Malacopedia

São Paulo, SP, Brazil
Volume 4(5): 50-58

ISSN 2595-9913
October/2021

The mollusk buccal mass – generalities

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Abstract

The buccal mass is an outstanding character of the Mollusca. It is the first digestive component and is very complex, bearing several muscles, hard structures as the radula, etc., in such general features are explained. Some phylogenetic inferences are performed, preparing the subject for future papers dealing with most of the buccal mass components, particularly the odontophore. The basic buccal mass model is explained, as well as the main basic modifications in all classes, including its loss.

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Keywords: morphology, anatomy, evolution, taxonomy, phylogeny.

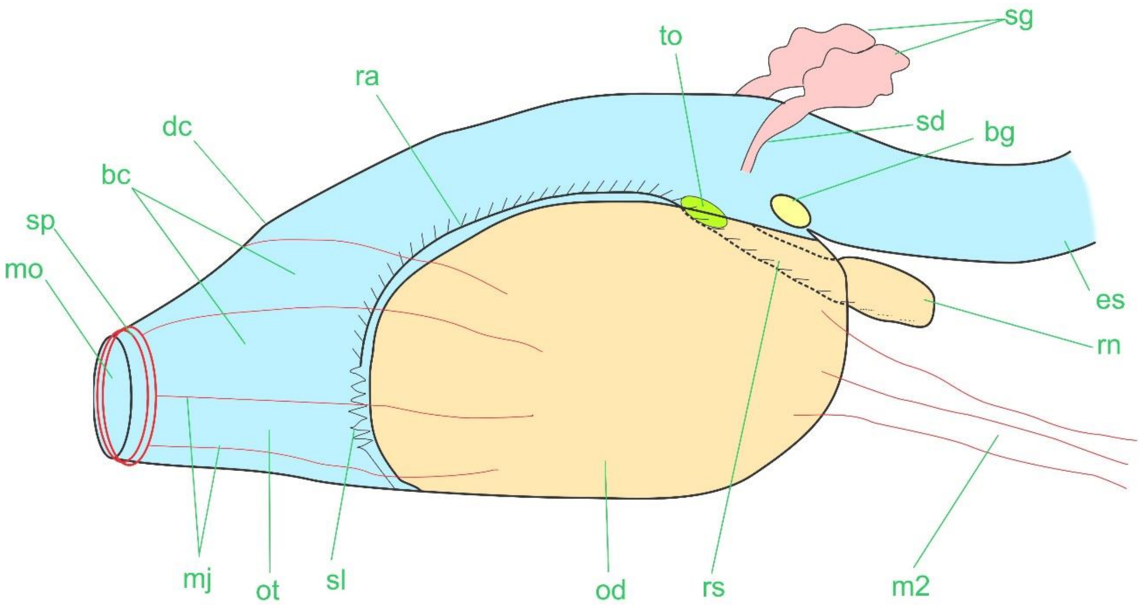
Introduction

The mollusks' buccal mass is the first internal structure of the digestive system. It more rarely is referred to while "pharynx". It is the organ that captures and first processes the food. For that, the buccal mass has different parts that catch, grip, smash, crash, and direct the processed food to the esophagus. To do all these activities, the organ has a complex arrangement of muscles, glands, epithelium reinforcements, hard structures done of chitin and conjunctive tissue, and good coordination of nerves to produce the best performance possible, avoiding auto-injuries. The buccal mass is so important that it has its own nervous command, provided by a pair of usually large buccal ganglia. This pair has a commissure and short connections with the central nerve ring; from these ganglia, several nerves arise, running to all buccal mass components.

The mollusk buccal mass is so complex that it is impracticable to explore all its components in a single paper. Hence, future Malacopedia issues will be devoted to each of its components, particularly the odontophore, jaw, etc. The present paper is, thus, concerned with generalities. Accordingly, the diverse main components, usually present in most mollusk classes, will be here introduced in a comparative and phylogenetic scenario.

The buccal mass is usually located just posterior to the mouth, as a swollen anterior region of the digestive tubes. Despite being an outstanding synapomorphy (exclusive character) of Mollusca, it was lost in several internal branches, particularly in all Bivalvia, and in some Gastropoda and even in Cephalopoda. The possible reasons are discussed below.

