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The intrinsic odontophore cartilages' muscles – m8

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Abstract

The odontophore muscle pair coded as m8 comprises muscles intrinsic to the odontophore cartilages. Two types are recognized. The most common type occurs in the four basal gastropod clades (Patellogastropoda, Cocculiniformia, Vetigastropoda, and Neritimorpha) and connects the anterior and posterior pairs of cartilages; accordingly, these muscles are termed cartilage approximators. The second type lies longitudinally along the outer anterior edges of the cartilages. This condition occurs in Neogastropoda, particularly in Buccinoidea and possibly throughout Volutoidea, and may represent a character uniting these groups. It also occurs convergently in the eupulmonate genus *Kora*. Additionally, a distinct, unpaired muscle connecting the radular nucleus to the adjacent dorsal surface of the odontophore in some cerithioidean lineages has also been designated as m8.

Keywords: odontophore, phylogeny, morphological modifications, anatomy.

Introduction

The odontophore muscle pair coded as "m8" comprises those intrinsic to the cartilages, i.e., muscles whose origin and insertion are both on the cartilages. This paper is part of a series dedicated to odontophore structures. The series began with general considerations (Simone, 2021) and subsequently focused on specific muscle groups, including the jugal muscles (group m1) (Simone, 2022); the buccal mass retractors (m2) (Simone, 2023a); the muscle pairs m3 and m9 (Simone, 2023b); the radular ventral tensor muscles (m4 and m5) (Simone, 2024); the horizontal muscle (m6) (Simone, 2025a); and the radular sac muscles (m7) (Simone, 2025b).

Two types of the m8 muscle pair are recognized, both so far detected only in Gastropoda. The first type occurs exclusively in taxa bearing two pairs of odontophore cartilages, i.e., an anterior, larger pair and a posterior, smaller pair. In these cases, the m8 pair connects the anterior cartilages to the posterior ones.

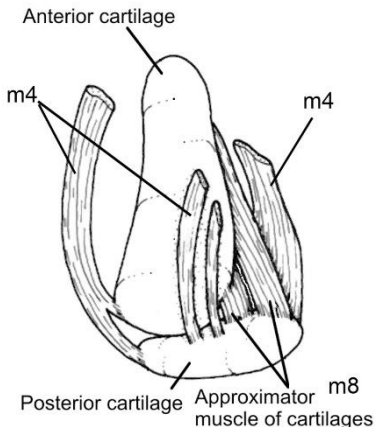
The second type is found in some Neogastropoda and certain Eupulmonata, where it is located along the outer edge of the cartilages. These two types are non-homologous and are discussed in more detail below.

Additionally, a distinct radular muscle present in some Cerithioidea has also been referred to as m8; this condition is likewise addressed below.

Pair m8 located between anterior and posterior cartilages

An odontophore bearing more than two pairs of cartilages occurs only in the four most basal gastropod clades (Sasaki, 1998; Simone, 2011), namely Patellogastropoda (Fig. 2D), Cocculiniformia (Fig. 2B), Vetigastropoda (Fig. 2C), and Neritimorpha (Fig. 2A).

Although there are a few exceptions (e.g., *Solariella*; Dornellas & Simone, 2015), as well as varying degrees of fusion between the anterior and posterior cartilages within derived members of these taxa, most species possess two pairs of cartilages—an anterior and a posterior pair. Some patellogastropods, however, exhibit additional cartilage pairs (Fig. 2D: lc).



1. Schematic representation of pair m8 and others. Odontophore sectioned in median line, only left side shown in right view, part of m4 removed. More superficial structures also removed.

