Malacopedia

São Paulo, SP, Brazil
Volume 3(5): 22-28

ISSN 2595-9913
May/2020

Molluscan gizzards: evolution, development, distribution

Luiz Ricardo L. Simone

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

Abstract

Gizzards, or muscular structure to smash food, was developed independently in several branches of the Mollusca digestive system. Examples of different kind of gizzards are explored herein. The gizzards are classified in (1) buccal (e.g., in doricadean nudibranchs); (2) odontophoral/buccal mass (e.g., in scaphopods); (3) esophageal (e.g., in aplysiomorphs, cephalaspideans and chilinids); and (4) gastric (e.g., in megalobulimids, systellomatophorans, some olivids among the gastropods, and verticordiids in bivalves). A brief description and discussion are performed.

DOI: 10.13140/RG.2.2.26385.66406

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

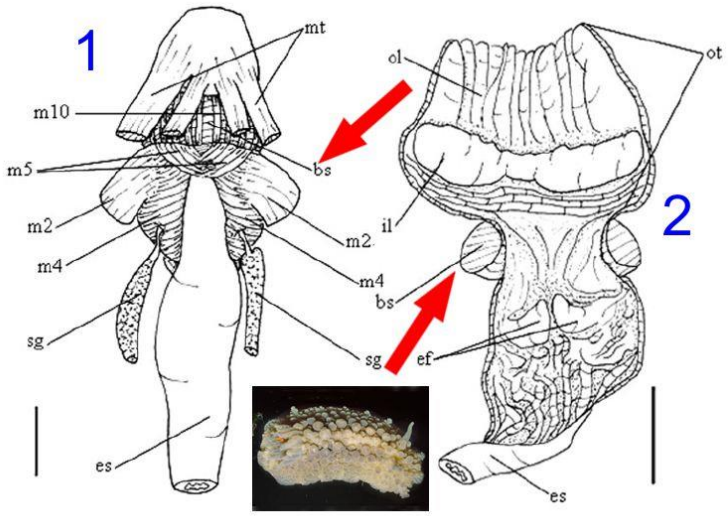
Introduction

Gizzards can be defined as a muscular located region of the digestive system specialized to smash the food, helping its processing. Molluscan gizzards occur at least in four classes – Gastropoda, Bivalvia, Scaphopoda and Cephalopoda – and can be located from pre-oral region up to the stomach. Despite in being an important taxonomical structure, gizzards appeared several times in molluscan evolution, in different ways, and are not always called 'gizzards'. This is explained in this paper, despite having no intention of exhausting the subject and the taxa that have the structure.

Gizzards usually are constituted by a bulged portion of the digestive tube, usually along the axis of it, with thick, strong walls of mostly circular muscular fibers. Their internal lumen surface usually is reinforced by a thick chitinous layer, sometimes even forming plates or spines. Their function usually is further mechanically processing the food, which was not properly crumbled in anterior structures, like the radula. As happens in birds, which lack teeth, the gizzard promotes mechanical crush, making the food goes further more properly processed.

The several kinds of gizzards and the taxa that possess them are discussed below. At first, the gizzards are classified by its localization along the digestive tube, the taxa that possess each type are duly reported, despite the survey is not exhaustive. The gizzards are, thus, classified in the following categories: 1) buccal; 2) odontophoral/buccal mass; 3) esophageal; and 4) gastric gizzards.

1. Buccal gizzard



1-2. Example of buccal gizzard (red arrows) in the nudibranch *Doris verrucosa* (extracted from Lima & Simone, 2015): **1.** Foregut, dorsal view; **2.** Same, opened longitudinally, ventral view, odontophore removed. Scales= 1 mm. Lettering: bs, buccal sphincter as anterior gizzard; ef, esophageal folds; es, esophagus; il, inner lip; m2-m5, odontophore muscles; mt, oral tube muscles; ol, outer lip; ot, oral tube; sg, salivary gland.

The buccal gizzard is more than a simply buccal sphincter, which usually is inconspicuous, normally seen in serial sections of transition mouth-integument.

Both, anyway, are usually constituted by circular muscular fibers, and are called buccal sphincter in current literature (e.g., Lima & Simone, 2015). A much more developed buccal sphincter, in order of being easily seen in dissection, actually works as a gizzard, and can be called "buccal gizzard".

