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Modifications in adductor muscles in bivalves

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Abstract

The bivalve adductor muscles are responsible for the shell closure, with the ligament as its antagonist. The possible evolution of this muscle from foot retractor is suggested. The modification of the adductor muscles are also explored, mainly the isomyarian, anisomyarian and monomyarian conditions, including functional, taxonomical and phylogenetical implications, being this a possible evolutionary line. Further modifications of the muscles are also discussed, as division, change of location and function, and appearance of secondary adductors.

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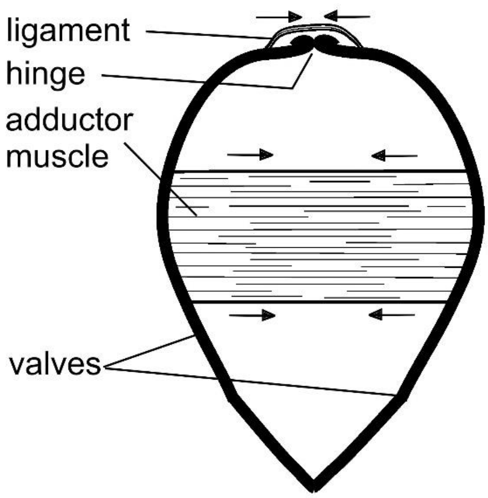
Keywords: adduction, abduction, Bivalvia, main musculature, evolution.

Introduction

Every bivalvia have adductor muscle(s), responsible for the adduction movement, i.e., the closure of the valves. Adductor muscles are attached to both valves, in order to provide their approach during contraction. They are strategically positioned in order to provide the best and quick power for valve's closure.

The Fig. 1 shows a scheme representing the valves (thick lines) and the forces exerced in them by the adductor muscle and the ligament. The



1. Schematic representation of a generic bivalve, a transverse axial section in level of adductor muscle. Arrows show the force done by the ligament and by the muscle, articulating at hinge.

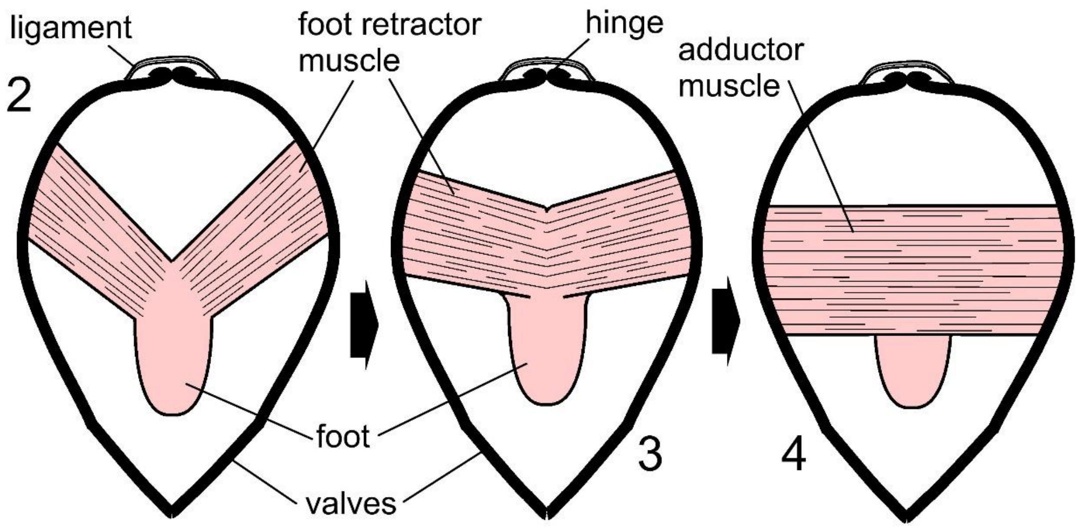
scheme shows that the antagonistic of the adductor muscle is the ligament, i.e., there is no "abductor muscle", this function is done by the ligament.

The ligament features, function, characters and evolution will be goals of future papers. Presently the more important information is that the ligament and adductor muscles compose a system of transferece of elastic energy, as the contraction of the adductor muscle creates tension at the ligament, that gets contracted (internal ligament) or distended (external one). When the adductor muscle relaxes the valves open (or abduct, or diduct) by means of the ligament, articulating in the hinge and distending the adductor muscle (Fig. 1).

The adductor muscles origins, as well as plethora of this muscle's modifications and adaptations, can be traced using the registered bivalves evolution. Some of these ideas are explored in the present paper.

Origin of bivalve adductor muscles

Mostly probably the adductor muscles are originated from pairs of foot retractor muscles. Foot retractor muscles, in all mollusks, usually are attached to the shell and have their insertion

