Malacopedia

São Paulo, SP, Brazil
Volume 7(9): 70-76

ISSN 2595-9913
December/2024

Molluscan gliding muscle attachments

Luiz Ricardo L. Simone

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

Abstract

This study explores the ability of certain mollusk muscles to reposition their attachments during development, referred to as molluscan gliding muscle attachments. One type involves gliding muscles that are directly attached to structures such as the shell, with examples drawn from bivalves and gastropods. The other type occurs when gliding muscles are not directly attached to a structure, such as the radula. In this case, the gliding phenomenon takes place between the subradular cartilage and the subradular membrane. Despite being understudied, these mechanisms are crucial for understanding molluscan physiology.

DOI:

Keywords: anatomy, organic function, taxonomy, phylogeny, evolution.

Introduction

Muscles are remarkable structures whose capacity for contraction generates movement, distinguishing the Animal Kingdom from other life forms. Our understanding of the complex constitution of muscles has progressively advanced, revealing their intricate and multifaceted nature. The traditional subdivision of muscles into striated and smooth types has been primarily studied in vertebrates. However, in mollusks, both types appear to be present. Striated muscles are associated with rapid or forceful movements, such as the ‘quick closure’ component of bivalve adductor muscles. In contrast, smooth muscles are involved in slow, sustained movements or maintaining tension, such as the crawling motion of gastropods’ feet and the ‘slow component’ of bivalve adductor muscles, which allows for prolonged closure with minimal energy expenditure.

Muscles are typically described anatomically as having three parts: (1) the origin, which is the fixed end attached to a structure that remains stationary during contraction; (2) the body, encompassing features such as size, shape, length, topology, and overall anatomy; and (3) the insertion, which is the opposite end attached to a structure that moves during contraction.

Simplistically, a muscle's function can be interpreted, and its name derived, by considering its 'origin, body, and insertion.' However, not all muscles exhibit these characteristics clearly. For example, in bivalves, determining the origin and insertion of the adductor muscle can be ambiguous. Nevertheless, this challenge is absent in the majority of muscles.

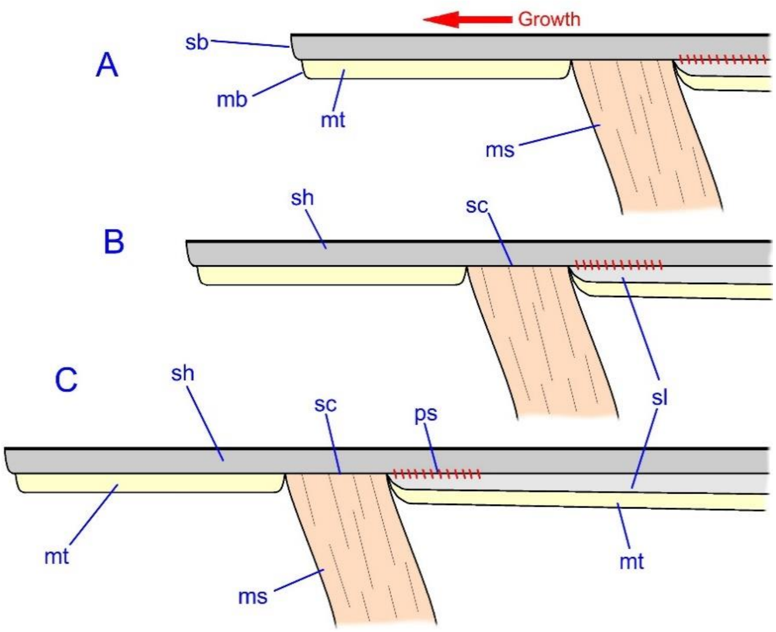
The muscular structure, types, and classifications of mollusks will be explored in future issues of *Malacopedia*. This issue, however, focuses on an extraordinary characteristic of certain molluscan muscles: their ability to adjust their attachment points, a phenomenon referred to as 'gliding attachment.' This term describes the capacity of molluscan muscles to shift their points of attachment in tandem with the animal's growth and development.