A group that developed buccal gizzards are the doridid nudibranchs (Figs. 1-2). The structure is a strong and thick layer of circular muscles preceding the buccal cavity and the odontophore (bs). It certainly has the function of smashing the food, in order of being the first step in the food processing. The muscular layers that move the beak of the cephalopods also has a crush function, and can be classified as buccal gizzard.

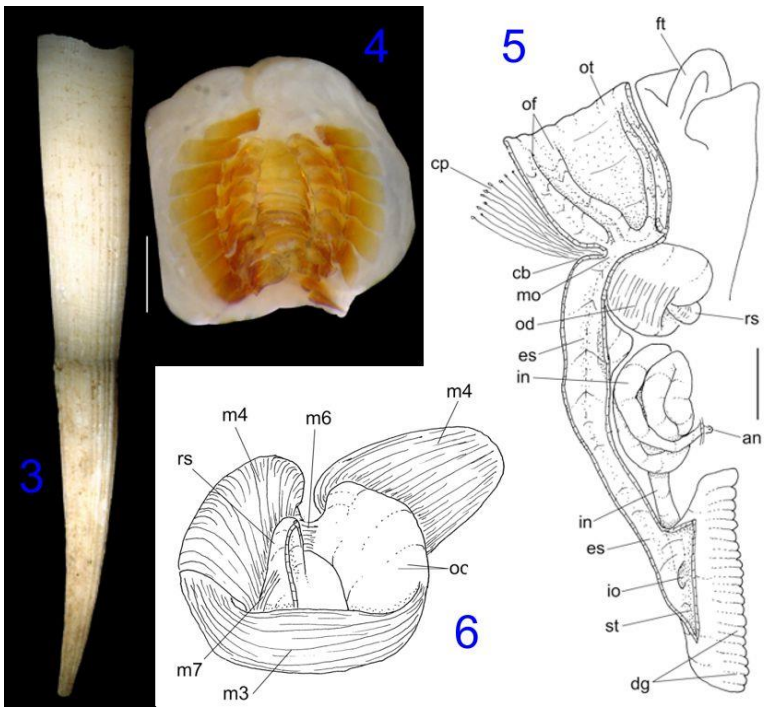
2. Odontophoral/buccal mass gizzard

The mollusk odontophore, *per si*, jointed to the remaining structures adjacent to it, works as a gizzard, as one of function of the buccal mass is to smash the food while the radula grinds it. The odontophore, as ventral structure, usually works opposite to the jaw plates in gastropods, which are dorsal, as a clip, removing pieces of the food, which will be further crumbed in odontophore posterior level. Jaws also occur in cephalopods as the beak, but are absent in other mollusk classes; they will be aim of other papers.

In the meantime, and despite the smash function of the buccal mass, which is an extraordinarily complex structure that will be addressed in future papers, a gizzard-like odontophore is

focused herein. A gizzard-like odontophore is found in scaphopods (Figs. 3-6). Analyzing the structure and appearance of the scaphopod radula (Fig. 4), it is possible to deduce that it has a crush function, rather than to grind.

The radula itself has the teeth organized as a pavement, adapted to quilt instead of sanding the food (Fig. 4). The odontophoral muscle organization also suggests a gizzard-like function, as it perform a complete ring, having the cartilages in lateral position, m3 and m6 in respective ventral and dorsal position (Fig. 6). Contracting, they promote the crash of the inside matter. The scaphopod odontophore is placed somewhat outside of the digestive tube main axis (Fig. 5: od), suggesting that the food enters in it, it is crushed, and returns to the esophagus to proceed the remaining digestive process.