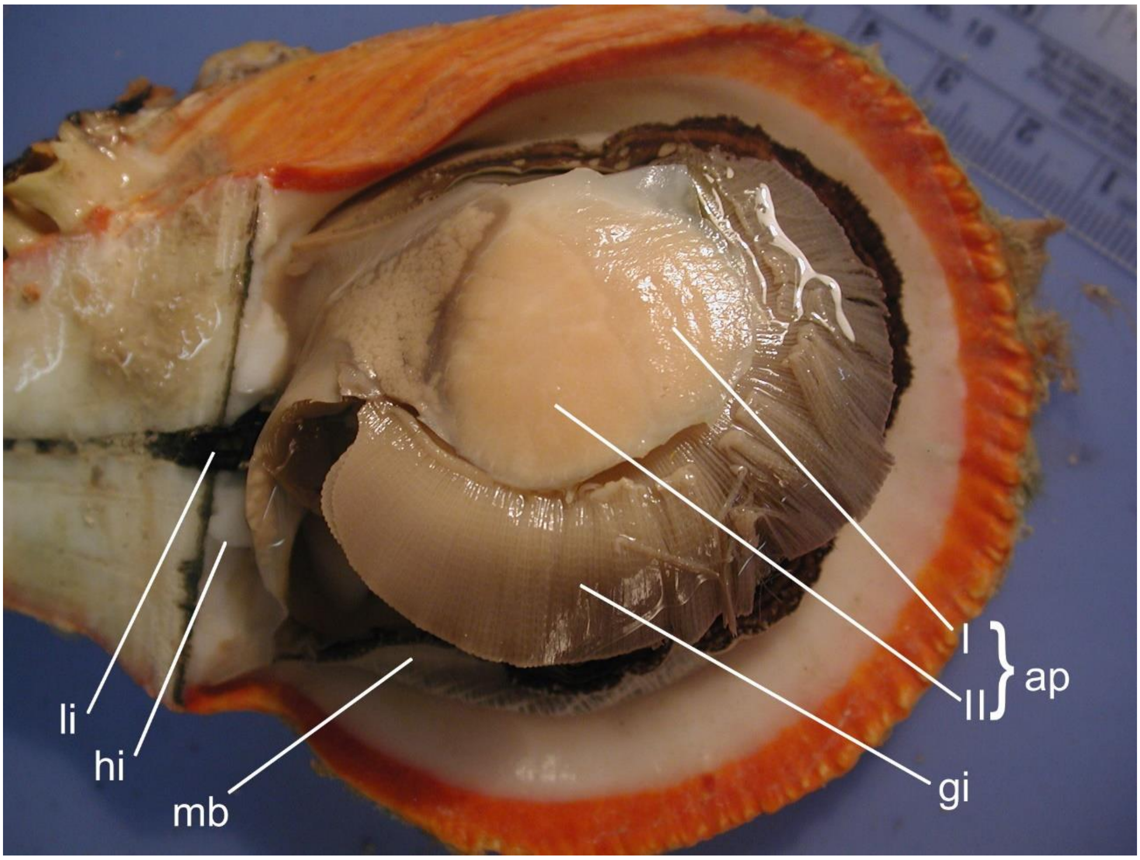


2-4. Possible evolution of the adductor muscles. **2**, transverse axial section in a hypothetical ancestor in level of anterior or posterior pair of foot retractor muscles, both still in a V-shape; **3**, same for an intermediary form, in such pair of muscles is becoming almost straight; **4**, a true adductor muscle derived from straightened pair of anterior or posterior foot retractor pair. Not to scales or proportions.

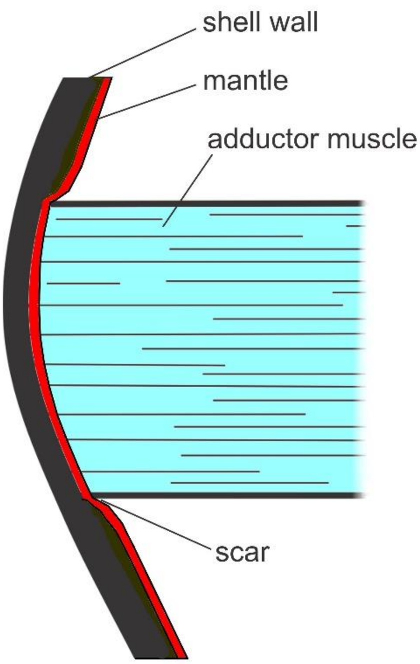
along the foot base (Figs. 2-3), in order to retract the foot inside the shell. As the bivalves are usually laterally flattened, and with the articulation of the hinge (which needs to be free of muscle insertions), the foot retractors became more and more lateralized and widely separated. Certainly, lateralized origins of both retractor muscles produced a more aligned and straightened pattern of the pair (Fig. 3), which could be also used for valves' adduction (closure). From this model to a true adductor muscle looks a simple step, with the previous pair totally straightened, working as a single muscular bundle (Fig. 4).

Despite any embryological approach can prove this scenario, it is more plausible observing some bivalve taxa, such as, e.g., Anomiidae (Fig. 20), in such some foot retractor muscles effectively work in the valve's closure, being a clue for this speculation.

Adductor muscles details



5. *Spondylus americanus* (from Florida). Right view, right valve and right mantle lobe removed to show adductor muscle and pallial structures. Lettering: **ap**, posterior adductor muscle and its two components I (quick) and II (slow); **gi**, gill; **hi**, hinge; **li**, ligament; **mb**, mantle border.

