

Physical defense strategies of South American land snails

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Abstract

A discussion on the singular physical strategies of defense against predators in South American land snails is exposed, mainly against other carnivore land snails of the families Streptaxidae, Scolodontidae and Spiraxidae, common in the continent. They are (1) apertural barriers (teeth, etc); (2) change in the direction of the shell growth; (3) hypercoiling; (4) hyper-retraction inside the shell; and (5) alterations of size, including giantism and miniaturization; (6) sinister-coiling. Examples, short description and discussion of them are included.

Introduction

Land snails have a series of strategies to defend against predators. Some are beyond the usual well-known tactics, such as:

- (1) The **shell**, which are a hard, protective involucre for the soft inner tissue.
- (2) The **operculum**, which encloses the shell aperture, making the shell a small safe-box (the clausilium and hard epiphragm of some pulmonates also work similarly).
- (3) Chemical repellents, venom or poison mainly found in slugs with reduced or absent shell (which are not physical properly).
- (4) Behavioral traits, such as nocturnal and fossorial habits, leaping movements, etc. (which also are not physical).

This paper deals with additional sort of physical strategies found in South America land snails, which possibly can be extrapolated to malacofauna from other continents.

Land snails are preyed upon by several small and large animals in South America, a feeding habit known as malacophagy. Birds and mammals are typical snail predators, but there are also several invertebrate predators, such as wasps, ants, beetles, flatworms, and even other snails. In



1: *Streptaxis decussatus* preying on *Bulimulus tenuissimus* (from Simone, 2006) (diameter ~20 mm)

the mainland, 3 pulmonate families are known as predators of their counterparts: Streptaxidae (Figs. 1, 2), Scolodontidae (Systrophiidae in older literature) (Fig. 3), and Spiraxidae. Representatives of the latter family are more common in the north regions of the mainland, Amazon Rainforest in particular, while the other 2 families have representatives widespread along the tropical and subtropical regions of it.

The streptaxids differ from the other 2 families in possessing an eversible proboscis (Simone, 2013), allowing the animal keeping its head and tentacles close to, or even outside of their prey's aperture, while the proboscis does its job. The scolodontids, on the other hand, have a clear protruded gland in dorsal

region of posterior end of the foot (Fig. 3).

The typical radula of these 3 families has a character in common – their teeth are tall, pointed, hook-like, very efficient for carnivory. The Fig. 4 shows an example of it.

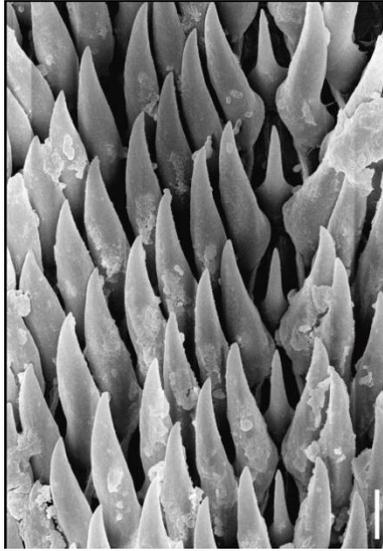
For more information about morphological defense (at least in aquatic snails) can be checked elsewhere (e.g., DeWitt et al, 2000; Preisser et al, 2005; Bourdeau, 2009, 2012); and Barker (2004 – terrestrial).



2: *Streptaxis capillosus* preying on *Solaropsis* sp (courtesy Femorale) (diameter ~20 mm)



3: *Happia* sp crawling on a flask border, note posterior dorsal pedal gland (from Simone, 2006) (diameter ~10 mm)



4: radula of *Huttonella bicolor* (from Simone, 2013) (scale= 10 μ m)

The text below presents the more common physical methods which are found in South American land snails.