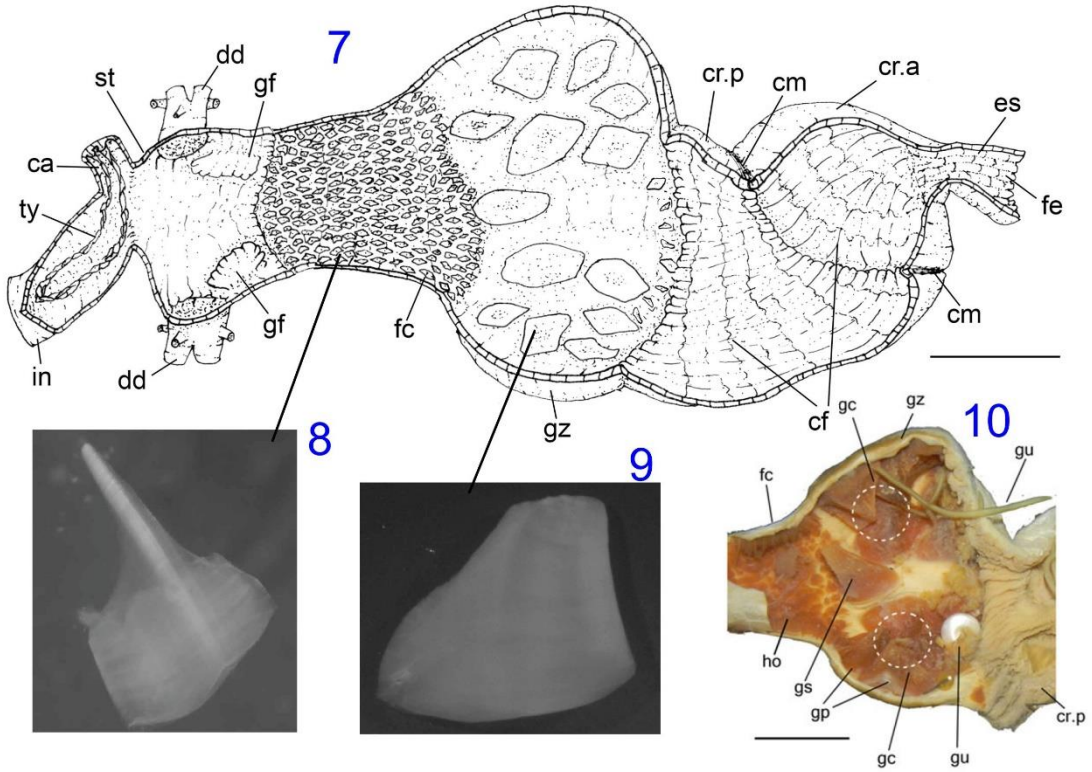
3-6. Example of odontophore gizzard in the scaphopod *Coccodentalium caduum* (extracted from Simone, 2009): **3.** Shell, right view (L ~60 mm); **4.** Radula, frontal view, scale= 1 mm; **5.** Digestive tubes as in situ, left view, scale= 2 mm; **6.** Odontophore, posterior view, radula completely removed, left portion of radular sac shown in situ, right m4 deflected. Lettering: an, anus; cb, captacula base; cp, captacula; es, esophagus; dg, digestive diverticula; ft, foot; m2-m5, odontophore muscles; in, intestine; io, intestinal origin; mo, mouth; of, inner fold of oral tube; oc, odontophore cartilage; od, odontophore; ot, oral tube rs, radular sac; st, stomach.

Scaphopods eat small shelled invertebrates living in interstitial space on the sediment, captured by the captacula. Mostly, and this is easily seen analyzing the content of the oral tube that works as a prey reservoir, the preys are foraminifers; more rarely young bivalves and gastropods are also found. The foraminifer testa are easy smashed, and their nutritive content can be more easily processed.

3. Esophageal gizzard

Gizzard located along the esophagus are the most common, and usually occurs in heterobranch gastropods. It can be present along any level of the esophagus length, but usually gizzards occur in posterior esophagus, in its region preceding esophageal insertion in stomach.

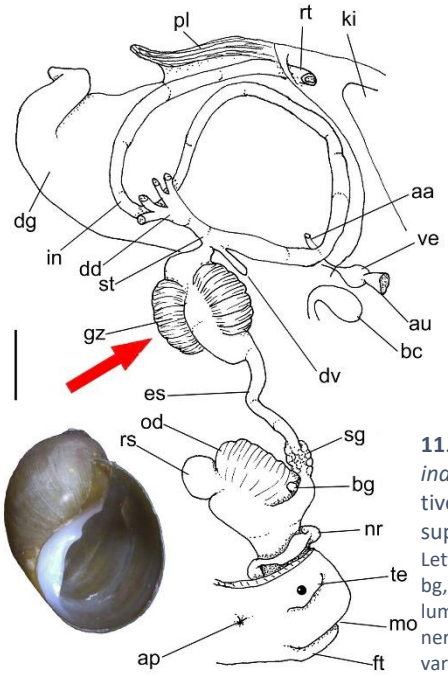
The esophageal gizzards are the more typical ones, and are the result of a muscular specialization of a given region, becoming a protruded, spherical hypertrophy of the esophagus, standing out from the rest of the organ.