Gliding muscle attachments are categorized into two types: (1) muscles attached to the shell and (2) muscles attached to the radula. Although both involve gliding mechanisms, the details and processes differ, warranting their separate treatment. An example of shell-attached gliding muscles is the columellar muscle in gastropods, whose attachment slides along the surface of the columella as the shell grows. Similarly, in bivalves, both the adductor and pallial muscles migrate their attachments along the inner surface of the shell during growth. These aspects will be explored in detail below.

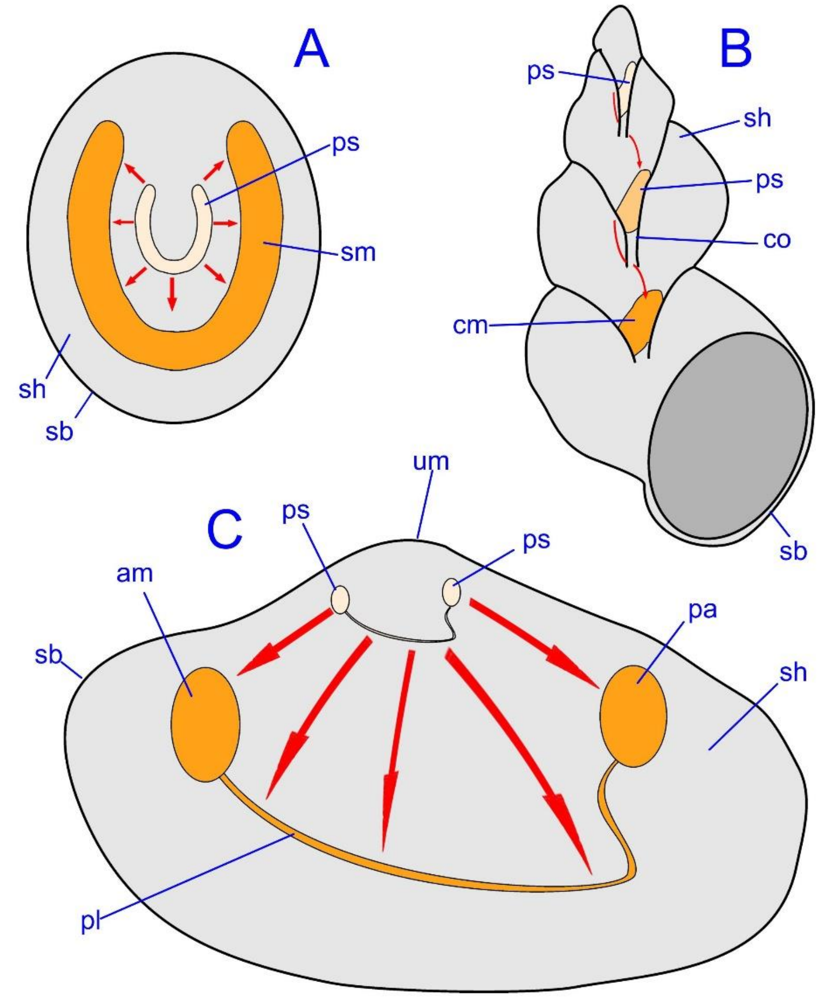
In the radula, housed within the odontophore, certain muscles are directly attached to the radular ribbon, facilitating its back-and-forth motion. Since the radular ribbon is continuously replaced, the muscles attached to it must also adjust their points of attachment through a gliding mechanism. This process will be discussed in greater detail below.

Gliding of muscles attached to the shell

The shell serves as the origin for several molluscan muscles. In some cases, such as the radular muscles (m2) of polyplacophorans and the adductor muscle of monomyarian bivalves, the muscular attachment to the shell appears stationary, remaining in the same location throughout the animal's development, with only a proportional increase in size being noticeable. Other muscles, however, clearly shift their attachment points along the shell as it grows (Fig. 1), a phenomenon referred to here as gliding attachment (Fig. 1A–C).