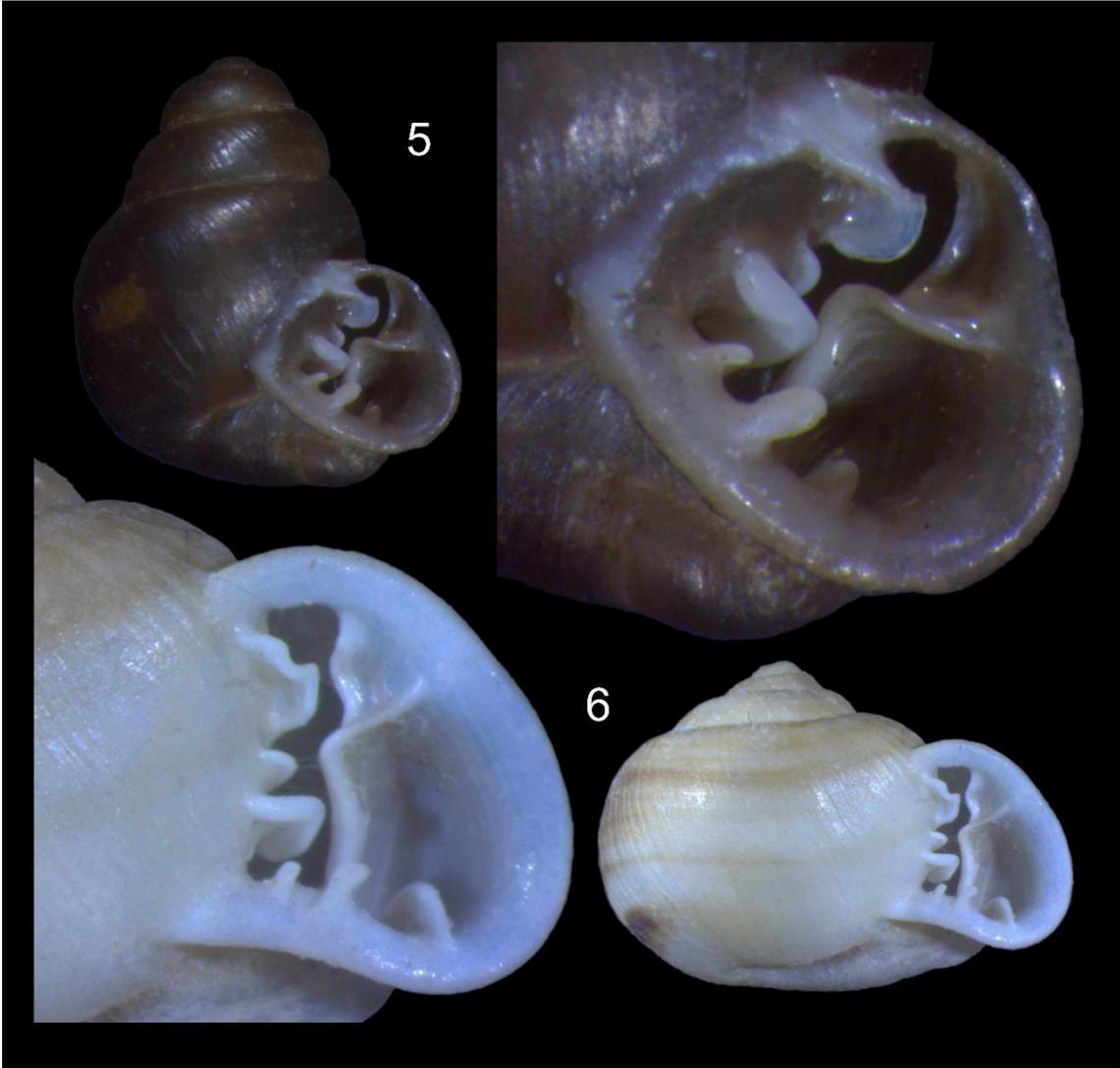
1. Apertural barriers (teeth, etc.)

Representatives of most South American families of pulmonates have developed teeth and lamellae on the shell aperture in different degrees of size and number. The placement and design of these apertural teeth strongly hampers any attack by another land snail and even arthropods and worms. Depending on the form, quantity and complexity of the teeth arrangement, the penetration of the predator's head-foot or proboscis can be hampered, as well as its withdraw. The same can be inferred to armored bugs, like ants, beetles and their larvae.

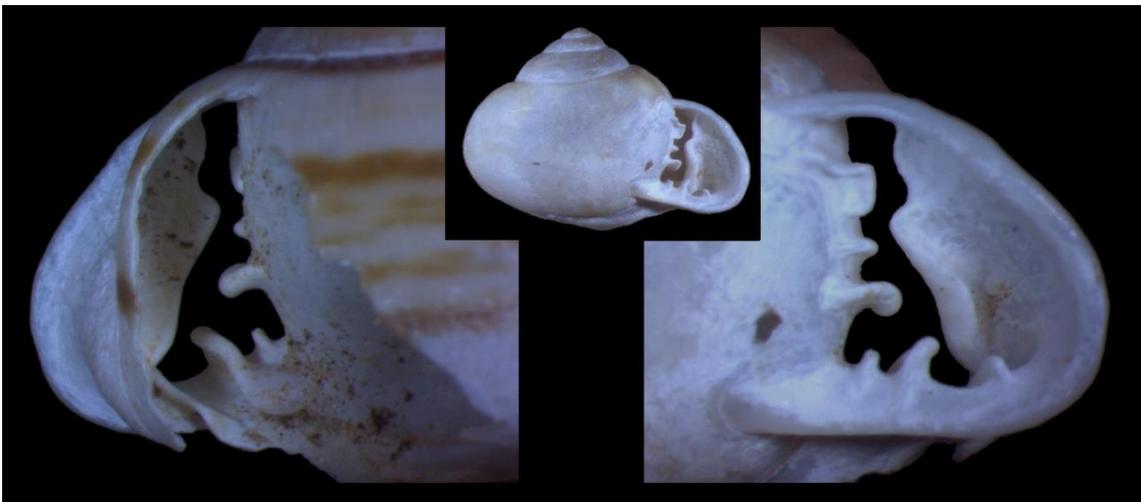
The Figs 5-6 show odontostomids with a high development of apertural teeth. The teeth are well-developed in all peristome surfaces, mainly a central undulating flap in the middle level of the outer lip. This profusion of teeth also precludes the own animal, as it delays a lot for retracting or protruding; but it should be worth it.

