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The molluscan jugal muscles – m1

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Abstract

Jugal muscles in Mollusca are a net of minute fibers that maintain the organs in their correct place inside the haemocoel, an important issue for contracting organisms. The haemocoel is the main cavity in the mollusks, as the celomatic cavity is restricted to the reno-pericardial region, the place in which the structures, when present, are hidden by the peritoneum. Jugal muscles can hypertrophy and become distinct pair of muscles (m1), mainly as protractor and retractor muscles of buccal mass, characterized by insertions in the surface of the organs. They can also originate transverse muscles (tm) in bivalves, which help in hydrostatic digging mechanism.

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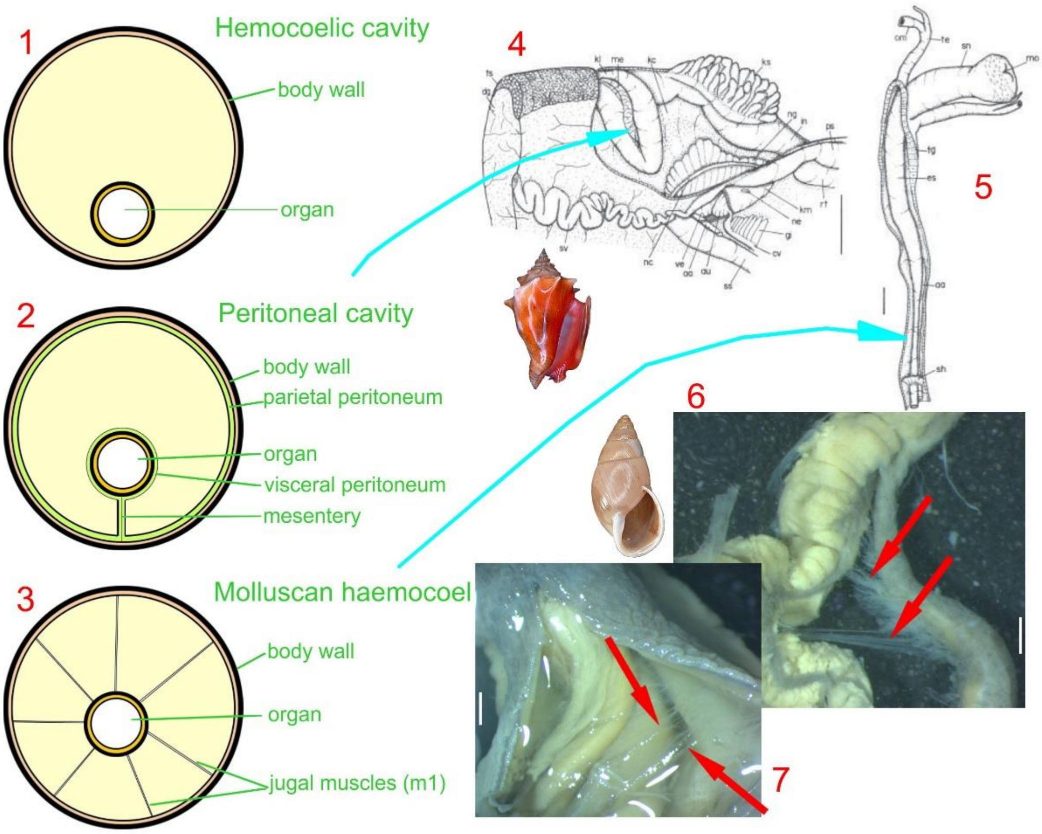
Introduction

The so-called **jugal muscles** in Mollusca differ from those present in other zoological branches. In vertebrates, for example, jugal muscles have origin in cranial jugal bones, that originate the zygomatic bones in mammals; in insects, in another example, jugal muscles are related to forewings. In mollusks, however, the current literature usually calls jugal muscles a tridimensional net of muscles that connect the organs lying in the haemocoel cavity with the adjacent inner walls of the haemocoel, and the organs to each other (Simone, 2011). This net of jugal muscles is less (e.g., aplacophorans) to very (e.g., higher conchiferans) dense, but present in all mollusks, and its main function is maintaining the haemocoelic organs in their correct place both, in activity and contracted phases, and, mainly, during retraction. Otherwise, if it weren't for the jugal muscles, the retraction would cause a truly chaos in the internal organs, causing denting, tearing and damages.