As each main buccal mass component will be explored in future Malacopedia papers, only generalities and the main evolutionary trends in the mollusk classes are presented here.



1. Schematic representation of generic morphology of a typical mollusk buccal mass, left view, some structures seen by translucency. Lettering: bc, buccal or oral chamber; bg, buccal ganglion; dc, dorsal wall of buccal chamber; es, esophagus; m2, buccal mass retractor muscle; mo, mouth; mj, peribuccal muscles; ra, radula; od, odontophore; ot, oral tube; rn, radular nucleus; rs, radular sac; sd, salivary duct; sg, salivary glands; sl, sublingual organ; sp, buccal sphincter; to, tissue on radula in anterior region of radular sac.

General anatomy of a typical molluscan buccal mass

The generic structures usually present in a mollusk buccal mass are shown in Fig 1. The buccal mass is represented in its left view, with an anterior region left and posterior right. The dorsal region is up. Basic explanations on its components are given below, from anterior to posterior order.

Mouth (mo): this is the anteriormost aperture of the digestive system. It usually is in the tip of a snout, proboscis, or some anterior projection. It works in the capture of the food, directing it to the oral tube for processing. It naturally has a capacity of closing and opening, mostly it works opening up, permitting the protrusion of the odontophore, which is exteriorized to contact the food. Despite the mouth usually being the first structure of the digestive system, in gastropods the snout or the proboscis is mostly discussed as part of it (Simone. 2011).

Buccal sphincter (sp): composed of circular muscular fibers, it surrounds the mouth. It is responsible for the mouth closure when contracts. Buccal sphincters rarely are anatomically visible. Its muscular tissue is thin and mostly detectable in serial sections only. An exception is some nudibranchs (e.g., doridids), which bear enormous buccal sphincters (e.g., Lima & Simone, 2018).

Oral tube (ot): is a tubular, usually conic connection between the mouth and remaining buccal mass components. Its walls are richly muscular. Despite oral tubes being usually well defined, sometimes it is very short (e.g., polyplacophores – Jardim et al, 2020), and sometimes very long, connecting a buccal mass located far from the mouth (e.g., conoideans – Simone, 1999, 2011). The oral tube usually is internally covered by a relatively thick transparent chitin layer. This layer works as a protection against potential injuries done by the food and the radula. Localized thickenings of this chitinous layer are called jaws. The chitin layer also works as a skeleton for the oral cavity, avoiding contact with the radula, and optimizing the organs' functioning.

Peribuccal muscles (mj): they are immersed in the oral tube walls, or sometimes they cover the oral tube externally. Their longitudinal and oblique fibers work as odontophore protractor muscles, as buccal dilatator muscles (opening the mouth), and also moving the jaw(s) when present (thus the abbreviation: mj, as muscles of the jaw). The mj insertion is slightly posterior to the anterior end of the odontophore. Thus, its contraction causes the protrusion of the odontophore, with the exposure of the radula. The protruded radula can be used grinding the food directly in the environment.

Dorsal wall of the buccal chamber (dc): like continuation of the oral tube, lying further posterior, dorsally to odontophore. The inner layer of chitin is still present, but thinner. Its anterior border with the oral tube, in cyrtosomans (gastropods + cephalopods), usually have a strong thickness called jaw (one of the cyrtosoman synapomorphies). The dorsal wall anterior region, usually reinforced by chitin and even by jaw(s), is typically used by the animal as a dorsal component of something as forceps. The ventral component of it is the anterior end of the odontophore. Both structures can be used tearing off pieces of food, which are swallowed by radular movements. This is another way for catching food beyond the direct radular action on it.

The dorsal wall of buccal mass mostly possesses a pair of wide dorsal folds. Both folds are separated by usually a wide furrow. In some basal gastropods, for example, this dorsal interspace between the folds is deep, with glandular mucosa, called the "dorsal chamber". The dorsal chamber, when present, is a step of the digestive process of the food.

Odontophore (od): is the structure that builds, stocks and moves the radula. The odontophore, with a consequent radula, are outstanding synapomorphies of Mollusca. The structure is a complex set of intrinsic and extrinsic muscles, cartilages, chitinous membranes, chitinous teeth, ligaments, nerves, blood vessels, etc., which are extremely important for comparative studies. Despite this, odontophores are very rarely included in the descriptions. On the contrary, it is mostly destroyed for radular extraction.