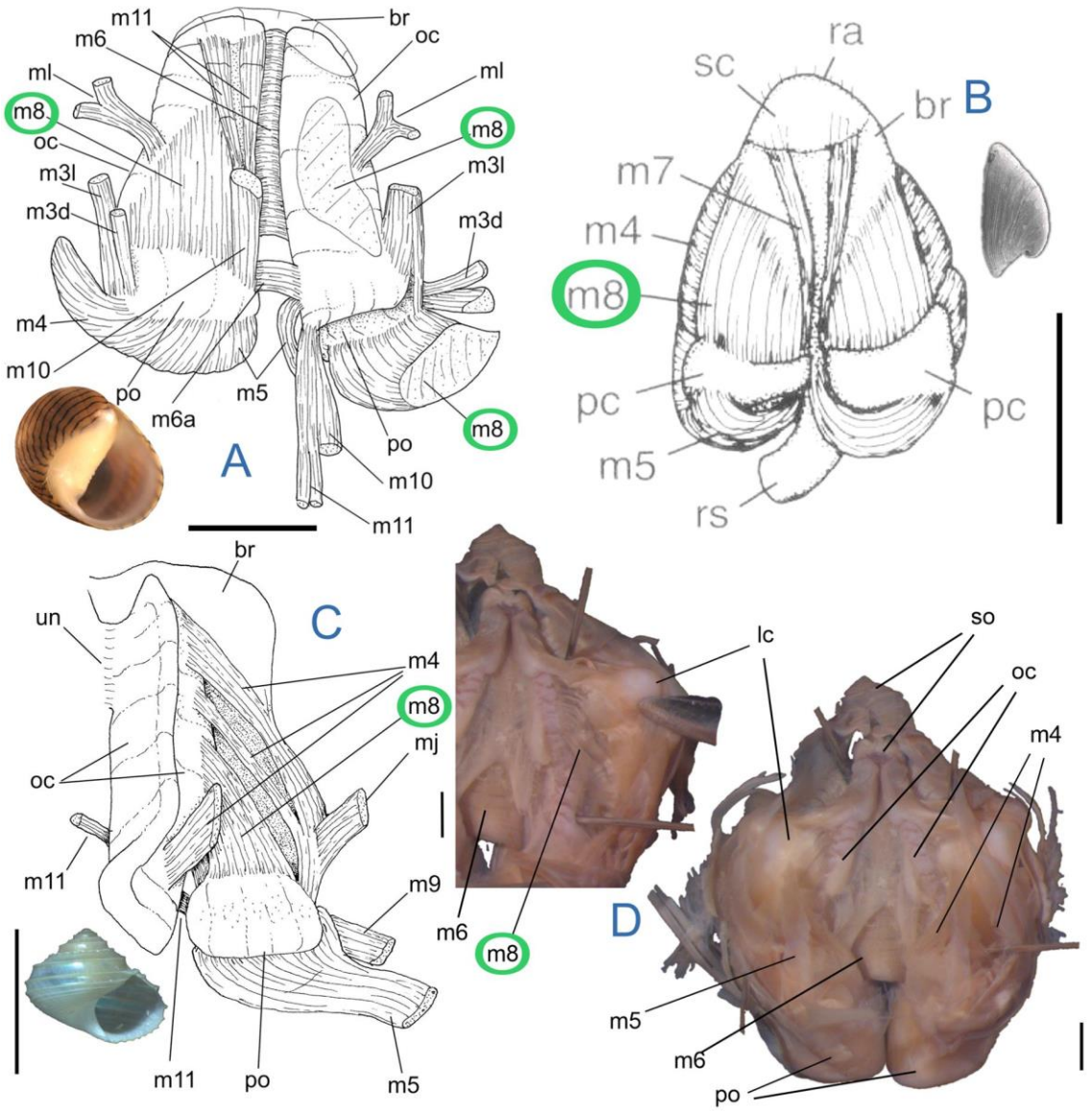
Each corresponding anterior–posterior cartilage pair possesses an m8 muscle connecting them (Fig. 1: m8). For this reason, this muscle is termed the cartilage approximator, as its contraction brings the two cartilages closer together.

The evolution of the m8 pair from basal to more derived gastropods remains unclear. As higher gastropods, i.e., the Apogastropoda, possess only the structure homologous to the anterior pair of odontophore cartilages, two possibilities arise, as discussed elsewhere (Simone, 2011).

The first is the loss or atrophy of the posterior cartilages and, consequently, of the m8 pair and other associated structures. The second explanation, which appears more plausible, is the fusion of the posterior cartilages with the posterior region of the anterior cartilages. This would result in the incorporation of the m8 pair into the m4 pair. Under this hypothesis, the m8 pair did not disappear but instead became part of the larger m4 musculature.

This second interpretation is favored because it also explains the positional relationships of the m4 and m5 pairs: in basal gastropods, these muscles are attached to the posterior cartilages, whereas in more derived gastropods they are attached to the posterior region of the anterior (and single) cartilages. Furthermore, as noted above, partial to complete fusion between anterior and posterior cartilages is not uncommon in some groups within the four most basal clades, suggesting that this may be a recurrent evolutionary pattern (e.g., *Propilidium curumim*, a patellogastropod, possesses a single pair of cartilages—Leal & Simone, 1998).

As no other molluscan group possesses more than one pair of odontophore cartilages, the condition of two pairs is regarded as a synapomorphy of Gastropoda (Simone, 2011), retained in the four basal clades of the class mentioned above. A reversion to a single pair of cartilages occurs