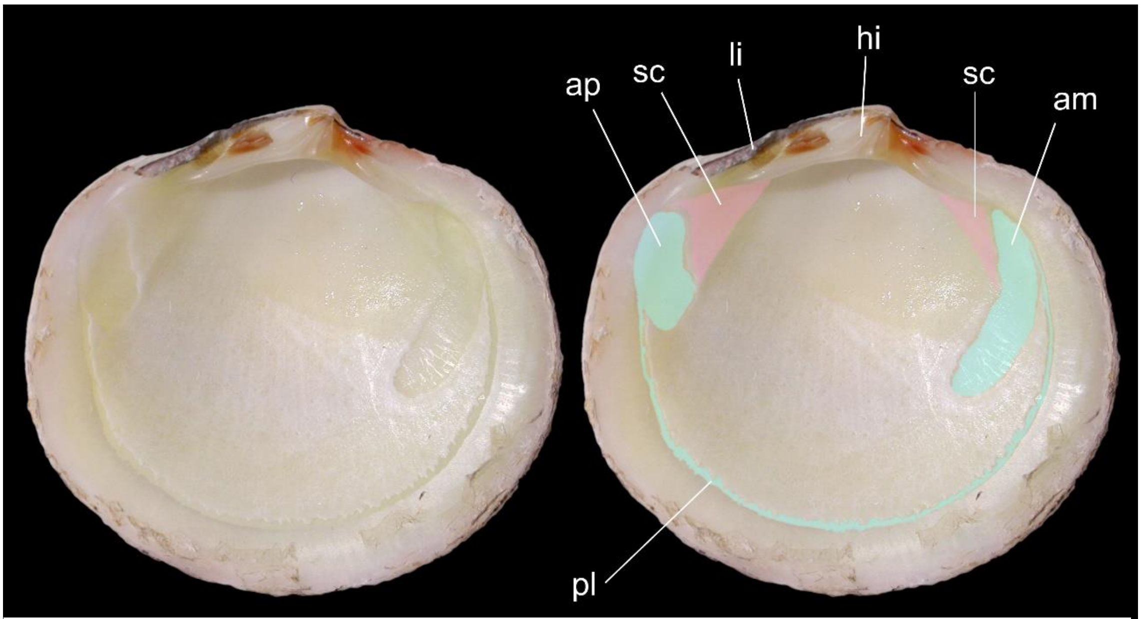


The adductor muscles usually have two components, which usually can easily identified as two different textures (Fig. 5: ap I and II). They are the quick and slow components. The quick component is a part of the muscle usually in dark color, which contracts quickly, closing the valves in an emergency. The quick component is rapid, but it is not strong. A strong grip is performed by the slow component, which takes some time to contract, but it is more powerful to maintain both valves strongly closed, usually with a light and opaque texture.

There is no evidence of two components in the adductor muscles of the protobranchs. Possibly the adductor division into two components is another synapomorphy of the lamellibranch (i.e., non-protobranch) bivalves (Simone, 2009).

6. Schematic representation of adductor muscle attachment. Detail of connection of the muscle with the shell, artificially colored. Only one side shown.

Checking the details of the adductor muscle structure, it is easy to see its origin connected directly to the shell. However, as the shell must be constructed to grow, a small portion of the mantle is interposed between the muscle and the shell. As this region of the mantle must be thin, and as the constant contraction of the muscle precludes the mantle metabolism, the shell wall just in the region of the muscle connection usually is thinner, with an excavated aspect, than the adjacent areas (Fig. 6). This specific mark caused by muscular insertion in the shell wall is called **scar**. The muscular scars in the inner surface of the bivalve shell usually are evident, and a useful taxonomical tool. Although, muscular scars can be almost invisible in small or thin-walled bivalves.

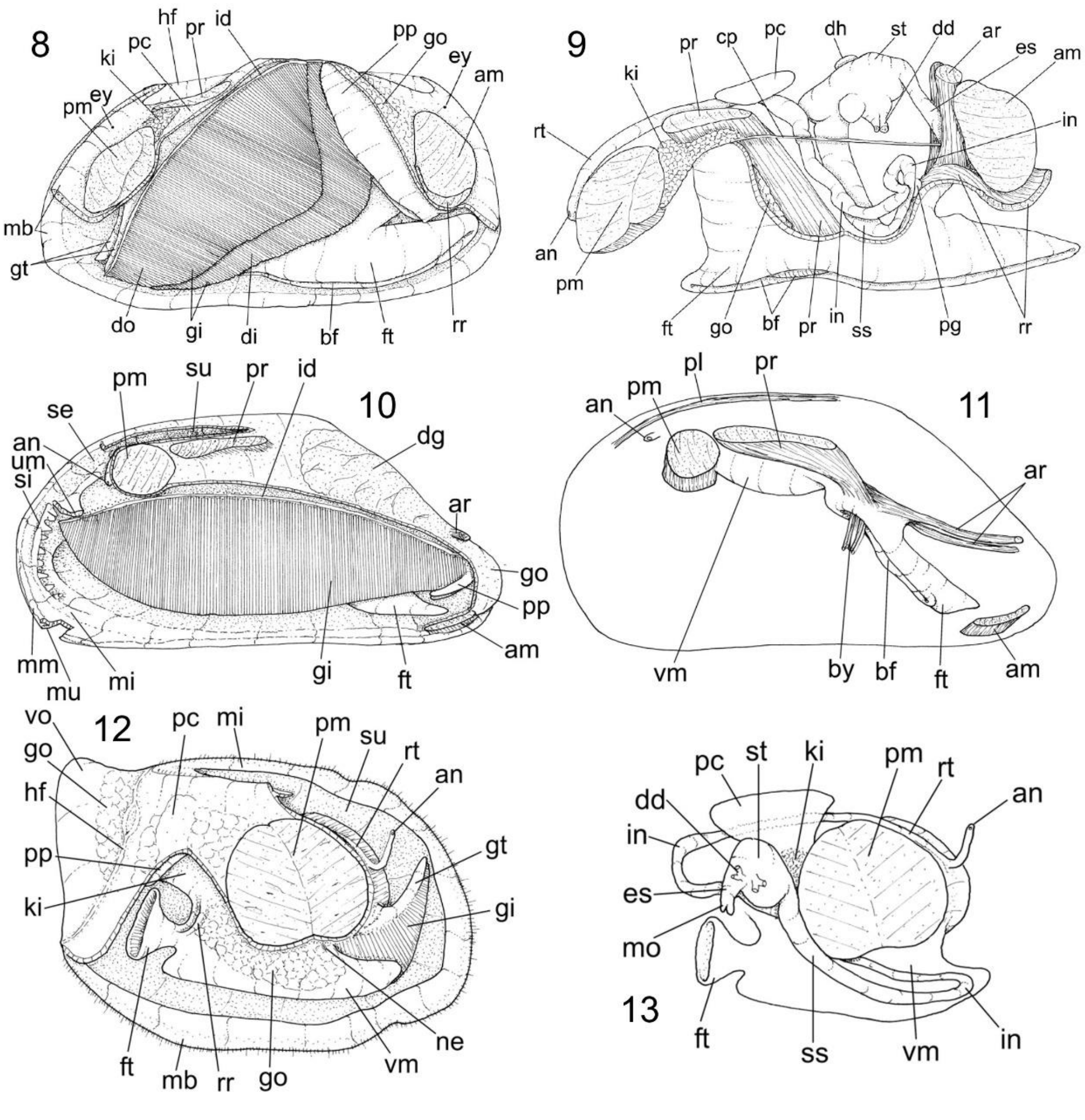


7. *Codakia orbicularis* (from Florida). Left valve, inner view. Right image with main muscle scars painted green and scars of previous allocations of the adductor muscles painted pink. Lettering: **am**, anterior adductor muscle; **ap**, posterior adductor muscle; **hi**, hinge; **li**, ligament; **pl**, pallial line; **sc**, scar of previous allocations of adductor muscles, done during growth.