A study of the aperture of these shells with profuse apertural teeth (Fig. 7) shows that some teeth are long flaps, called lamellae or plicae, running internally along $\frac{1}{4}$ whorl, while other are single short protrusions, looking really a tooth.

More examples of species which developed protective teeth at aperture are shown in the Figs. 8-11. The more notorious are the odontostomids (Figs. 5-10), in such the name is a clue, but other South American families also have representatives with that convergent character (e.g., *Labyrinthus* - Fig. 11 - a camaenid/pleurodontid). Figure 12 shows the usual terminology for apertural teeth. The inner lip is divided into parietal (superior half) and columellar (inferior half) regions; while the outer lip is simply called palatal region (yellow words); the localization of the teeth in each region is used to name them (white words).



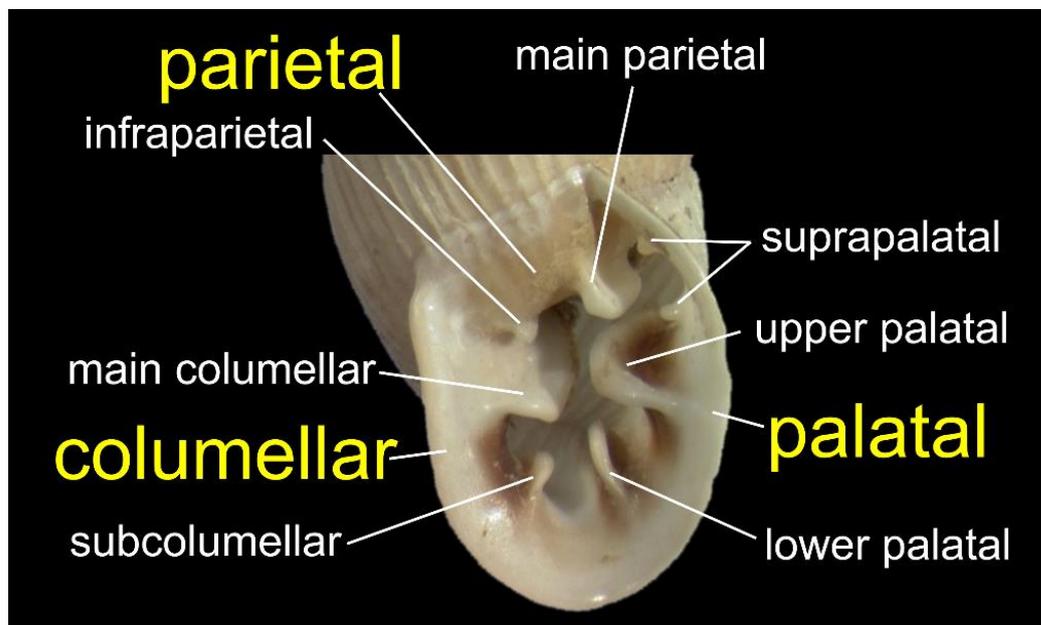
5: Shell of *Biotocus ubajarensis*, with a detail of aperture (L 5.5 mm); 6: the same for *Tomigerus clausus* (W 15.5 mm)



7: Apertural study of a shell of *Tomigerus clausus* (W 14.1 mm), with detail of outer view (left), and inner view (right) through an artificial window done in shell last whorl.



Additional examples of shells with protective teeth in aperture: 8, *Ringicella luetzelburgi*; 9, *Macrodonates leniusculptus*; 10, *Cyclodontina gemellata*; 11, *Labyrinthus diminutus*



12, Usual terminology of peristome teeth, example in *Cyclodontina gemellata*. Yellow: regions; white: specific tooth (adapted from Burch, 1962).