1-7. Explanations on zoological somatic cavities, left schematic representations of transverse sections of the body, right actual examples in gastropods. 1, a typical hemocoel, with internal organs not connected of, e.g., aschelminth worms; **2**, a typical peritoneal cavity of triploblastic metazoans, showing the peritoneum and its components holding the internal organs; **3**, the hemocoel region of a generic mollusk with internal organ held by the jugal muscles (m1); **4**, *Strombus pugilis* shell (L ~50 mm) and anterior region of visceral mass, ventral view, ventral wall of kidney sectioned along its left edge and deflected to right (superior in Fig.), a true peritoneal (celomatic) cavity, scale= 5 mm; **5**, same, detail of head-foot, ventral view, foot and columellar muscle removed, showing haemocoel, scale= 5 mm (both from Simone, 2005); **6**, *Kora* sp 151817, m1 between spermoviduct and duct of bursa, scale= 1 mm, 7, *Kora rupestris*, shell (L ~40 m), MZSP 151890, anterior region of head foot, opened dorsally, integument just opened, scale= 1 mm, both Figs with some jugal muscles indicated by red arrows. Lettering: aa, anterior aorta; au, auricle; cv, ctenidial vein; dg, digestive gland; es, esophagus; gi, gill; in, intestine; kc, kidney chamber; ki, kidney; km, kidney membrane; me, mesentery; mo, mouth; nc, nephridial vessel; ne, nephrostome; ng, nephridial gland; om, ommatophore; ps, prostate; rt, rectum; sh, diaphragmatic septum; ss, style sac; te, cephalic tentacle; tg, integument; ts, testis; ve, ventricle.

Before we go further, it is important to explain that there are 2 kinds of cavities in metazoans: 1) the haemocoelic cavity, and 2) the peritoneal or celomatic cavity:

Haemocoelic cavity

The classic haemocoelic cavity is that of the aschelminths, also known as pseudocoelom (Fig. 1). This cavity is usually hollow, fulfilled by blood, from which the name derivates – as haemocoel literally means "cell of blood" – and the internal organs run "free" inside, i.e., they are not connected with the surrounding structures.

Peritoneal or celomatic cavity

This is similar to the haemocoelic cavity, but the peritoneum is present. The peritoneum (Fig. 2) is a membrane of mesoderm origin that surrounds everything inside the cavity. Its portion surrounding the cavity walls themselves is called parietal peritoneum, while the remaining portions, surrounding the internal organs, are the visceral peritoneum. Its connection between both, parietal and visceral peritoneum is known as mesentery. The embryological formation of a celomatic cavity is complex, and beyond the scope of this text. But it is considerably more complex than a haemocoelic cavity, and is present in all higher metazoans, including mollusks, annelids, arthropods and vertebrates.

The case of the Mollusca

The mollusks are special. They have, in general, both, a celomatic and a large haemocoelic cavities. The molluscan celomatic cavity is restricted to the reno-pericardial region, which usually is not large in most mollusks. However, if it is large, and has intestinal loops inside, the peritoneal nature of it clearly appears. An example are the strombids (Fig. 4), the large intestinal loop inside the renal chamber (kc) is covered by a visceral peritoneum, even including a vascularized mesentery (me).