The Fig. 7 shows an example of an inner view of a valve with typical muscular scars in a bivalve (they are painted in the right image). The main visible scars are from the adductor muscles, the anterior (am) and the posterior (ap) (Fig. 7), and the pallial line (pl), which are composed of multiple small scars of the insertions of the pallial muscles. These muscles are responsible for the retraction of the mantle border inside the shell. A small portion of the adductor muscles' scars edges the foot retractors scars can be present, almost fused to the adductors or slightly separated. In several bivalves, scars of previous positions of the adductor muscles are also possible to be seen (Fig. 7: sc). They show regions in such the adductor muscles were attached when the specimen was smaller. Obviously, they are successively smaller and smaller towards umbos, forming a rather triangular shape.

Dimyarian and monomyarian bivalves

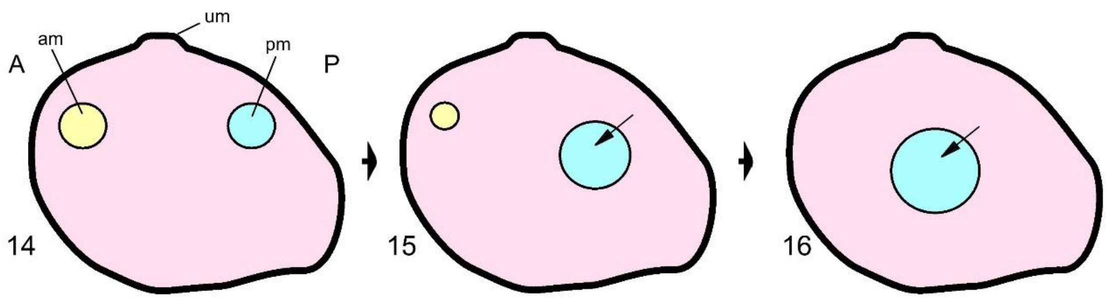
The basal condition of the class Bivalvia is to be **dimyarian**, possessing a pair of adductor muscles, an anterior muscle and a posterior one, strategically located in order to permit the articulation of the hinge, being antagonized by the ligament (responsible for the valves' abduction). All protobranchs are dimyarian. Several lamellibranchs, however, became **monomyarian**, i.e., a single adductor muscle is present. In the case of the monomyarian taxa, always the posterior adductor muscle is preserved, and the anterior muscle is lost. Of course, there are lots of taxa that have the



8-13. Anatomical drawing of some bivalves as example of different adductor muscles' size and number (all from Simone et al, 2015). Left column specimen just removed from shell with mantle lobe removed; right column figures with focus in main muscular system and some adjacent structures. **8-9**, *Arcopsis adamsi*, right view (L~15 mm); **10-11**, *Brachidontes exustus*, right view (L ~20 mm); **12-13**, *Spondylus americanus*, left view (L ~50 mm). Lettering: **am**, anterior adductor muscle; **an**, anus; **ar**, anterior foot retractor muscle; **bf**, byssal furrow; **by** byssus; **cp**, cerebrovisceral connective; **dd**, duct to digestive diverticula; **dg** digestive diverticula; **dh**, dorsal hood; **di**, inner demibranch; **do**, outer demibranch; **es**, esophagus; **ey**, pallial eye; **ft**, foot; **gi**, gill; **go**, gonad; **gt**, gill suspensory stalk; **hf**, hinge fold of mantle; **id**, insertion of outer demibranch in mantle; **in**, intestine; **ki**, kidney; **mb**, mantle border; **mi**, mantle border inner fold; **mm**, mantle border middle fold; **mo**, mouth; **mu**, mantle border outer fold; **ne**, nephropore; **pc** pericardium; **pg**, pedal ganglion; **pl**, pallial muscles; **pm**, posterior adductor muscle; **pp**, palps; **pr**, posterior pedal retractor muscle; **rr**, pedal protractor muscle; **rt**, rectum; **se**, excurrent aperture; **si**, incurrent aperture; **ss**, style sac; **st**, stomach; **su**, supra-anal chamber; **um**, fusion between left and right mantle lobes; **vm**, visceral mass; **vo**, mantle portion occupying umbonal cavity

intermediary condition, the so called **anisomyarian**, i.e., non-equal pair of muscles holders, in apposition to the **isomyarian** bivalves, which have both muscles of equal or of similar size. The anisomyarian bivalves have the anterior adductor muscle (am) clearly smaller than the posterior one (pm) (Figs. 10-11).

Observing the allocation of the monomyarian bivalves in some phylogenies, they mostly are preceded by anisomyarian taxa. Then, possibly the anisomyarian condition may be an intermediary between the isomyarian and the monomyarian conditions. Sometimes, some families can present more than one muscular conditions amongst their species. An example is Mytilidae, as some genera are anisomyarian (e.g., *Brachidontes* – Figs. 10-11), while others are monomyarian (e.g., *Perna*).