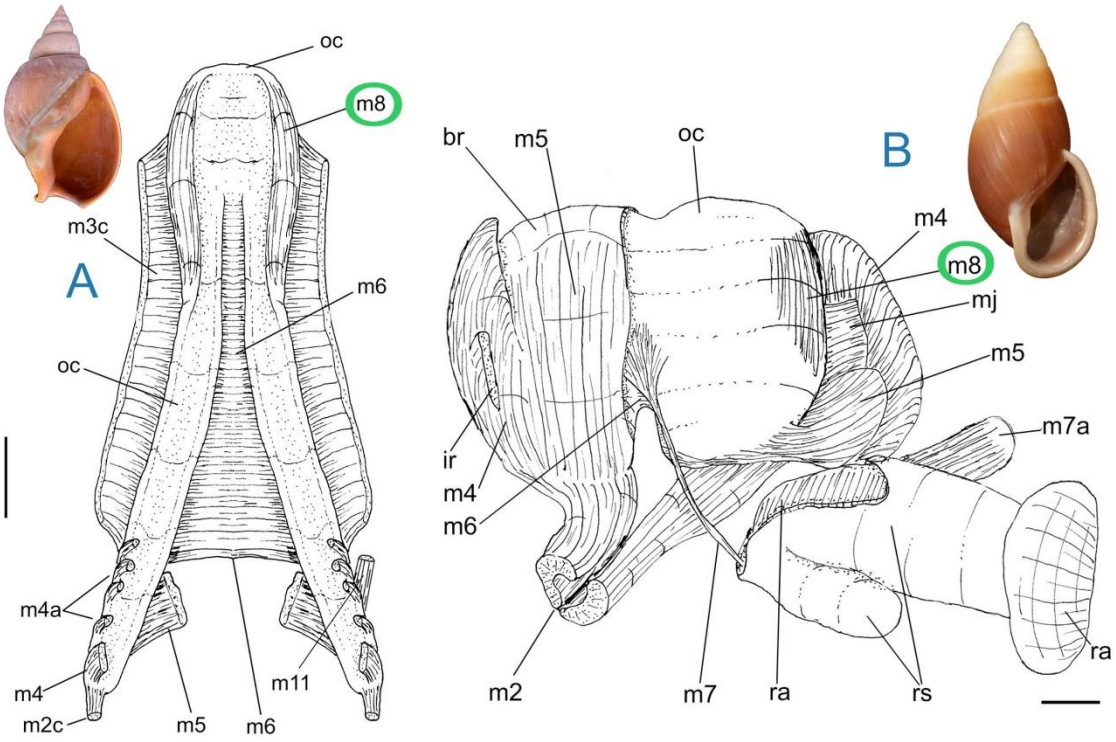


2. Examples of intrinsic odontophore cartilages muscles – m8 – in archaeogastropods. A, *Vitta zebra* (Neritimorpha, Neritidae) odontophore, dorsal view, both anterior cartilages slightly deflected, right structures partially removed and deflected (mainly m8) in order to show inner structures, scale= 1 mm, shell CMPHRM 2673 (W 18 mm) (from Barros et al., 2012); B, *Copulabyssia riosi* (Cocculiniformia, Pseudococculinidae) odontophore, ventral view, superficial layer of muscles and membranes partially removed, scale= 0.5 mm, shell MZSP 32150 (L 3 mm) (from Leal & Simone, 2000); C, *Vaninia imperialis* (Vetigastropoda, Calliostomatidae) odontophore, detail of right side with anterior cartilage deflected upward, separated from posterior cartilage to show intrinsic muscle origins and insertions, scale = 1 mm, shell MZSP 36783 (W 10 mm) (from Simone & Dornellas, 2026); D, *Nacella concinna* (Patellogastropoda, Nacellidae) odontophore, dorsal view, superficial layer of structures removed, both cartilages deflected, radula removed, left image with m4 further deflected to right for exposing m8, scales= 1 mm. Lettering: br, subradular membrane; lc, lateral extra cartilage; m1-m11, intrinsic and extrinsic odontophore muscles; mj, jaws and peribuccal muscles; ml, longitudinal muscle; oc, odontophore anterior cartilage; pc-po, posterior odontophore cartilage; ra, radula; rs, radular sac; sc, subradular cartilage; so, sublingual organ; un, connection between both anterior cartilages.

in Apogastropoda and, as far as is known, is not reversed, although some lineages have completely lost the odontophore.

The m8 pair, functioning as an approximator between the anterior and posterior cartilages, is therefore considered a basal feature of Gastropoda. This muscle pair was possibly incorporated into the m4 pair following the probable fusion of the posterior cartilages, as discussed above.

Pair m8 in the outer edge of the cartilages



3. Examples of intrinsic odontophore cartilages muscles – m8 – in outer cartilage edges. A, *Buccinanops cochlidium* (Neogastropoda, Buccinanopsidae) odontophore cartilages, dorsal view, most intrinsic muscle partially removed, showing only their origin and some adjacent muscles, scale= 2 mm, shell MZSP (L 83 mm) (from Pastorino & Simone, 2021); B, *Kora corallina* (Eupulmonata, Bulimulidae) odontophore, dorsal view, radula removed and deflected downwards (m7a, located inside radular sac, slightly deflected), left muscles as in situ, right muscles deflected externally, scale= 1 mm, shell holotype MZSP 103910 (L 43 mm) (from Simone, 2024). Lettering: br, subradular membrane; ir, insertion of m4 in radular sac; m1-m8, intrinsic and extrinsic odontophore muscles; mj, jaws and peribuccal muscles; oc, odontophore anterior cartilage; ra, radula; rs, radular sac.