The complex odontophore characters, radula included, will be treated in future Malacopedia issues. As practically all its structures have interesting features to be discussed in the comparative morphology, physiology, and phylogeny viewpoint, each one will be explored separately. Even the generic features of the odontophore are issues of a proper paper.

The important information for this paper is that the odontophore is a solid, ventral, bulged structure usually located at the postero-ventral end of the buccal mass. The radula is built in the radular nucleus (**rn**), stored along with the radular sac (**rs**), and becomes exposed in the buccal cavity (**ra**) to be used along the odontophore dorso-anterior region. Especial sets of muscles move the radula anteriorly and posteriorly, as well as move the odontophore itself forwards, backward, and other positions, and the other buccal structures. Several pairs of muscles are used for these movements. The muscles are generally originated from the odontophore pair of central cartilages, and in the surrounding structures of buccal mass and haemocoel.

Sublingual organ(sl): is an accordion-like, multi-folded region of the ventro-posterior surface of the oral tube, in its border with the odontophore. It is posteriorly connected to the radular anterior end, being stretched out and wrinkled according to the coming and going movement of the radula. Its main function is to permit the radular movement, protecting against food entrance to the haemocoel. In some basal gastropods, the sublingual organ has a thick mucosa, with some unknown digestive function. This differentiated structure of those taxa raised the name.

The tissue on the radula in anterior region of radular sac (to): is mostly an elliptic, hard, solid set of conjunctive tissue strategically located in the region in such the radular sac opens for the radular exteriorization inside the buccal mass. It usually stays surrounded by the radular ribbon, in its region at end of the radular sac. This tissue has the special function of avoiding the entrance of food inside the radular sac. However, it does not need to be attached to the surrounding structures, as the radula must flow through it, replacing the more anterior teeth eroded by the usage.

Salivary glands (sg): a pair, usually located in the dorso-posterior region of buccal mass. The salivary glands can be a pair of deep dorsal diverticula, connected to the oral cavity by a simple aperture. But in several taxa of most molluscan classes, the connection is done via salivary ducts (**sd**), which are more derived, differentiated, non-glandular structures.

Salivary glands have different digestive functions amongst the molluscan branches. The function is usually the first step for food processing. However, in some predatory gastropods and cephalopods, the saliva can have numbness function on the prey, proteolytic function, and even venom. All these will be explored in future Malacopedia issues.

Buccal ganglia (bg): are a pair of the central nervous system responsible for coordination of movements and sensorial stimuli in the buccal mass. Such an important and complex structure deserves its coordination center. The usual region in such buccal ganglia is located in the postero-dorsal surface of the buccal mass, in each side of the esophageal origin. In pulmonate gastropods, for example, they are located just in the penetration of the salivary ducts in the buccal mass wall. A long, thin, and most difficult detection commissure connects both buccal ganglia with each other, as well as long connectives connect them with the central nerve ring, mostly in the pair of cerebral ganglia.

The pair of buccal ganglia is usually easy to be detected in most groups that possess buccal mass. Some branches, however, have modified this condition. Neogastropods, for example, have their pair of buccal ganglia located closer to the nerve ring, sometimes even as part of it; their innervation to the buccal mass is done via very long nerves.

