. 5D).

Conclusion

The molluscan horizontal muscle (m6), like any anatomical structure, exhibits a typical morphology along with a wide range of evolutionary modifications. These variations make m6 a valuable feature for comparative studies in taxonomy and phylogeny. This study highlights the most common modifications, though many others—and the taxa in which they occur—remain unexplored due to a general lack of detailed anatomical knowledge. The odontophore, in particular, is a poorly studied structure, often destroyed during radula extraction—an unfortunate loss of valuable comparative data.

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