This type of m8 is rarer and its functional interpretation is less clear. It occurs in some Neogastropoda and appears to be a synapomorphy of Buccinoidea. In this taxon, the odontophore is often highly modified and typically elongated; the cartilages are slender and widely fused anteriorly (Fig. 3A).

The m8 pair is located along the free edge of the anterior region of the cartilages, adjacent to the fused portion (Fig. 3A). Its function remains uncertain. As the muscle fibers run longitudinally along the edges, their contraction may cause this region of the cartilages to arch. So far, all buccinoideans examined in detail with respect to the odontophore possess the m8 pair.

Another taxon exhibiting similar modifications of the odontophore is Volutoidea. It is possible that Buccinoidea and Volutoidea together form a single clade within Neogastropoda; however, too few volutoideans have been anatomically studied to confirm this hypothesis. Likewise, it remains uncertain whether the presence of the m8 pair is as widespread in Volutoidea as it is in Buccinoidea.

At least one volutoidean species, *Volvarina tripartita*, has been reported to possess an m8 pair (Souza & Simone, 2019), but its occurrence in other members of the group remains unclear.

Surprisingly, a similar m8 pair has been identified in the unrelated eupulmonate genus *Kora* (Orthalicoidea, Bulimulidae) (Fig. 3B). To date, *Kora* is the only pulmonate known to exhibit

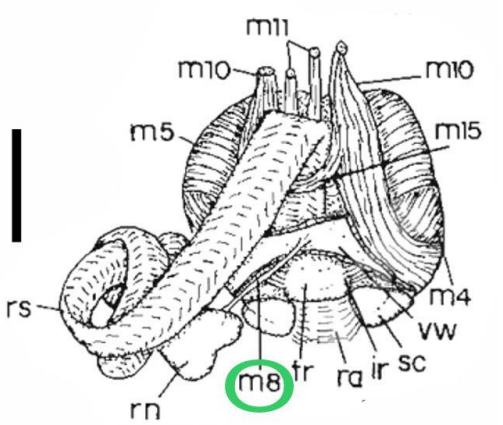
this condition. As the location and arrangement of the fibers are analogous to those of the neogastropod m8, the function of these muscles may be similar. However, they are certainly not homologous between the two groups.

Muscle m8 of some Cerithioidea branches

In early studies of the molluscan odontophore, a muscle occurring in some cerithioidean lineages was designated as m8 (Simone, 2001, 2011). However, this cerithioidean "m8" does not conform to the definition adopted in the present study.

First, it is unpaired, typically narrow and slender. Second, it is not associated with the odontophore cartilages; instead, it lies on the outer surface of the odontophore, connecting its dorsoposterior region to the radular nucleus at the tip of the radular sac, which is usually long and coiled in these animals (Fig. 4: m8).

This cerithioidean "m8" is a synapomorphy of certain internal lineages within the superfamily and exhibits additional modifications. It appears to represent a modification of a local vessel that typically irrigates the radular nucleus, a structure commonly present in many mollusks.



4. Example of cerithioidean model of m8. *Doryssa ipupiara* (Cerithioidea, Pachychilidae) odontophore with first layer of muscles and membranes partially extracted, dorsal view, scale= 1 mm (from Simone, 2001). Lettering: ir, insertion of m4 in radular sac; m1-m15, intrinsic and extrinsic odontophore muscles; ra, radula; rn, radular nucleus; rs, radular sac, tr, tissue on middle region of radula, vw, dorso-posterior surface of buccal mass.

As a region of intense cellular activity, the radular nucleus requires substantial oxygenation and nutrient supply to perform its fundamental role in the formation of radular teeth. Accordingly, a specialized vessel is directed to this region. However, in mollusks it is not uncommon for vessels to acquire muscularization, and in some cases their contractile function becomes more prominent than their original circulatory role. This seems to be the case for the cerithioidean "m8" (Simone, 2001, 2011).

In the comprehensive phylogenetic analysis of Caenogastropoda (Simone, 2011), m8 features were coded under both interpretations: as an intrinsic structure of the odontophore cartilages (e.g., p. 193) and as part of the organization of certain internal lineages of Cerithioidea (p. 253; characters 375, 376). Both interpretations are relevant for phylogenetic inference and support several clades, as do other odontophore structures.

This highlights the critical importance of studying the odontophore—a structure that is all too often destroyed or dissolved during radula extraction, resulting in the irreversible loss of valuable anatomical and phylogenetic information.

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