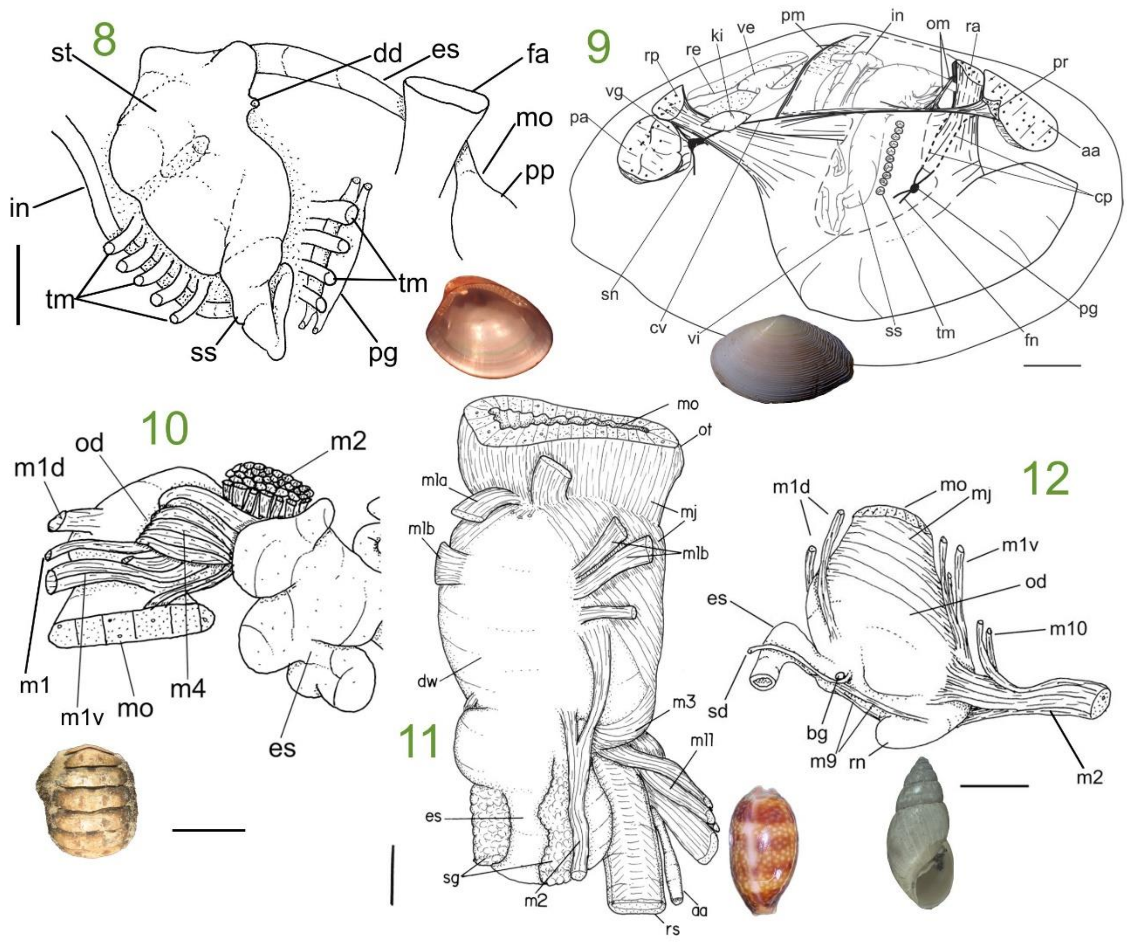
Except for the reno-pericardial region, the remaining hollow regions of the mollusks' bodies are haemocoels. The more conspicuous haemocoel is adjacent to the foot, which is usually simply called "haemocoel" in the molluscan jargon, especially in the gastropod head-foot. However, different from other haemocoels found in other more basal metazoan fila, the organs held inside the Mollusca haemocoel are not "free", on the contrary, as referred above, they are all connected with neighboring structures by the tridimensional net of jugal muscles (m1) (Figs. 3, 6, 7).

The haemocoel of other fila constituents are usually more rigid, i.e., non-contractile. However, mollusks are mostly contractile creatures. The contraction usually is a protective movement, and it must be efficient and quick. For that, as also referred above, one of the problems is the internal organs lying inside the cavities. In a quick retraction, the internal organs can be dented, torn and damaged both, by the muscles and by themselves. If the cavity was celomatic, the internal organization of the organs, and the consequent damage protection, should be provided by the peritoneum. However, as the main mollusk cavity is haemocoelic, the molluscan evolutionary solution was the jugal muscles (m1). The jugal muscles are poorly developed in the 3 aculiferan classes and in the monophacophorans, as they are not great contractors of the entire body. But, in the Euconchifera (non-monophacophoran cochiferans), which are highly contractile animals, the jugal muscles are much more developed (Figs. 3, 6, 7).

