Malacopedia

São Paulo, SP, Brazil
Volume 6(1): 1-6

ISSN 2595-9913
February/2023

Main processes of body modification in gastropods: the miniaturization

Luiz Ricardo L. Simone

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

Abstract

Miniaturization is an evolutive process of great reduction of a gastropod to an adult form smaller than 1 mm. This process is not organically totally proportional. There are structures that became proportionally large, like stomach and pallial gonoducts. Other structures are simplified (e.g., genital structures), reduced and even lost (e.g., pallial structures, mainly the gill). While some structures, like the posterior pedal gland and the endostracum, are apparently exclusive of miniaturized forms. Despite the truly miniaturization looks exclusive of some branches of Apogastropoda, inferences in other gastropod groups and other mollusk classes are also provided.

DOI:

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

Introduction

The process called "miniaturization," as the name indicates, is the evolutive process in which the animal exaggeratedly diminishes its size. The miniaturization was partially approached in Simone (2018), as well as the giantism, as a method against predation in landsnails.

Although miniaturization can perfectly be a good anti-predator strategy, observing the mollusks as a whole, the usual apparent reason for the great size reduction is the adaptation to the environment. Habitats of scanty space or resources, like phreatic groundwater, caves, islands, interstitial sediment, etc., usually look more persuasive reason for leading such kind of evolutionary pathway.

A lot of controversy exists about the "normal" size of a mollusk. Informally, focusing on Testaria (non-aplacophoran mollusks), the "normal", or usual body size apparently is 30-40 mm. If the animal is bigger than this, it usually is considered "large;" if it is over 200 mm, "giant". If the animal is smaller than that "normal," it usually is considered "small," and if it is smaller than 10

mm, it is “micro”. Of course, this informal size classification excludes the cephalopods. Their body constitution, mainly mostly closed circulatory system, make them exceptions in body size considerations. These features predispose to body increment, as cephalopods are usually large beasts. Smaller ones, such as *Pickfordiateuthis* of 30-40 mm, are almost exceptions.

However, in the context of this paper, a true miniaturized gastropod are those taxa in such adult usually are smaller than 1 mm. species in which the adult has 0.6-0.8 mm in length or width, and a specimen of 1.0-1.2 mm are the giant individuals, are the focus here.

Practically only gastropods reached these minuscule proportions, and they did so in several branches independently. Some bivalves (e.g., *Pisidium*), caudofoveates and monoplacophores are minute, but they are larger than 1 mm. Even so, the miniaturization of these classes will be treated in a future Malacopedia issue.

The miniaturization evolutive process, from a 30-40 mm adult organism to a smaller than 1 mm, as observed by the comparative anatomical studies, is not a simple proportional diminishment of the structures, if the animal was put in a theoretical miniaturization machine. The miniaturization process is followed by a great disproportionate reduction of the different organs and systems, the simplification and even disappearance of some structures, etc. Some of these processes are explored below, including examples and phylogenetic inferences.