1: Schematic representation of a portion of the shell in transverse section, region of attachment of a muscle, in 3 different stages of the growth A to C (arrow). Details in text. Lettering: mb, mantle border; ms, muscle; mt, mantle; ps, previous muscle scar covered by new shell layer; sb, shell edge; sc, muscle scar; sh, oldest shell layer; sl, newest shell layer



2: Schematic representation of two (A, C) and three (B) stages of the main muscular attachment in the shell of a limpet (A), a generic coiled snail (B) and an ordinary dimyarian bivalve (C). The older previous scars are in lighter colors which is covered by newly secreted shell inner layers. The coiled snail (B) is represented as transparent; red arrows indicate gliding ways of each structure. More details in text. Lettering: am, anterior adductor muscle scar (and pedal retractor and protractor); co, columella; pa, posterior adductor muscle scar (and pedal retractor); pl, pallial line; ps, previous muscle scar covered by new shell layer; sb, shell edge; sh, shell; sm, shell muscle; um, umbo.

A detailed examination of muscular attachments to the shell reveals that no mantle layer is present. This indicates that the muscle is directly attached to the shell surface (Fig. 1) and that the corresponding portion of the shell neither grows nor thickens while the muscle remains attached. The muscle-shell attachment is not composed solely of muscular tissue; it includes a specialized epithelial layer and a mucous-like material at the interface, which likely serves an adhesive function (Frescura, 1990). Additionally, this specialized epithelial layer appears to facilitate the sliding of the muscle toward younger portions of the shell, enabling growth in accordance with the individual's development.

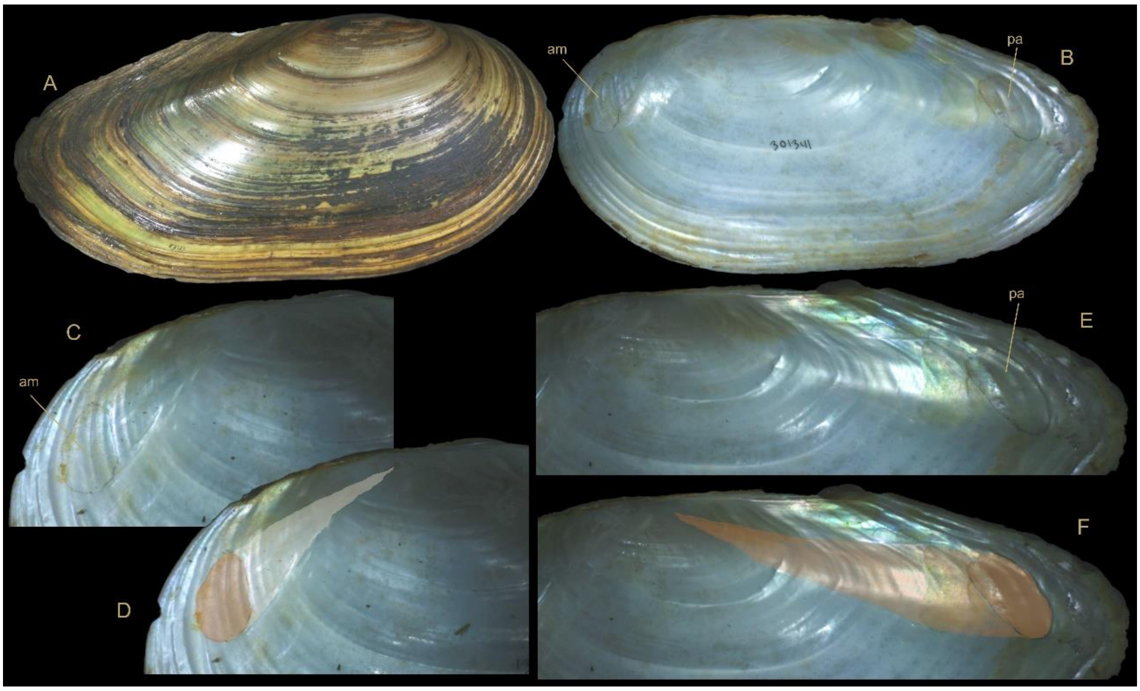
As shown in Figs. 1–2, the muscle (Fig. 1: ms) migrates its attachment to maintain the same proportional position relative to the animal's growth. The region of muscular attachment, known as the scar (sc), lacks a mantle layer, which prevents this area from growing. However, the surrounding regions grow both in length (area) and thickness (right side of Fig. 1). When the muscle glides forward, the previous scar (ps) is abandoned and subsequently covered by new shell layers (sl) secreted by the mantle (mt). Simultaneously, the new site of muscle attachment displaces the mantle tissue originally present in that location.