Thus, during the retraction of the molluscan body, the animal does not only contract the retractor muscles of the body walls, but also it performs an elaborate wave of retraction of the jugal muscles in order of the internal organs maintain an optimum position, and their functionality, even in retracted condition. This is easily deduced by dissecting retracted animals; all the internal organs are in the almost exact same position inside the haemocoel in all specimens of a same species. As much that details of the organization of the internal organs can be used as taxonomic characters to differentiate taxa in morphological studies.

Specializations of jugal muscles (m1)

The usual style of the jugal muscles (m1) conformation is of a scanty to dense tridimensional net of tiny muscular fibers (Figs. 6-7), sometimes difficult to visualize, which break with



8-12. Examples of specialized jugal muscles (m1, tm) in different mollusk classes, dissected structure (drawing) and a shell: 8, *Ennucula pulchella* (bivalve, nuculid), midgut and adjacent structures as in situ, right view, scale= 1 mm, shell MZSP 19101 (L 13 mm) (from Simone, 2009); **9**, *Phyllodina persica* (bivalve, tellinid), topology of visceral structures, pericardial region, main muscle system and central nervous system, right view, scale- 1.5 mm, shell MZSP 96780 (L 25 mm) (from Marques & Simone, 2013); **10**, *Acanthopleura gemmata* (polyplacophoran, chitonid), foregut, left view, scale= 2 mm, shell MZSP 54475 (L 30 mm) (from Jardim et al., 2020); **11**, *Macrocypraea zebra* (gastropod, cypraeid), buccal mass, dorsal-slightly lateral-right view, radular sac only partially shown, scale= 2 mm, shell MZSP (L 80 mm) (from Simone, 2004); **12**, *Bulimulus sula* (gastropod, bulimulid), buccal mass, right view, scale= 1 mm, shell MZSP 134374 (L 19 mm) (from Simone & Amaral, 2018). Lettering: aa, anterior aorta or anterior adductor muscle; bg, buccal ganglion; cp, cerebro-pedal connective; cv, cerebro-visceral connective; dd, duct to digestive diverticula; dw, dorsal wall of buccal mass; es, esophagus; fa, anterior pedal retractor muscle; fn, pedal nerve; in, intestine; ki, kidney; m1, jugal muscles; m2-m10, extrinsic and intrinsic odontophore muscles; mj, jaw and peribuccal muscles; mo, mouth; od, odontophore; om, oblique protractor muscle; ot, oral tube; pa, posterior adductor muscle; pg, pedal ganglia; pm, posterior transverse muscle; pp, palps; pr, foot protractor muscle; ra, anterior pedal retractor muscle; re, rectum; rn, radular nucleus; rp, posterior pedal retractor muscle; rs, radular sac; sd, salivary duct; sg, salivary gland; sn, siphonal nerve; ss, style sac; st, stomach; tm, transverse muscles; ve, ventricle; vg, visceral ganglia; vi, visceral sac.

simple manipulation. However, as everything in Biology, specializations can appear, and some hypertrophy of a given set of fibers happens. These specializations cause the appearance of a developed muscle inside haemocoel, mostly in pairs, connecting an organ or structure to the internal haemocoelic wall, or the organs with each other. From the diverse hypertrophied jugal muscles found in mollusks, two kinds are selected as examples to be explored herein: the bivalve transverse muscles in visceral sac (Figs. 8, 9: tm), and the m1 pairs related to the buccal mass (Figs. 10-12). A given muscle present in haemocoel can be called as “jugal” as long as it is inserted in the surface of the organ; if, on the contrary, it goes further, penetrating inside the structure, it is not “jugal”, but something else. Thus, to be classified as “jugal”, a muscle, or mostly a pair of muscles, must be inserted to the surface of the organ; its origin can be both, the surface of other organs or the inner surface of the haemocoel.