14-16. Schematic representations of bivalves, showing their adductor muscles' size and position, left view. **14**, dimyarian-isomyarian; **15**, dimyarian-anisomyarian; **16**, monomyarian. Narrow arrows showing migration of posterior adductor muscle for changing from a condition to another. Wider arrows indicating suggestive pathway of evolution. Lettering: **A**, anterior; **am**, anterior adductor muscle; **P**, posterior; **pm**, posterior adductor muscle; **um**, umbo.

The Figs 14-16 represent schematically the transformation from a dimyarian-isomyarian bivalve (Fig. 14) to a true monomyarian one (Fig. 16), with a dimyarian-anisomyarian bivalve as intermediary condition (Fig. 15). In this process of modification, which could be called "**monomyarization**", two phenomena are observed:

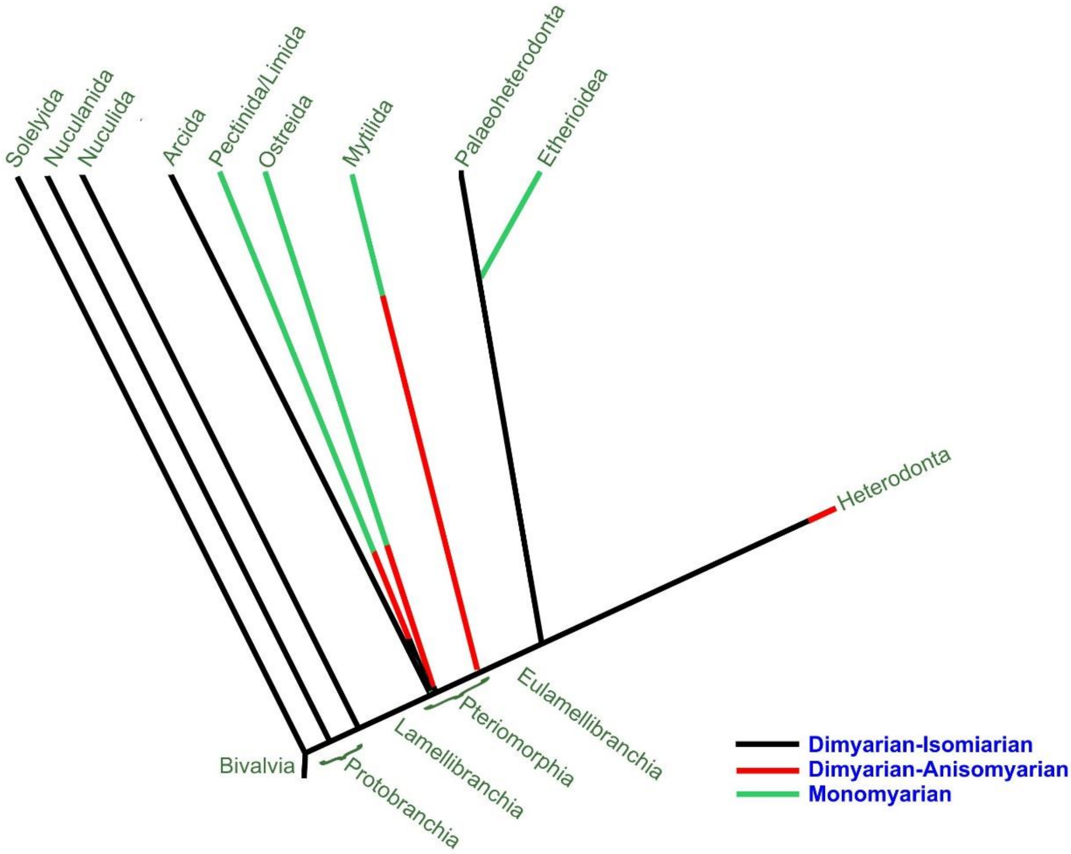
(1) **Change of position**: the posterior adductor muscle, which is the single remaining in the monomyarian bivalves, gradually migrates from a posterior portion towards a more central position. This is a physical strategy for a better efficiency of the muscular action. A more centrally located muscle distributes more efficiently the valves' grip function and avoids a weakening of any side of the shell that could be forced to open.

(2) **Change of size**: with the diminishment of the anterior adductor muscle, the posterior one must increase as in compensation. In an approximation, the remaining posterior adductor muscle of the monomyarian bivalves should have the sum of the insertion area of both adductors of a correspondent dimyarian bivalve. The same can be extrapolated to anisomyarian condition. Check, for example, the huge size of the adductor of a *Spondylus* (Fig. 5: ap).

Main branches that suffered monomyarization

The Figure 17 shows an unpretentious cladogram representing the main branches of the Bivalvia phylogeny in which the monomyarization process occurred to any degree. The cladogram is mostly based on Simone (2009, 2011), Simone et al (2015), with some information from WoRMS.

In that representation it is possible to see that most of the bivalve branches are isomyarian, as the Heterodonta branch is highly simplified, including the most basal branches the protobranchs. The Pectinida/Limida branch, which possibly are a single branch, has a basal taxon that practically is isomyarian – the Dimyoidea. Additionally, some limids apparently have reminiscences of an anterior adductor muscle (all this information is mostly inedited, in papers in preparation). But most of Pectinida/Limida branch is of monomyarian taxa (Figs. 5, 12-13).