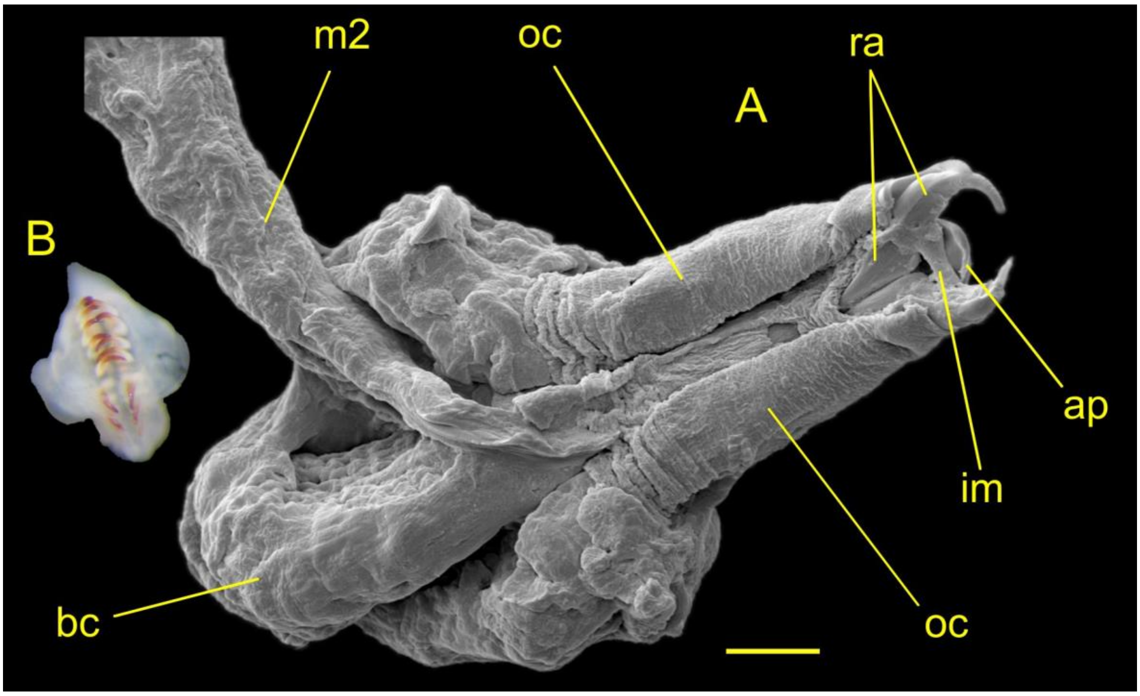
Pair of buccal mass retractor muscles (m2): is responsible for the retraction of the buccal mass back inside the haemocoel when the animal ends its feeding activities. It is not always present. In these cases, its function is, thus, substituted by other extrinsic muscles, mainly jugal muscles (m1), or by the contraction of peri-buccal muscles, mainly the buccal sphincter; or a mixture of them.

The typical m2 pair originates in the inner haemocoelic walls, in their posterior regions. It runs anteriorly inserted in the postero-lateral surface of the buccal mass. This insertion can be superficial, or it can go further inside, penetrating through odontophore muscles, inserting in one of them or the odontophore cartilages. All these kinds of m2 modifications, and their occurrence, will be explored in future Malacopedia issues.

Esophagus (es): its origin marks the end of the buccal mass and the beginning of what usually is called “midgut”, which is the set esophagus-stomach-intestine, and their eventual annexed structures. The esophagus is a long tube that connects the buccal mass, anteriorly located, to the stomach, posteriorly located inside the visceral mass. The esophagus is also a structure that suffered high modification along with the mollusk evolution, particularly in the gastropods, and will also be explored in future Malacopedia issues.

The typical buccal mass of the molluscan classes

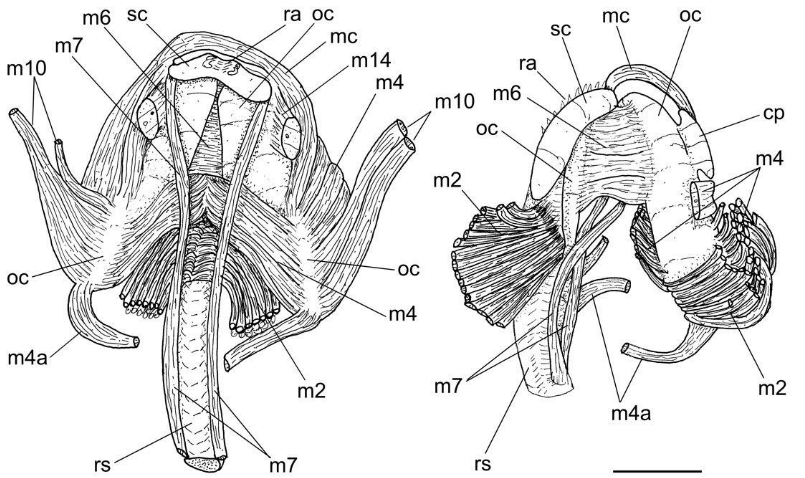
The buccal mass is present and rather ordinary, i.e., as above described, in the 4 more basal mollusk classes – Caudofoveata, Solenogastres, Polyplacophora, and Monoplacophora.