The **bivalve transverse muscles** in visceral sac (Figs. 8, 9: tm): they are particularly well-developed in digger taxa, in which the foot must be introduced inside the sediment. For that, the visceral sac at the foot base works as a hydrostatic reservoir, its contraction propels the blood to the foot as a piston. In digger forms, the transverse muscles (tm) are reinforcement structures to this digging mechanism. The transverse muscles are connected inside the haemocoelic walls and run straight from side by side, passing through all visceral structures, like gonad, digestive diverticula and intestinal loops. In some taxa, e.g., they can be clustered in a given region, like surrounding stomach in nuculids (Fig. 8), or aligned anterior to it in *Phyllodina* tellinid (Fig. 9).

The **buccal mass jugal muscles** (Figs. 10-12: m1) are another usual specialization of jugal muscles, obviously present in the taxa that possess buccal mass, odontophore and radula. Different from other extrinsic and intrinsic buccal mass and odontophore muscles, the jugal muscles (m1), as above mentioned, always insert in the surface of the buccal mass, neve penetrating inside it.

Usually, the most common m1 specializations are as buccal mass protractors and retractors. They are protractor muscles when their origin is more anterior than their insertions; and, on the contrary, they are retractor muscles when their origins are more posterior than their insertions on the buccal mass.

They usually are named according to their position in the buccal mass. If they are lateral, they are named as “m1l” (l of lateral). If they are ventral, they are named as “m1v” (Figs, 10, 12), and if dorsal, as “m1d” (Figs. 10, 12). However, in some cases in which there are several m1 pairs, they are merely named “m1a”, “m1b”, etc. (Fig. 11).

The m1 pairs in buccal mass are relatively uniform in a same species, but they are of great importance to be compared among species, as they have reasonable interspecific variation. Thus, they are a good source of taxonomic and phylogenetic data. This is different from other buccal and odontophore muscles, which usually are relatively uniform in closely related species.

References

Jardim, JA; Almeida, SM & Simone, LRL, 2020. Towards understanding a confusing and widespread species: an anatomical study of *Acanthopleura gemmata* (Polyplacophora, Chitonidae) from Thailand. Strombus 26(1-2): 1-14.

Marques, RC & Simone LRL, 2013. Anatomy of *Phyllodina persica* (Bivalvia: Tellinidae), and its first occurrence in southeastern Brazilian waters. Papéis Avulsos de Zoologia 53(9): 115-127.

Simone, LRL, 2004. Morphology and phylogeny of the Cypraeoidea Mollusca, Caenogastropoda. Papel Virtual. Rio de Janeiro, 185 pp. http://www.moluscos.org/trabalhos/2004/Simone%202004%20-%20Cypraeoidea.pdf

Simone, LRL, 2005. Comparative morphological study of representatives of the three families of Stromboidea and the Xenophoroidea (Mollusca, Caenogastropoda), with an assessment of their phylogeny. Arquivos de Zoologia 37(2): 141-267. http://www.moluscos.org/trabalhos/2005/Simone%202005-Stromboidea.pdf

Simone, LRL, 2009. Comparative morphology among representatives of main taxa of Scaphopoda and basal protobranch Bivalvia (Mollusca). Papéis Avulsos de Zoologia 49(32): 405-457. http://www.moluscos.org/trabalhos/2009/Simone%202009%20Diasoma.pdf

Simone, LRL, 2011. Phylogeny of the Caenogastropoda (Mollusca), based on comparative morphology. Arquivos de Zoologia 42(4): 161-323. http://www.moluscos.org/trabalhos/Caenogastro/Simone%202011a%20Caenogastropoda%20Phylogeny%20LIGHT.pdf

Simone, LRL & Amaral, VS, 2018. Insular life: new endemic species from São Paulo oceanic islands, Brazil (Pulmonata, Bulimulidae), as example of endemicity. Journal of Conchology 43(7): 167-187.