7-10. Example of esophageal gizzard in the aplysiomorph gastropod *Aplysia depilans* (extracted from Cunha & Simone, 2018): **7.** Fore and midgut, dorsal view, almost completely sectioned longitudinally to show inner surface, scale= 10 mm; **8.** Gastric hook (L~1 mm) of indicated level; **9.** Gizzard plate (L ~8 mm) of indicated level; **10.** gizzard, dorsal view, opened longitudinally to show inner surface, dotted circle indicating clusters, scale= 10 mm. Lettering: ca, caecum; cf, crop folds; cm, circular muscle of crop; cr.a, crop anterior chamber; cr.p, crop posterior chamber; dd, duct to digestive gland; es, esophagus; fc, filter chamber; fe, esophageal folds; gc, gizzard cluster; gf, gastric fold; gp, gizzard plates; gs, gizzard plates; gu, contents of digestive system; gz, gizzard; ho, gastric hooks; in, intestine; st, stomach; ty, typhlosole;

Esophageal gizzards are the rule in aplysiomorphs and cephalaspideans. In the former the gizzard is almost entirely covered by chitinous plates (Figs. 7-10), being the larger ones in the middle level of the structure. While in the cephalaspidean, almost invariably the gizzard contains only three rather triangular plates (e.g., Eilertsen & Malaquias, 2013: fig 2D).

The usual esophageal gizzard of the aplysiomorphs is relatively complex, preceded by a crop (Fig. 7: cr), and succeeded by a filter chamber (fc), containing small hook-like plates (Fig. 8). The gizzard itself (Figs. 7, 10: gz) has muscular walls and the inner surface possessing large, tall, rather pyramidal plates (Figs, 9, 10: gs).



11. Example of esophageal gizzard in the chilinid basommatophoran *Chilina megastoma* (arrow)(extracted from Simone, submit.): most of digestive tubes and some adjacent structures as in situ, inferior in right and superior in ventral views, scale= 1 mm, and shell of paratype (L ~19 mm). Lettering: aa, anterior aorta; ap, penial aperture; au, auricle; bc, bursa copulatrix; bg, buccal ganglion; dd, duct to digestive gland; dg, digestive gland; dv, diverticulum; es, esophagus; ft, foot; gz, gizzard; in, intestine; ki, kidney; mo, mouth; nr, nerve ring; od, odontophore; pl, pallial muscle; rs, radular sac; rt, rectum; sg, salivary gland; st, stomach; te, cephalic flap; ve, ventricle.

Another heterobranch in such well-developed esophageal gizzard is found are the basommatophoran chilinids (Fig. 11: gz – arrow)

In chilinids, the gizzard is proportionally huge, and, strangely, has a pair of opposed muscular pistons, connected with each other my thick circular muscles. These pistons have a flat, chitinous inner surface adapted to smash the content more efficiently.

4. Gastric gizzard

The so called "gastric gizzard" is more commonly called muscular stomach. The gastric portion of the mollusk digestive system is easily marked by the presence of the duct(s) to the digestive gland (usually abbreviated "dd"). Some taxa developed highly muscular gastric walls, in order to work as a gizzard. Usually, the mollusk stomach is a selection zone of the digestive tube, selecting the food particles to take them to the duct(s) to the digestive gland, or to the intestine, or to be crushed to the crystalline style (Fig. 14: sy). All them will be subject matter of future papers. The muscular stomach, or gastric gizzard, has, thus, the additional function of smashing the food.