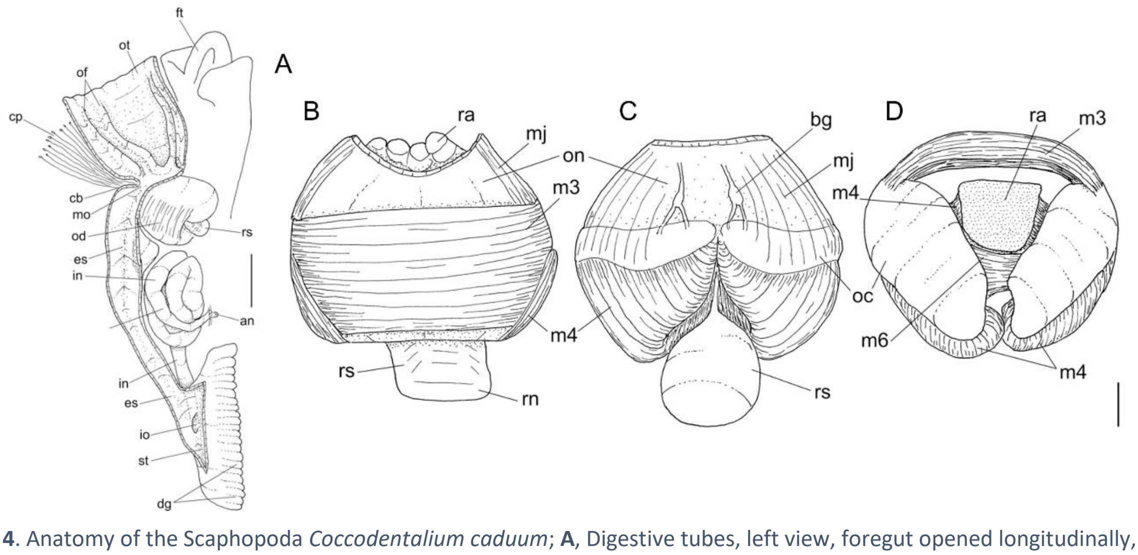
2. Caudofoveata odontophores: **A**, scanning electron micrography of an odontophore of *Chiastofalcidens* sp, representing a more advanced model of the class, in which the radula modified to a pair of hooks, ventral view. Scale= 0.1 mm; **B**, odontophore of *Prochaetoderma* sp, a more basal model, anterior view, light photography (L 0.5 mm). Lettering: ap, anterior triangular plate; bc, basal cone or cartilage; im, interdental muscle; m2, main retractor muscle; oc, odontophore lateral cartilages; ra, radular tooth (all MZSP material).

Of course, the buccal mass, the odontophore in particular, has modifications along with each class’s evolution. The more notorious it iswhat occurred in the Caudofoveata, the more basal taxa, e.g., procaetodermatids (Fig. 2B) still possess a relatively ordinary odontophore, with several rows of teeth. However, the more advanced caudofoveates, e.g., chaetodermatids (Fig. 2A), modified this conformation to a single pair of teeth. Each tooth has its hook-like distal half (ra), which, jointed to its counterpart, works pinching the food and its substrate. This movement is helped by an interdental muscle (im), as well as the arrangement of the cartilages (oc + bc), which promote their closure when the retractor muscle (m2) contracts.

The odontophore of the polyplacophorans is usually strong, large, and complex (Fig. 3). The complexity of muscles and annexed structures are explained in the given reference, as the details are not important in the present context. Whilst more interesting features are the fact that the main pair of retractor muscles (m2) originated from the second shell plate, runs directly to the odontophore cartilages (oc). This direct connection between odontophore and the shell is found in monoplacophorans (Wingstrand, 1985) and more basal gastropods – the patellogastropods (e.g., Leal & Simone, 1998). By the way, this pair of m2 originated from the shell is important in ancient fossils to determine if a fossil limpet is a gastropod or a monoplacophore. As it is detected in a fossil by a pair of small anterior scars, called "radular muscles" in the inner shell surface. If the beak of the shell is directed as opposed to the scars, the animal is a gastropod, as denotes torsion. If, on the contrary, the shell beak is directed to the same side of the scars, i.e., anterior, the animal is a monoplacophore, as denotes lack of torsion (see Simone, 2021).