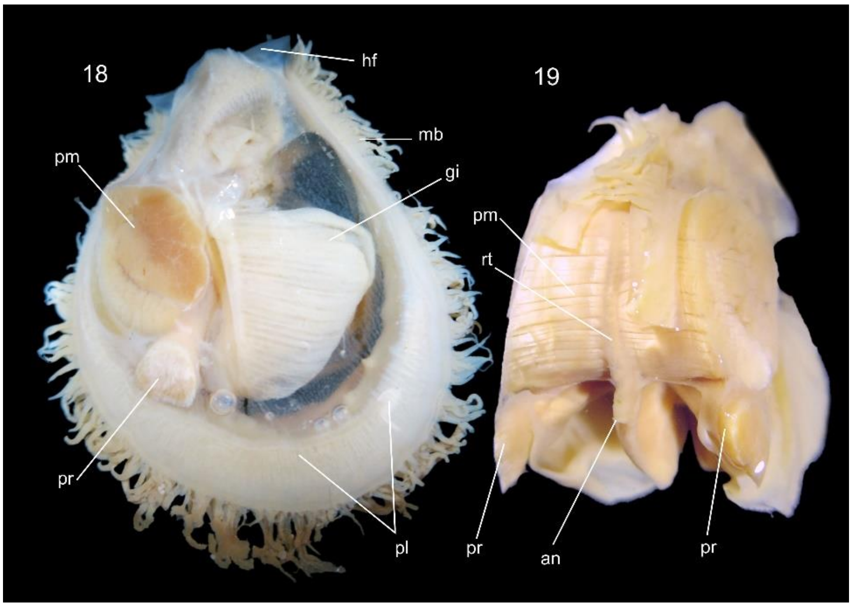
17. An unpretentious cladogram of Bivalvia, mostly based on Simone (2009,2011), Simone et al (2015) and WoRMS, showing important taxa that suffered monomyarization during evolution. Black lines represent dimyarian-isomyarian taxa; remaining colors as indicated in bottom-right of the figure. The survey is not exhaustive.

The Ostreida branch is also mostly constituted by monomyarian taxa (Amaral & Simone, 2014, 2016). However, it includes the Pinnoidea, which mostly have reminiscences of the anterior adductor muscle (Simone et al, 2015).

The Mytilida branch is more heterogeneous, as most of the taxa has a small anterior adductor muscle (Figs. 10-11), being, then, anisomyarian, while some taxa have actually lost it at all (e.g., *Perna*).

In the remaining branch, the Eulamellibranchia, mostly included isomyarian taxa. They are a huge branch of Bivalvia, with high biodiversity, in such the isomyary is almost a rule. The exceptions are the African freshwater oysters of the family Etheriidae, which are monomyarian palaeoheterodonts. Amongst the Heterodonta, the isomyary condition is also almost absolute. Some exceptions are, e.g., the Lucinidae (Fig. 7), which most species presenting the anterior adductor muscle higher than the posterior one, and the aberrant groups like Clavagellidae, Teredinidae, Galeommatidae, and allies, which have extremely modified shells, with difficult standardization (e.g., Morton, 2007; Silva & Narchi, 2007; Simone, 2008 respectively).

Weird adductor muscles

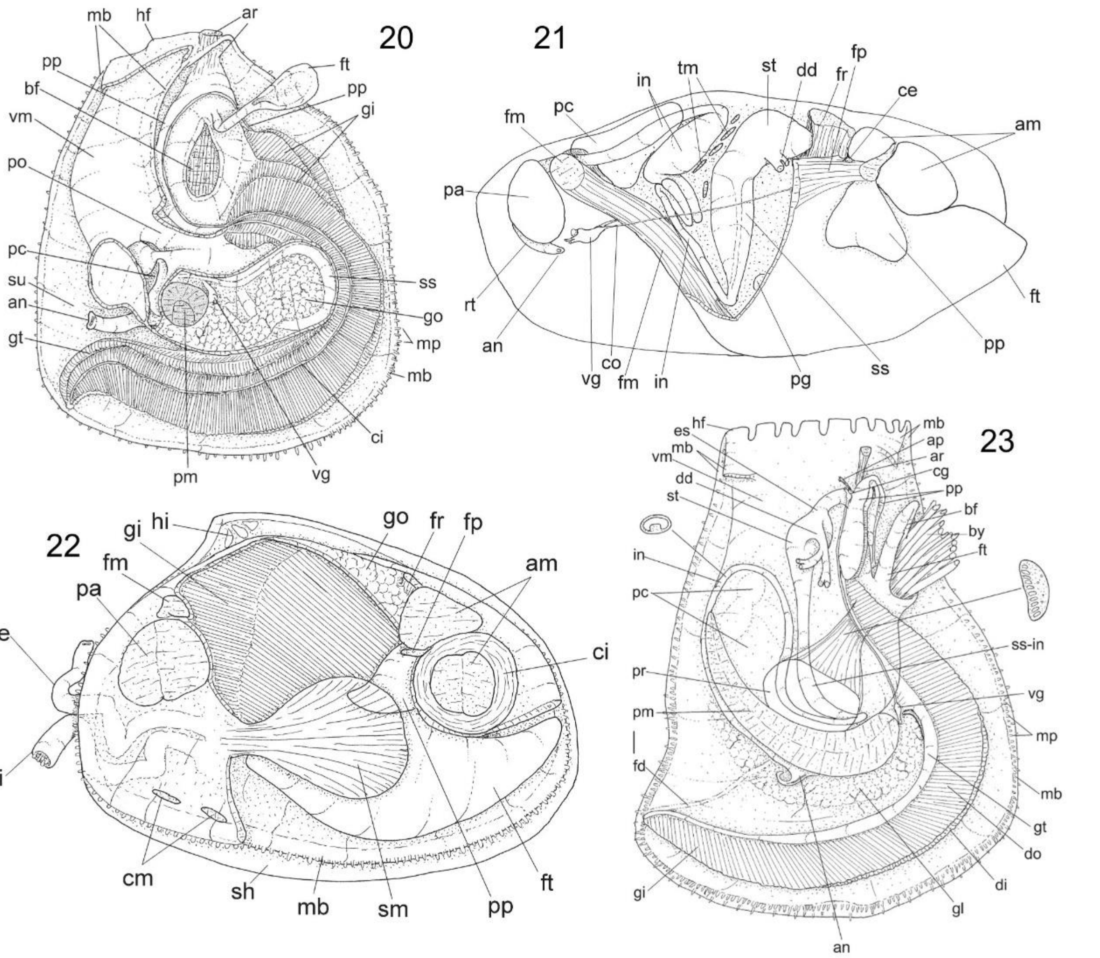


18-19. ***Ctenoides* sp (Limidae from República Dominicana)**: **18**, specimen removed from shell, right view, structures seen by transparency of mantle lobe (L ~30 mm); **19**, region of adductor muscle, posterior-slightly right view, mantle lobe removed (L ~10 mm). Lettering: see Figs. 8-13.