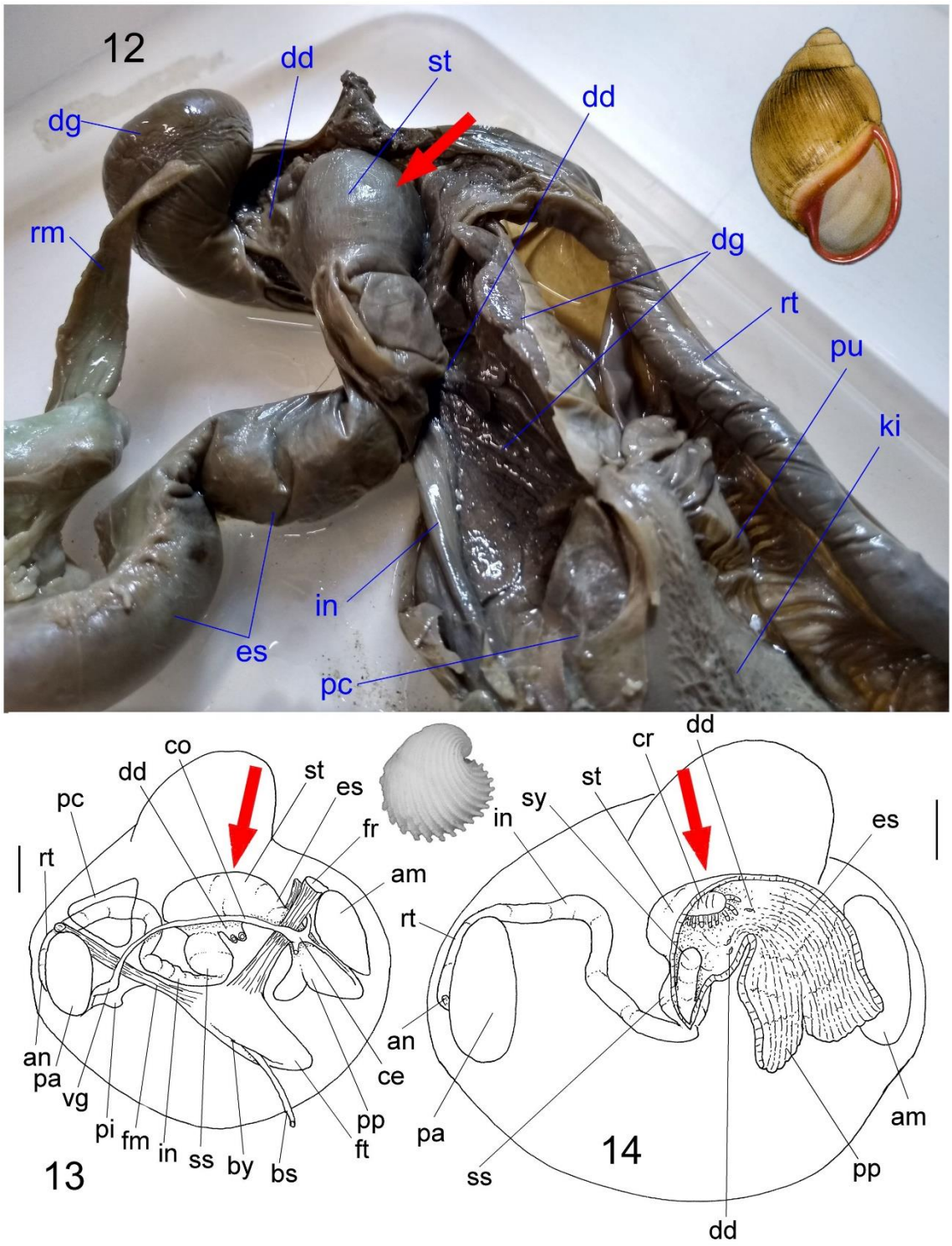
Gastric gizzards are found in several heterobranch gastropods, being an interesting convergence. One of them is the stylommatophoran strophocheilids of the genus *Megalobulimus* (Fig 12). The *Megalobulimus* have a strong muscular stomach, bulging in the esophageal-intestinal transition (Fig. 2: st). It has the duct to the posterior lobe of the digestive gland (left dd), while to the anterior lobe is originated from the distal region of the esophagus (right dd). the thick gastric walls in rich in muscular fibers apparently randomly organizes, with obvious predominance of circular fibers. The internal gastric surface has a clear chitinous layer, showing the mechanical attribution (gizzard-like) for the organ; selection ciliary areas are restricted to the folds surrounding the main chitinous surface.