Although muscular shell gliding attachments also occur in polyplacophorans, monoplacophorans, scaphopods, and shell-bearing cephalopods, the phenomenon is most evident in bivalves and gastropods, as shown in Fig. 2. These two groups are discussed in more detail here.

Muscular shell gliding attachment appears to be another synapomorphy of the Testaria (Polyplacophora + Conchifera).

In Gastropoda, the shell muscle of limpets (Fig. 2A) and the columellar muscle of coiled snails (Fig. 2B), which are homologous structures (Simone, 2018), as well as other muscles connecting the head-foot to the shell in different gastropod morphologies, clearly migrate their attachment points in accordance with the animal's growth. In limpets, the earlier shell muscle attachments are positioned closer to the shell apex (Fig. 2A: ps), while more recent attachments shift toward the shell edge (Fig. 2A: sm). In coiled snails, the columellar muscle, which is responsible for retracting the head-foot into the shell, migrates from regions near the apex (Fig. 2B: ps) to regions closer to the aperture in later developmental stages (Fig. 2B: cm). The columellar muscle in gastropods clearly slides forward as the animal grows.

A more complex scenario is observed in Bivalvia, particularly in classic dimyarian forms. In monomyarian species, the more central positioning of the remaining posterior adductor muscle (Simone, 2019) obscures the gliding phenomenon. The initial positions of the muscular attachments of the adductor muscles (Fig. 2C: ps), as well as the pallial line where the muscles originating



3: *Anodonta cygnea* (Unionidae), shell, as example of preservation of previous scars of adductor muscles. (MZSP 301341, Czech Republic, L 150 mm). **A**, right valve, outer view; **B**, same inner view; **C**, same, detail of region of the anterior adductor muscle scar; **D**, same, with anterior adductor scar artificially painted brown, its previous attachments in light beige; **E**, same valve, detail of postero-dorsal region; **F**, same, posterior adductor scar artificially painted brown, its previous attachments in lighter brown. Lettering: am, scar of anterior adductor and foot retractor muscles; pa, scar of posterior adductor and foot retrator muscles.

from the mantle edge attach, are located much closer to the umbo (um) – the oldest region of the shell. As the animal grows, these structures glide in the direction indicated by the red arrows. The anterior adductor muscle (Fig. 2C: am) migrates toward the anterior, carrying with it the attachments of the retractor and protractor muscles of the foot. Conversely, the posterior adductor muscle (Fig. 2C: pa) migrates toward the posterior, along with the attachment of the posterior retractor muscle of the foot. Meanwhile, the pallial line (Fig. 2C: pl) shifts toward the ventral side.