Some bivalves have further modified their adductor muscles, beyond the allocation and size. Some examples are presented here, such as the limid *Ctenoides* sp (Figs. 19-20). In species of this genus the single (posterior) adductor muscle is large (pm), but slightly dislocated dorsally, as it is helped by also well-developed pair of posterior foot retractor muscles (pr), which has a design almost straight (Fig. 19: pr) and has its main function of helping the adductor muscle, rather than foot retraction itself, as the foot size is minute.

Other examples of strange shaped adductor muscles are shown in the Figs 20-23. The anomiid *Anomia simplex* is monomyarian, but its adductor muscle is relatively small (Fig. 20: pm). The minuteness of the (posterior) adductor muscle is due to the very modified foot retractor muscles (Simone et al, 2015), in such design also helps the valves' closure. Its main foot retractor (located in the Fig. 20 below the region indicated by "bf") attaches directly to the left valve; its opposite portion attaches to the wide, calcified byssus, which is attached to the substrate; its contraction approaches the left valve to the substrate, causing the shell's closure as long as the adductor itself.

Another group that also usually has a modification of the anterior adductor muscle (as they are isomyarian) are the Tellinidae. One of the synapomorphies of the family is the division of the anterior adductor muscle (Fig. 21: am) into two portions, caused by the position where the anterior foot protractor muscles (fp) originates. Some tellinids have this foot protractor encased in the adductor, while in other species the foot protractor penetrates further, dividing the adductor completely, as the case of *Moerella* cf. *nitens* illustrated in the Fig. 21. Then, some tellinids in fact have three adductors, being two of them anterior. An extreme of this kind of tellinid division of the completely divided, but also have an enigmatic thick layer of circular muscle (ci) surrounding its



20-23. **Anatomical drawings of selected bivalves with weird adductor muscles** (see text for details), **20**, *Anomia simplex* (Anomiidae from Florida – Simone et al, 2015), right view, left mantle lobe removed (L~25 mm); **21**, *Moerella* cf. *nitens* (Tellinidae from Thailand – Simone & Wilkinson, 2008), topology of visceral structures and main muscles, right view (L ~15 mm); **22**, *Cadella* cf. *semen* (Tellinidae from Thailand – Simone & Wilkinson, 2008), right view, left mantle lobe mostly removed (L~6 mm); **23**, *Isognomon alatus* (Pteriidae from Florida – Simone et al, 2015), right view, left mantle lobe removed (L~25 mm). Lettering: **ap**, auxiliary pedal retractor muscle; **ce**, cerebral ganglion; **cg**, cerebral ganglion; **ci**, ciliary connection of gill with mantle lobe (Fig. 20) or circular muscle fibers (in Fig. 22); **cm**, cruciform muscle; **co**, cerebrovisceral connective; **fd**, fold; **fm**, posterior foot retractor muscle; **fp**, anterior foot protractor muscle; **fr**, anterior foot retractor muscle; **gl**, gland; **hi**, hinge; **mp**, mantle papillae; **po**, promyal chamber; **se**, excurrent siphon, **sh**, shell; **si**, incurrent siphon; **sm**, siphonal retractor muscles; **tm**, transverse visceral muscles; **vg**, visceral ganglion; other abbreviations see Figs. 8-13.

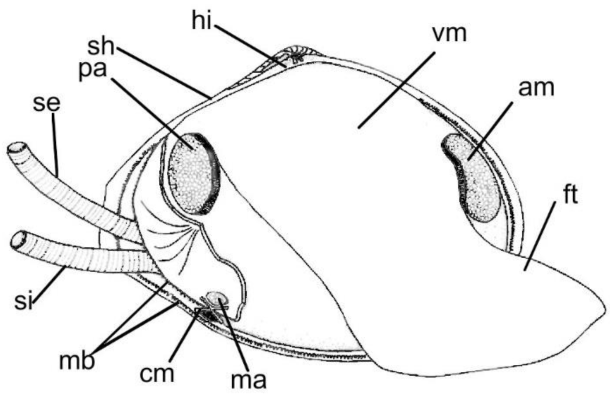
anterior unity anterior adductor muscle is found in *Cadella* (Fig. 22: am). The adductor muscle not only is.

Another strange-shaped adductor muscle it that of the pteriid *Isognomon* (Fig. 23: pm), which is crescent-moon (or banana) shaped in cross section, with a slightly thicker ventral end. This strange shape is caused by the position of the posterior foot retractor muscles (pr), which is also called as retractor of the byssus.

Auxiliary muscles of the adductor muscles

Other bivalve muscles also help the adduction movement of the shell valves, working as adductors' auxiliary. The main of them, already explored above, are the foot retractor muscles. Their arrangement also helps the shell closure, mainly those arranged more straightened from each other (Figs 2-3), as have been detected, for example, in anomiids (Fig. 20), limids (Figs. 18-19: pr) and pteriids (Fig. 23: pr).