3. Odontophore of the polyplacophore *Acanthopleura gemmata*; **left**, ventral view, some extrinsic muscles deflected; **right**, dorsal view, radular ribbon deflected to left, right muscles mostly deflected to show cartilage. Scale= 2 mm (extracted from Jardim et al 2020). Lettering: cp, cartilage projection; m2-m14, intrinsic and extrinsic odontophore muscles; mc, buccal sphincter; oc, odontophore cartilages; ra, radula; rs, radular sac; sc, subradular cartilage



4. Anatomy of the Scaphopoda *Coccodentalium caduum*; **A**, Digestive tubes, left view, foregut opened longitudinally, the topology of some adjacent structures also shown, scale= 2 mm; **B**, Odontophore, dorsal view; **C.** Same, ventral view; **D.** Odontophore, anterior view, superficial layer of muscles and membranes removed, part of radula also removed (except portion inside radular sac), scale=0.5 mm (extracted from Simone, 2009). Lettering: cb, captacula base; cp, captacula; es, esophagus; dg, digestive diverticula; ft, foot; in, intestine; io, intestinal origin; m3, transverse muscle of odontophore; m4, pair of ventral tensor muscles of radula; m6, horizontal muscle; mj, protractor muscle of odontophore; mo, mouth; oc, odontophore cartilage; od, odontophore; of, inner fold of oral tube; on, odontophoral connection with esophagus; ot, oral tube; ra, radula; rn, radular nucleus; rs, radular sac; st, stomach

In the Euconchifera (non-monoplacophoran Conchifera) the buccal mass was totally lost in one of the main groups – the Bivalvia. No vestige of this structure is found in any of its representatives, even in their embryology. Thus, the buccal mass of the Scaphopoda is used to understand how buccal mass evolved in Diasoma. In scaphopods, the buccal mass looks like an appendix of the anterior digestive tube (Fig. 4A), instead of being along it, as the usual model. It is located only connected to the mouth (mo) by a small orifice, and it is located by side of the esophagus. The arrangement of the odontophore muscles and structures (Figs. 4B-D) is so that the only interpretation of its function is crushing the prey, instead of scraping it, as a usual radula (Simone, 2009, 2011). The muscles m3 and m6, joined to the odontophore cartilages (oc) form a circle, a prey located inside it is, thus, crushed when these muscles contract. The scaphopod radula looks more like a protective pavement, rather than an abrasive structure. Scaphopods usually eat small shelled invertebrates (e.g., young mollusks) and protozoans (e.g., foraminifers). It looks logical an odontophore works squeezing them to facilitate the subsequent digestion.

Abstracting the odontophore, the scaphopod foregut becomes similar to those of the bivalves. It is not difficult to imagine an appendix-like odontophore atrophying in a microphage animal like the bivalves' ancestor, in such the radula looks unnecessary.

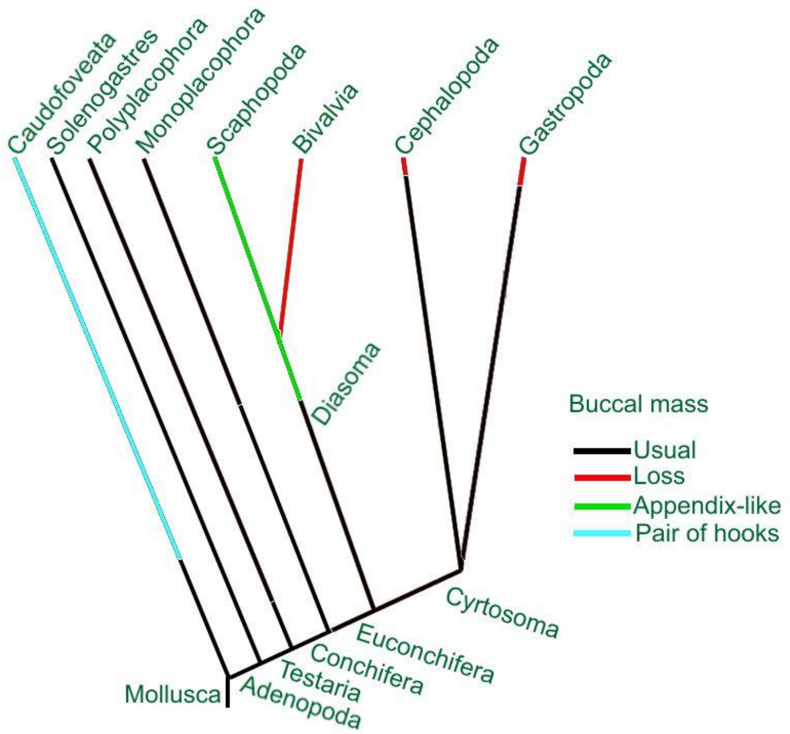
In the Cyrtosoma (Gastropoda + Cephalopoda), the buccal mass suffered all kinds of modifications, from an increment of complexity, up to its total loss. Groups lacking buccal mass, i.e., the mouth is connected to the stomach by a simple tubular esophagus, lacking buccal cavity as the first digestive stage, occurred in cephalopods at least once (Spirulidae), and several times in gastropods, such as, e.g., in coralliophilines, eulimids, some turriforms, some terebrids, some marginellids, amathinids, some pyramidellids, etc. Interestingly, the buccal mass loss is generally associated with parasitism (e.g., eulimids) or with predators that eat tender prey (e.g., some marginellids and the turriform *Daphnella*, preying delicate polychaetes).