Other taxa that also have surprisingly similar muscular stomach are the also stylommatophoran achatinid *Lissachatina fulica*. The systellommatophoran veronicellids also have similar muscular gastric organization. Possibly other eupulmonates also have similar gizzard-like stomachs. At least these three taxa reported herein have converged in this character (*Megalobulimus*, achatinids and veronicellids), as they are phylogenetically separated by taxa lacking muscular walls.

Amongst Gastropoda, gizzard-like stomach is also found in the caenogastropod olivids of the genus *Olivella*, which the protruded stomach can possess a narrow band of circular muscles or the stomach almost completely muscular.

The bivalves also have at least a group with muscular, gizzard-like stomach. The anomalodesmatan verticordiids also have a stomach with strong muscular walls (Figs. 13-14: st), and no apparent internal selection area. Verticordiids, as septibranchs, are carnivorous predators. They stay in the prowl with their strong siphons, capturing prey, normally small crustaceans (Fig. 14: cr) conducting them to the pallial cavity. The prey is, thus, swallowed whole, catched by the palps. The smashing work is done by the stomach itself, as a gizzard.

Discussion



12-14. Examples of gastric gizzards (muscular stomachs) (red arrows) **12**.Pulmonate gastropod *Megalobulimus oblongus* MZSP 136679 (Mortugaba, Bahia) (shell L ~120 mm, photo Fernanda S. Santos), dissected specimen, detail of transition pallial cavity and visceral mass, ventral view, visceral whorls partially uncoiled, genital structures removed, foregut deflected, midgut and hindgut in situ. **13-14**. Septibranch bivalve *Spinosipella deshayesiana*, shell (MNHN, Fiji, L ~12 mm) and anatomical drawings of whole right view; **13**. Digestive tubes, central nervous system and main musculature, including topology of some adjacent structures; **14**. Same, emphasizing digestive tubes, with their anterior region opened longitudinally. Scales= 1 mm. Lettering: an, anus; am, anterior adductor muscle; bs, byssus; by, byssal furrow; ce, cerebral ganglion; co, cerebro-visceral connective; cr, crustacean inside stomach; dd, duct to digestive gland; dg, digestive gland; es, esophagus; fm, posterior foot retractor muscle; fr, anterior foot retractor muscle; ft, foot; in, intestine; ki, kidney; pa, posterior adductor muscle; pc, pericardium; pi, papilla of excurrent chamber roof; pp, palp; pu, pulmonary cavity; rm, radular muscle; rt, rectum; ss, style sac; st, muscular stomach (gizzard-like); sy, crystalline style; vg, visceral ganglia.

Gizzards and gizzard-like structures appeared several times in the mollusk evolution. Some

examples are explored herein, but the survey is far in being exhaustive, possibly other taxa also developed gizzards in their digestive types. as explained above, gizzard can appear in different levels of the digestive system, from pre-buccal area up to the stomach, getting different names, but always functioning as food crusher by means of strong circular muscle fibers.

Acknowledgements

This paper was peer-reviewed by Patricia Oristanio V Lima, MZUSP, in such I am thankful.

References

Cunha, CM & Simone, LRL, 2018. Morphological re-description of *Aplysia depilans* (Gastropoda: Anaspidea): new insights into the anatomy of the anaspideans. Journal of the Marine Biological Association of the United Kingdom 99(3): 1-16. doi:10.1017/S0025315418000528

Eilertsen, MH & Malaquias, MAE, 2013. Unique digestive system, trophic specialization, and diversification in the deep-sea gastropod genus *Scaphander*. Biological Journal of the Linnean Society 109(3): 512-525.

Lima, POV & Simone, LRL, 2015. Anatomical review of *Doris verrucosa* and redescription of *Doris januarii* (Gastropoda, Nudibranchia) based on comparative morphology. Journal of the Marina Biological Association of the United Kingdom 95(6): 1203-1220. doi:10.1017/S0025315415000296

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, submitted. Freshwater micro-gastropods from Iguaçu National Park, Brazil: two new truncularioidean caenogastropods and anatomy of *Chilina megastoma* (Hygrophila, Chilinidae). Memórias do Instituto Oswaldo Cruz.