Beyond the foot retractor muscles, sometimes some bivalve groups develop extra muscles that directly or indirectly works as adductor auxiliaries. A classic example is the cruciform muscle, a Tellionoidea synapomorphy (Figs. 22, 24: cm). As the name suggests, the cruciform muscle is composed of muscular bands positioned in a X-shape pattern, and is located in the ventral base of the incurrent siphon. Indifferently of its function in the siphonal functionality, its contraction certainly helps in the valves' closure. Of course, the cruciform muscle looks too narrow to have a considerable adduction function, however, its localization far from the articulation (the shell hinge), potentialize its power, as normally the more powerful is the muscle as long as it is far from the articulation. The cruciform muscle stamps easily detectable scars at the shell, which can be interpreted as an important and strong muscle.

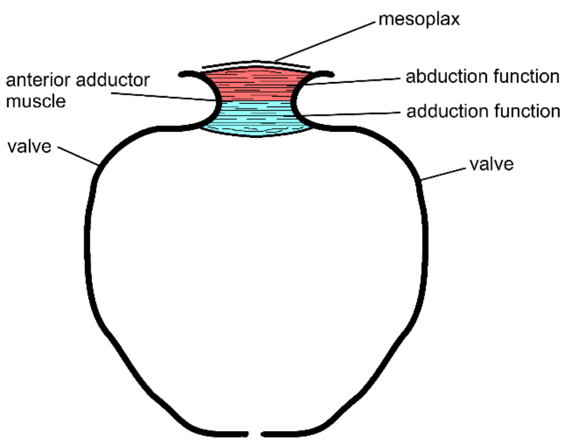


24. ***Macoma biota* (from Brazil)**: schematic representation of a specimen with right valve and pallial structures remove, and extended foot, with main concern to main musculature (L ~40 mm). Lettering: see Figs. 8-13 & 20-24; **ma**, auxiliary ventral adductor muscle. Modified from Piffer et al 2011.

Beyond cruciform muscle, some tellinids also develop extra muscles which can be called as secondary adductors. An example is *Macoma biota*, which developed a strong transverse muscle just dorsal to the cruciform muscle (Fig. 24: ma) (Arruda & Domaneschi, 2005; Piffer et al, 2011). Observing its shape and localization, no other function can be attributed to it instead of valves' adduction.

Abductor muscles

Despite the introduction above stated that the abduction, or diduction, of the valves is provided by the ligament, and the single function of the adductor muscle(s) is to be opposite to the ligament, some bivalves modified this function. Particularly, the Pholadidae and allies have very modified shells that have lost the ligament. The anterior adductor muscle migrated dorsally to an intermediary position between both valves. The valves dorsal edge is curved, producing a convex surface in such the adductor muscle attaches (Fig. 25). It then works as ligament in both ways: (1) it connects the valves to each other and (2) it also works as abductor muscle. The abduction function of the muscle is provided by its dorsal region, as the arrangement



25. ***Cyrtopleura costata* (Pholadidae)** (Brazil): schematic representation of its anterior region, a transverse section just in middle level of anterior adductor muscle; no other structure shown except for shell and adductor muscle (W ~40 mm).

of the valve allows this movement (Fig. 25: red region). On the other hand, its ventral portion (Fig. 25: blue region), continues with adduction function. The dorsal allocation of the anterior adductor muscle keeps it somewhat exposed. It is, at that time, protected by an isolated position of the shell called mesoplax (Fig. 25). More details in Purchon (1955), Röder (1977) and Savazzi (1987).

It is recognized the paradox of calling "adductor" a muscle that also has abduction function, however, the name is only to show the homology to the anterior adductor muscle of the remaining bivalves.

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References

Amaral, VS & Simone, LRL, 2014. Revision of genus *Crassostrea* (Bivalvia: Ostreidae) of Brazil. Journal of the Marine Biological Association of the United Kingdom doi:10.1017/S0025315414000058

Amaral, VS & Simone, LRL, 2016. Comparative anatomy of five species of *Saccostrea* Dollfus and Dautzenberg, 1920 (Bivalvia: Ostreidae) from the Pacific Ocean. Nautilus 130(2): 53-71.

Arruda, EP & Domaneschi, O, 2005. New species of *Macoma* (Bivalvia: Tellinoidea: Tellinidae) from southeastern Brazil, with description of its gross anatomy. Zootaxa 1012: 13-22.

Morton, B, 2007. The evolution of the watering pot shells (Bivalvia: Anomalodesmata: Clavagellidae and Penicillidae). Records of the Western Australian Museum 24: 19-64.

Piffer, PR, Arruda, ERP & Passos, FD, 2011. The biology and functional morphology of *Macoma biota* (Bivalvia: Tellinidae: Macominae). Zoologia 28(3): 321-333.

Purchon, RD, 1955. The structure and function of the British Pholadidae (rock-boring Lamellibranchia). Proceedings of the Zoological Society of London 124: 859-911.

Röder, H, 1977. Zur Beziehung zvischen Konstruktion und Substrat bei mechanisch bohrenden Bohrmuscheln (Pholadidae, Teredinidae). Senckenbergiana Maritima 9: 105-213.

Savazzi, E, 1987. Geometric and functional constrains on bivalve shell morphology. Lethaia 20: 293-306.

Simone, LRL, 2008. A new species of *Chlamydoconcha* Dall, 1884, from southeastern Brazil (Bivalvia: Chlamydoconchidae). Nautilus 122(4): 252-258.

Simone, LRL, 2009. Comparative morphology among representatives of main taxa of Scaphopoda and basal protobranch Bivalvia. 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; Mikkelsen, PM & Bieler, R, 2015. Comparative anatomy of selected marine bivalves from the Florida Keys, with notes on Brazilian congeners (Mollusca: Bivalvia). Malacologia 58(1-2): 1-127.

Silva, MJM & Marchi, W, 2007. Functional anatomy of *Bankia fimbriatula* Moll & Roch, 1931 (Bivalvia, Teredinidae) Veliger 50(4): 300-325.

Worms – MolluscaBase, 2019, http://www.marinespecies.org/aphia.php