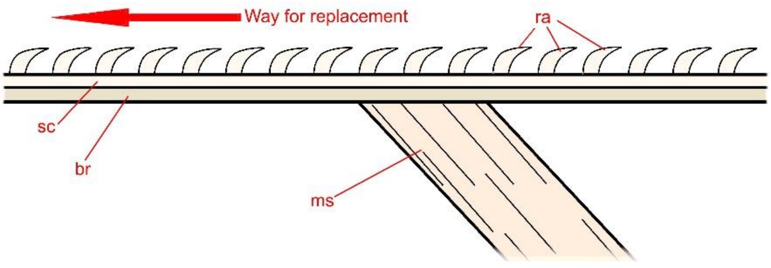
Previous muscle attachments are rarely visible in ordinary shells, whether in gastropods or bivalves. This is because the mantle covers the old scars with new inner shell layers, as illustrated in Fig. 1 (sl). However, in some cases where muscle scars are particularly pronounced and the successive inner shell layers are thin, the former attachment trail may be visible. In bivalves, this trail typically appears as a shallow, conical groove marked by successive low, arched folds. It is narrow near the umbo and snakes toward the current adductor scars (Fig. 3). This phenomenon is not observed in the pallial line of bivalves, nor has it been reported in the columellar muscles of coiled gastropods or the shell muscles of limpets. This absence is likely due to the less pronounced scars left by muscular attachments in these cases.

The ultrastructure and histological architecture of molluscan muscle attachments to the shell are relatively well understood. A review of the detailed literature, from Frescura (1990) to Castro et al. (2021), reveals a complex arrangement of cells in the attachment epithelium, including mucous cells, anchor cells, and even tendon cells. However, no evidence has been found to explain the mechanism underlying the gliding phenomenon of muscle attachments. At least for now, this remains an intriguing topic for a potential complementary project.

Gliding of muscles attached to the radula

As briefly explained elsewhere (Simone, 2011, 2021), the radula, one of the key synapomorphies of Mollusca, is constructed and operated by the odontophore. The odontophore is a complex structure composed of cartilages, membranes, and numerous muscles. It holds significant value for comparative biology, particularly in taxonomy and phylogeny, yet it has been relatively underexplored. Instead, it is often dissolved to isolate a clean radula for examination under scanning electron microscopy. In my studies, the odontophore has consistently been investigated as a source of comparative data, proving to possess valuable characters applicable across taxonomic levels, from species to higher clades. A useful overview is provided in Simone (2011), with additional explanatory details offered in various *Malacopedia* issues (Simone, 2021, 2022, 2023a, b, 2024). These efforts to highlight the odontophore's relevance remain ongoing.

The radula is a chitinous ribbon covered with numerous minute, chitinous teeth (Fig. 4: ra). The size, shape, composition, and number of these teeth vary widely among taxa, with possibilities ranging across a myriad of forms, including complete absence in some groups. The chitinous ribbon that supports the arrangement of teeth is known as the subradular cartilage (Fig. 4: sc). Both the teeth and the subradular cartilage are continuously replaced, as the teeth wear down during use. New teeth and subradular cartilage are produced at the posterior end of the radula, in a region called the radular nucleus. From there, they are stored in the radular sac, which varies in length depending on the species and the degree of radular wear. The radular sac leads to the buccal cavity, where the radula is exposed, allowing the teeth to be used and gradually worn down.



4: Schematic representation of a longitudinal section of the odontophore in a region in which an intrinsic muscle attaches in the radular ribbon. The thickness of membrane and cartilage is exaggerated. Arrow indicating the direction in which the teeth are lost and must be replaced. Lettering: br, subradular membrane; ms, generic intrinsic muscle; ra, radular teeth; sc, subradular cartilage.

The radular ribbon, composed of the teeth and the subradular cartilage, is continuously and gradually moved forward to replace worn teeth. Covering the entire subradular cartilage on the surface opposite the teeth is the subradular membrane (Fig. 4: br). The subradular membrane is fully attached to the subradular cartilage and is likely responsible for its formation. All intrinsic muscles—that is, the muscles responsible for moving the radula itself (ms)—are attached to the subradular membrane. These muscles are not attached to the subradular cartilage or the radular teeth, as both are continuously moving forward for replacement (red arrow).

Consequently, unlike the muscles attached to the shell (as described above), which are directly connected to the structure they move, the intrinsic radular muscles are attached to the subradular membrane rather than the moving structure—the radular ribbon. As a result, the gliding phenomenon occurs between the subradular membrane and the subradular cartilage.