The cyrtosoman buccal mass, odontophore in particular, is a true universe of issues to be explored. Some of them certainly will be done in future Malacopedia fascicles. Both, cephalopods and basal gastropods, share the dorsal jaw of a buccal cavity as a synapomorphy. In gastropods, however, the structure is usually a pair of small to large plates located in a dorsal region of a post-oral level. While the cephalopods have a single, huge, pointed dorsal jaw associated with another ventral similar component. Both joined to form the famous parrot-like beak, so characteristic to the class. The cephalopod beak has a muscular complexity comparable to that of the odontophore itself and is intimately anatomically related to them. Comparative and phylogenetic studies on these cephalopod buccal mass muscles and structures are interesting an issue for future papers, which are being developed in association with what exist in the literature. By the way, as told above the buccal mass of all classes will be further treated in future Malacopedia issues.

Phylogenetic inferences

Little can be added to the comparative discussion already performed above, with the notice that many details still will be covered in future Malacopedia issues, given the complexity and importance of the buccal mass components, the odontophore in particular.

Roughly, the basal type of buccal mass described above is found in almost all basal constituents of the classes, showing that the model is the basic, from which all other models evolved. This so-called "usual" model is represented in black in Fig. 5.



5. Morphology-based Mollusca phylogeny, mostly based on Simone (2011), showing different types of buccal masses as indicated by the colors (see text for details). The survey is not exhaustive.

Just the first molluscan branch – the Caudofoveata, modified the buccal mass bearing an odontophore with a single pair of hook-like teeth (Fig. 2). Ordinary odontophore is found only in more basal taxa (Fig. 2B).

More considerable modification is only found in Diasoma. The Scaphopoda haa an appendix-like buccal mass (green), evolving to the total loss in the Bivalvia (red). The black color (ordinary model) of the base of Diasoma is theoretical, a suggestion of how the buccal mass was in Rostroconchia, a fossil group that appears at the base of Diasoma (Simone, 2009). From a phylogenetic point of view, bivalves and scaphopods are modified rostroconchs, and only scaphopods presently have buccal mass to be studied.

As reported above, buccal mass loss is found both, in cephalopods and, more abundantly, in gastropods. This is the reason for the red color in the tip of both branches in Fig. 5. However, it is clear that, at least in gastropods, the phenomenon happened independently several times.

To summarize, the buccal mass is a fascinating structure with lots of important data to be studied in comparative biology, with crucial implications in Taxonomy and Phylogeny. The reasons for these changes are also intriguing goals to physiological studies. The main intention of this paper is to introduce the subject. Several other papers will be produced on various details of the buccal mass, mainly of the odontophore.

Acknowledgements

I thank to Claudia Heromy Guimarães, Australia, for comments and text corrections. Parts of the Fig. 2 were used in the PhD dissertation by Inês X. Martins, with my cooperation.

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Notice

This paper has as main intention of being popular scientific divulgation. However, the scientific rigor and accuracy is maintained. Opinions and feedbacks are always welcome, and even eventually can be added to the paper. Contacts in emails above.