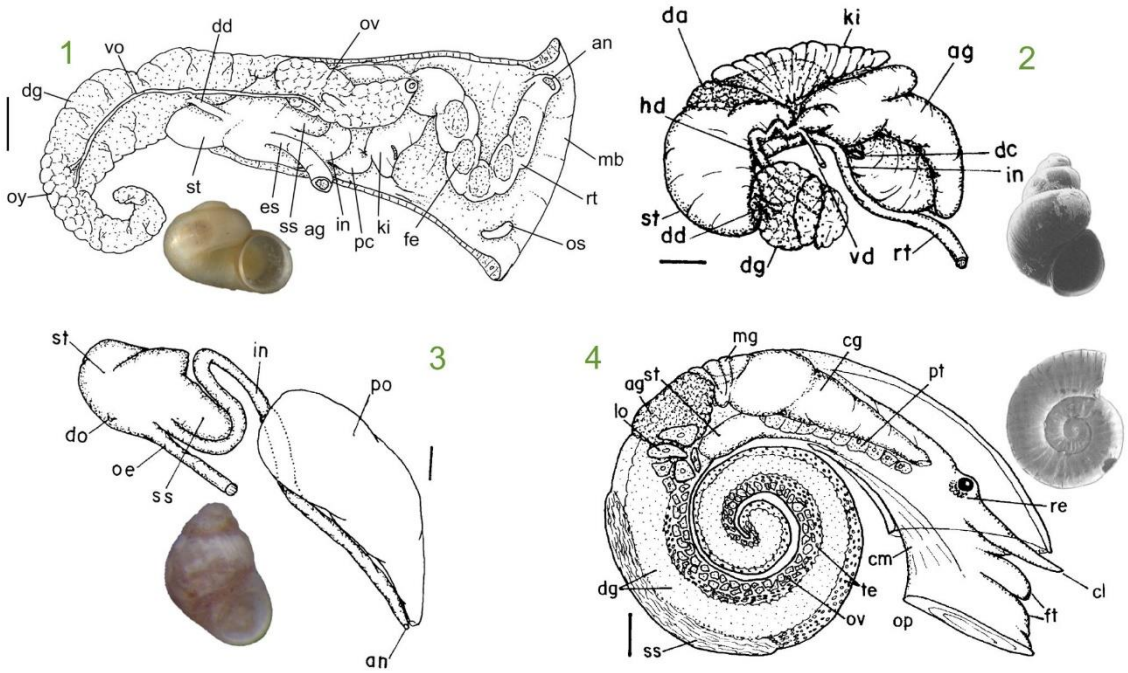
Anatomical idiosyncrasies of miniaturized gastropods

As referred above, several branches of Gastropoda evolved to a truly miniaturized form, i.e., adults smaller than 1 mm. In most of them, despite not being related, several anatomical coincidences appear, revealing that they are important to that minuscule form. These discrepancies, which can be called “idiosyncrasies” of the miniaturization evolutive process, can be divided into 3 categories: 1) organs proportionally larger than their non-miniaturized counterparts; 2) the contrary, organs proportionally smaller and even absent than their non-miniaturized counterparts; and 3) structures apparently exclusive of miniaturized forms:

1) Organs proportionally large

All the structures of the miniaturized forms are naturally small and simplified. However, two of them are usually outstandingly large among the others: the stomach and the pallial gonoduct, in special the female pallial oviduct (Figs. 1-4)

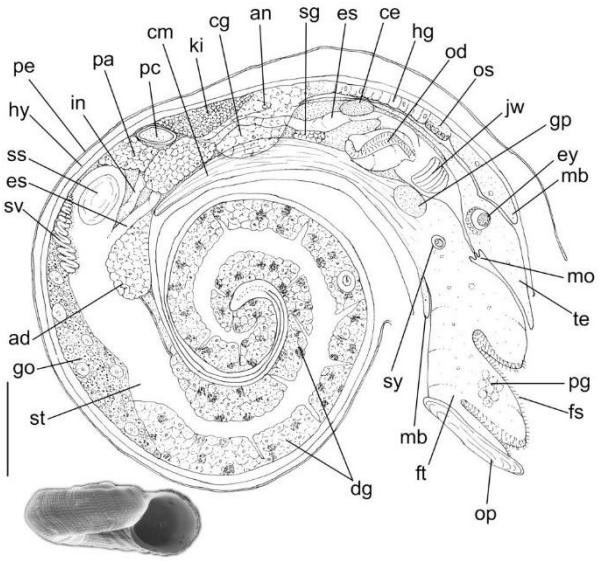
The disproportionality of these two structures stands out in anatomical studies compared to the remaining ones. This makes us interpret how important it is to process the meal and to reproduce even in such minute creatures, as much that they reserve 1/3-1/2 of their inner volume to them.