The radula is the third most studied molluscan structure, following the shell and operculum. Even its histological formation is relatively well understood (e.g., Vortsepneva et al., 2022). However, there is currently no information available regarding the gliding phenomenon involved in replacing worn teeth, as mentioned above. This undoubtedly represents another intriguing topic for future research.

Conclusion

As discussed above, molluscan gliding muscle attachments appear to be a phenomenon unique to Mollusca, specifically within Testaria. The structural differences between gliding muscle attachments in the shell and the radula suggest they represent distinct adaptations for muscle insertion in continuously growing structures. In the shell, the muscles attach directly to the shell, with the gliding capacity inherent to the muscle itself. In contrast, for the radula, the muscles are permanently attached to the subradular membrane, and the gliding movement occurs between the subradular membrane and the subradular cartilage—indirectly involving the muscle attachment.

These two types of molluscan gliding muscle attachments remain poorly understood and, in fact, are virtually absent from the malacological literature. They thus represent intriguing topics for further investigation.

References

Castro-C, JD; Checa, A; Lucena, C; Pearson, JR & Salas, C, 2021. Shell-adductor muscle attachment and Ca^{2}+ transport in the bivalves *Ostrea stentina* and *Anomia ephippium*. Acta Biomaterialia 120: 29-262. https://doi.org/10.1016/j.actbio.2020.09.053

Frescura, M, 1990. Aspects of the structure and function of some gastropod columellar muscles (Mollusca). PhD. Thesis; Rhodes University. https://commons.ru.ac.za/vital/access/manager/Repository/vital:5642?site_name=Rhodes+University&view=grid&f0=sm_format%253A%2522205+leaves%2522&sort=sort_ss_sm_creator+asc

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, 2018b. Main processes of body modification in gastropods: the limpetization. Malacopedia 1(4): 23-36. http://www.moluscos.org/trabalhos/Malacopedia/01-

04%20Simone%202018%20Malacopedia%20Limpetization.pdf

Simone, LRL, 2019. Modifications in adductor muscles in bivalves. Malacopedia 2(1): 1-12. http://www.moluscos.org/trabalhos/Malacopedia/02-01Simone%202019%20Malacopedia-AAM-Biv.pdf

Simone, LRL, 2021. The mollusk buccal mass – generalities. Malacopedia 4(5): 50-58. http://www.moluscos.org/trabalhos/Malacopedia/04-05Simone%202021%20Malacopedia-%20buccal%20mass.pdf

Simone, LRL, 2022. The molluscan jugal muscles – m1. Malacopedia 5(5): 43-48. http://www.moluscos.org/trabalhos/Malacopedia/05-05Simone%202022%20Malacopedia-jugal%20muscle%20m1.pdf

Simone, LRL, 2023a. The retractor muscles of buccal mass – m2. Malacopedia 6(2): 7-15. http://www.moluscos.org/trabalhos/Malacopedia/06-022023%20Malacopedia%20m2.pdf

Simone, LRL, 2023b. The unnamed odontophore muscles m3 and m9. Malacopedia 6(5): 29-34. http://www.moluscos.org/trabalhos/Malacopedia/06-052023%20Malacopedia%20m3-m9.pdf

Simone, LRL, 2024. The odontophore dorsal tensor muscles m4 and m5. Malacopedia 7(6): 49-57. http://www.moluscos.org/trabalhos/Malacopedia/07-06Simone%202024%20Malacopedia%20m4-m5.pdf

Vortsepneva, E; Mikhlina, A & Kantor, Y, 2022. Main patterns of radula formation and ontogeny in Gastropoda. Journal of Morphology 284: e21538. https://doi.org/10.1002/jmor.21538

*More in **Malacopedia** in http://www.moluscos.org/malacopedia_previous.html*

***Malacopedia** is both, is a popular scientific **journal**, and a **book**, published in topics, in which more than 40 years of Malacology are published.*