1-4 Examples of miniaturized (below 1 mm) gastropods: 1, *Atomicus inopinatus* (Caenogastropoda, Cochliopidae), pallial cavity roof, female, ventral-inner view, and uncoiled visceral mass, scale= 100 µm, shell MZSP 151667 (W 0.9 mm) (from Simone & Rolán, 2021); 2, *Risoella ornata* (Heterobranchia, Rissoellidae), two last whorls of visceral mass, ventral view, scale= 100 µm, shell (SEM) MZSP 28005 (L 0.8 mm) (From Simone, 1995a); 3, *Amphithalamus glabrus* (Caenogastropoda, Anabathridae), stomach and pallial oviduct as in situ, ventral view, scale= 100 µm, shell MZSP 28997 (L 0.8 mm) (from Simone, 1995b); 4, *Ammonicera plana* (Heterobranchia, Omalogyridae), entire semi-diagrammatic right view, scale= 10 µm, shell (SEM) MZSP 28225 (W 0.6 mm) (from Simone 1997). Lettering: ag, albumen gland; an, anus; cg, capsule gland; cl, cephalic lobe; da, anterior lobe of digestive gland; dc, duct to capsule gland; dd, duct to digestive gland; dg, digestive gland; cm columellar muscle; do, duct to digestive gland; es, esophagus; fe, fecal pellets; ft, foot; hd, hermaphroditic duct; ki, kidney; in, intestine; lo, large ova; mb, mantle border; mg, mucous gland; oe, esophagus; os, osphradium; ov, pallial oviduct or ovary portion of gonad; oy, ovary; pc, pericardium; po, pallial oviduct; pt, prostate; re, retina; rt, rectum; ss, style sac or sperm sac; st, stomach; te, testicular portion of gonad; vd, vas deferens; vo, visceral oviduct.

Despite proportionally large stomachs and pallial gonoducts can be faced as a rule in miniaturized forms, taxa with planispiral or almost planispiral shell (Figs. 4, 5), in which the internal space of the whorls is particularly tight, sometimes lack wide stomachs (Fig 4). But they are exceptions.

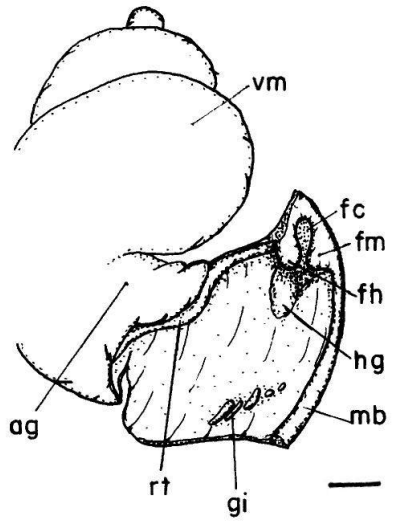
As referred before, the above-mentioned disproportion is possible to be detected in several non-related taxa. As exemplified here, there is heterobranchs (Figs. 2, 4, 5) and caenogastropods (Figs. 1, 3) that converged similar characteristics.



5. *Orbitestella patagonica* (Heterobranchia, Orbitestellidae), semi-diagrammatic longitudinal section, scale= 100 µm, shell MLP 6368 (W 0.6 mm) (from Simone & Zelaya, 2004). Lettering: ad, anterior lobe of digestive gland; an, anus; ca, capsule gland; ce, cerebral ganglion; cg, pallial genital gland; cm, columellar muscle; cs, style sac; dg, digestive gland; es, esophagus; ey, eye; fs, foot sole; ft, foot; go, gonad; gp, pedal ganglion; hy, endostracum; in, intestine; jw, jaw plate; mb, mantle border; mo, mouth; od, odontophore; op, operculum; os, osphradium; pa, posterior lobe of pedal gland; pe, periostracum; pg, posterior mucous gland; pt, prostate; sg, salivary gland; st, stomach; sv, seminal vesicle; sy, statocyst; te, cephalic lobe.

2) Organs proportionally small and even absent

With the extreme diminishment, the structures naturally became greatly simplified, which means that organs' branches, subdivisions, etc., tend to disappear in miniaturized forms. Examples are genital structures, usually having several glands, chambers, etc., particularly in heterobranchs, are much simpler in miniaturized forms (Figs. 2, 4, 5).



6. *Rissoella ornata* (Heterobranchia, Rissoellidae), whole extracted specimen, with special concern to pallial cavity (in frontal view), scale= 100 µm (from Simone, 1995a). Lettering: ag, albumen gland; fc, fecal chamber; fm-fh, mantle folds; gi, gill vestiges; hg, hypobranchial gland vestiges; mb, mantle border; rt, rectum; vm, visceral mass.

Being small-sized, the gas exchange for respiration of the miniaturized forms can be simply done by diffusion through the integument and mantle. Thus, a usually simplified and sometimes even atrophied structure is the gill in aquatic caenogastropods. Although it can be totally absent (Fig. 1), the more usual is to find vestiges of some gill filaments (Fig. 6: gi), even in very reduced snails.

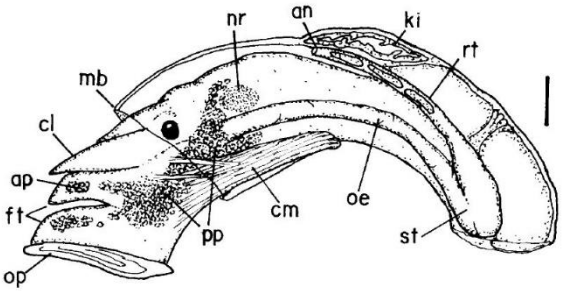
An interesting example is the cochliopid genus *Phreatodrobia*, in which some species have a well-developed gill, some have it vestigial, while others lack it at all (Hershler & Longley, 1986).

Other pallial structures, like osphradium (Figs. 1, 5: os) and hypobranchial gland (Fig. 6: hg), in the same amount as the gill, can also be reduced and also absent. All these structures are independent from each other, as one of them can be present, while others cannot. However, the osphradium can become microscopic, as a small set of preceptory cells, only detected by histological approaches. So far mostly caenogastropods are being evoked, the heterobranchs, as they have the pallial structures highly modified, are not good examples to study modifications in this region.

3) Organs apparently exclusive of miniaturized forms

Two structures are apparently exclusive of miniaturized gastropods: 1) the posterior pedal gland, and 2) the endostracum.

The posterior pedal gland, as the name indicates, is located posteriorly at the foot, in opposition to the current pedal gland, which, in those cases, are called "anterior pedal gland". The pedal gland, or anterior pedal gland (Fig. 6: ap), is virtually present in all crawling gastropods, and is responsible for the mucus production. This mucus permits the crawling movement and naturally must be located the most anterior possible.



6. *Ammonicera plana* (Heterobranchia, Omalogyridae), whole head-foot and adjacent region of pallial structures, left view, scale= 10 µm (from Simone, 1997). Lettering: an, anus; ap, anterior pedal gland; cl, cephalic lobe; cm, columellar muscle; ft, foot; ki, kidney; mb, mantle border; nr, nerve ring; oe, esophagus; op, operculum; pp, posterior pedal gland; rt, rectum; st, stomach.

The posterior pedal gland (Figs. 5: pg. 6: pp), on the other hand, are only found in very small snails. It is usually located from middle to posteriorly in the foot tissue, and its duct generally is located medially in the posterior third of the foot sole. Unlike the anterior gland, the posterior

pedal gland is not used to promote the locomotion of the animal, but so to anchor it into the substrate. It produces an adhesive mucus that is so efficient that permits minute snails to live on algae and rocks even in wavy regions.

Posterior pedal glands are found both, in miniaturized caenogastropods and heterobranchs, being an extraordinary convergence, and a clue that this structure is necessary for this life mode.

The other exclusive structure is the endostracum, also known as hypostracum. This is an organic layer that usually covers internally the shell of the miniaturized forms (Fig 5: hy). It is more properly seen when the shell is decalcified for anatomical study. The decalcification process keeps intact the organic layers of the shell, usually the periostracum (Fig. 5: pe). However, this process clearly shows the presence of the endostracum in most very small (micros) and miniaturized caenogastropods and heterobranchs as well, showing, thus, being another interesting convergence.

The function, and even the building of the endostracum are obscure matters, nothing intuitive can be inferred, except for any kind of protection against environmental acid or other chemical attack to the calcareous portion of the shell. In so minuscule shells, the calcareous layer is so thin that any environmental chemical reaction makes it disappear.

Micro-gastropods

Informally defining micro-gastropods as those species with adult shells ranging from 2 to 8 mm, and despite not being the focus of this paper, it is possible to infer some generalities that some of the processes described herein can be applied. Micro-gastropods are in the midst of miniaturization, and some of the above-mentioned phenomena are already present in them. They really already have disproportional stomachs and pallial gonoducts, mainly the smaller ones. Endostracum and posterior pedal glands are sometimes present, as well as the simplification and loss of some structures can be already detected. An example was already explored in the osphradium (Simone, 2021) with the presence of monopectinate ones.

Phylogenetic inferences

Truly miniaturized forms (below 1 mm) are practically exclusive of 2 groups of Apogastropoda (Heterobranchia + Caenogastropoda) (Simone, 2006, 2011). One of them is a grade called allogastropods, which are basal heterobranchs. Some of them evolved to miniaturized forms, particularly Omalogyroidea, Obistestelloidea and Rissoelloidea, possibly as convergences, and the slug Rhodopemorpha (Brezinger et al., 2013).

The other is a caenogastropod branch that in the Simone (2011) concept is a single taxon – Rissooidea, but in MolluscaBase (2023) it is divided into 3 branches: Littorinoidea, Rissooidea and Truncatelloidea. In this taxon, several families and genera, both in freshwater and marine habitats, evolved to miniaturization. The internal phylogenetic organization of this taxon is still unclear, but apparently the miniaturization process converged several times in this group.

The other gastropod branches have small-sized species, but usually larger than 1 mm. the Cocculiniformia, and some fissurellids, seguenzioideans, etc., among the Vetigastropoda (e.g., Kunze et al., 2008), have some small-sized examples.

Acknowledgements

This paper was partially criticized by José Leal, Balley-Matthews National Shell Museum, in such I thank for comments and corrections.

References

Brenzinger, B; Haszprunar, G & Schrödl, M. 2013. At the limits of a successful body plan – 3D microanatomy, histology and evolution of *Helminthope* (Mollusca: Hetreobranchia: Rhodopemorpha), the most worm-like gastropod. Frontiers in Zoology 10(37): 1-26.

Hershler, R & Longley, G, 1986. Phreatic Hydrobiids (Gastropoda: Prosobranchia) from the Edwards (Balcones Fault Zone) Aquifer Region, south-central Texas. Malacologia 27(1): 127-172.

Kunze, T; Hess, M; Brückner, M; Beck, F & Haszprunar, G. 2008. Skeneiform gastropods in Neomphalina and Vetigastropoda – A preliminary report. Zoosymposia 1: 119-131.

MolluscaBase (2023), http://www.marinespecies.org/aphia.php

Simone, LRL, 1995a. *Rissoella ornata*, a new species of Rissoellidae (Mollusca: Gastropoda: Rissoelloidea) from the southeastern coast of Brazil. Proceedings of the Biological Society of Washington 108(4): 560-567. http://www.moluscos.org/trabalhos/1995/Simone%201995-Rissoella.pdf

Simone, LRL, 1995b. A new *Amphithalamus* Carpenter, 1864 species (Gastropoda, Rissoidea, Barleeidae) from the Brazilian coast. Journal of Conchology 35: 329-333. http://www.moluscos.org/trabalhos/1995/Simone%201995-Amphitalamus.pdf

Simone, LRL, 2006. Accounts on the phylogeny of the Rissooidea (=Hydrobioidea) and Littorinoidea, based on some American representatives, as base for a future taxonomic revaluation (Mollusca, Caenogastropoda). Strombus 2(13): 18-26. http://www.moluscos.org/trabalhos/2006/Simone%202006%20Rissooidea%20Phylogeny.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, 2018. Physical defense strategies of South American land snails. Malacopedia 1(2): 3-11. http://www.moluscos.org/trabalhos/Malacopedia/01-02%20Simone%202018%20Physical%20strategies%20of%20defense.pdf

Simone, LRL, 2021. The mollusk osphradium, structure and evolution. Malacopedia 4(4): 38-49. http://www.moluscos.org/trabalhos/Malacopedia/04-04Simone%202021%20Malacopedia-%20Osphradium.pdf

Simone, LRL & Rolán, E, 2021. A new genus and three new species of freshwater cochliopids (Caenogastropoda) from Goiás, Brazil. Iberus 39(1): 1-21.

Simone, LRL & Zelaya, DG, 2004. A new *Orbitestella* (Gastropoda: Heterobranchia: Orbitestellidae) from tierra del Fuego, Argentina. Nautilus 118(4): 160-166.