2. Change in the direction of shell growth

Some terrestrial gastropods have weird shell growth, mainly in the last whorls, making them of strange shape if compared to species in such the shell growth is more uniform. Change of the growth direction certainly may confuse any fortuitous predator.

In south America, species of the genus *Anostoma* (Fig. 13) are the most famous, with half last whorl totally displaced from the expected position.



13, *Anostoma deshaysianum*, 4 views of its shell (from Simone, 2006) (W 27 mm)



14, *Clinispira insolita*, two views of holotype (from Simone & Casati, 2013) (L 14.6 mm)

Another example is a relative, *Clinispira insolita*, which also possesses the last half whorl very displaced (Fig. 14).

Of course, the aperture displacement is only found in the adult specimens, in such its growth is ended. Younger specimens look very different, and usually with ordinary shape. Young specimens of species with these adaptations are difficult to identify, and usually are in wrong places in collections.



15, *Opisthostoma secretum*, two views (from Cavallari et al, 2016) (L 0.9 mm)

Although not from South America, as curiosity, some Asian diplommatinids are famous by their very weird shell coiling, possessing great coiling displacement even before the last whorl. An example is in the Fig. 15.

3. Hypercoiling



16, *Polygyratia polygyrata*, two views (W 44 mm); 17, *Beckianum beckianum* (L 6 mm) (both from Simone, 2006)

Great quantity of coils of a shell looks another strategy for avoiding malacophagy. In these cases, the shell whorls become so tight, squeezed, that any predator can be discouraged.

There are two kinds of hypercoiling: (1) in a dischid shell, in such the more notorious are the species of *Polygyratia* (Fig. 16). (2) in a turritiform shell (Figs. 17, 18).

Hypercoiling also produces a more resistant shell to breaking and crushing (Salvador, pers.com.)

4. Hyper-retraction

Some species have a high capacity to retract inside the shell, deeply inside. The wide distance between the shell aperture and the retracted specimen looks another interesting strategy to avoid predation.

A photographed example is in Fig. 18, the subulinid *Lavajatus moroi*, in such the yellow bar indicates the high distance between the retracted specimen and the aperture of its shell, easily seen by translucency.

Of course, the capacity of retraction inside the shell depends of additional factors, such as the degree of nutrients stored in the digestive gland; and, sometimes, the degree of desiccation of the specimen.

18, *Lavajatus moroi*, subulinid with translucent shell showing a high capacity of retraction, indicated by the yellow bar (L 30.8 mm).



5. Alterations of size

Alterations of the body size can be also evoked as an adaptation for avoiding malacophagy. Both, giantism and miniaturization are found in some groups of land snails in South America.

Interestingly, giantism is the rule in the acavid genus *Megalobulimus*, widespread in the mainland with dozens of species (most undescribed). But large-sized species are present in other groups, such as, e.g., the megaspirid *Thaumastus*, the orthalicids *Porphyrobaphe* and *Sultana*, the subulinid *Neobeliscus*, and the amphibulimid *Plekocheilus*. A giant snail over 100 mm is difficultly predated by most invertebrates and carnivore snails, in the range of 10 mm.

In the other extreme, the miniaturization, here are several land snails, such as, e.g., the helicininid *Alcadia*, the diplommatinid *Adelopoma*, the strobilopsid *Strobilopsis*, the euconulid *Pseudoguppya*, and in the scolodontid *Entodina*. However, the miniaturization is remarkable in the charopids, with several genera and dozens of species (several new) of tiny dimensions.



19, the acavid *Megalobulimus grandis* (shell L 150 mm), 20, a helicodiscid *Radiodiscus* sp crawling on it in same proportion (W 1.5 mm), showing discrepancy of sizes (19= from Femorale).

6. Sinister-coiling

As most snails are dextral, i.e., right-coiling, a sinister, left-coiling snail can confuse a predator. A classical example is the African ampullariid *Lanistes*, which may be a problem to the snail-eating hawk, with beak adapted to dextral snails. However, sinister species are rare in South America. One of the few examples are orthalicids of the genus *Corona* (see Simone, 2006: 159-160), in such about half of the specimens are sinister.

Conclusion

It is important to keep in mind that the terrestrial gastropods are animals that are part of an ecosystem. As so, they are predated and need to defend against that. Here some interesting physical adaptations are exposed, although much others can be evoked. The fauna from other continents certainly has groups that also converged those strategies, as well as other kind of adaptations that are not included herein, which are welcome to be commented in correspondence with the author's email.

Acknowledgements

The referee of this paper was Rodrigo Brincalepe Salvador, presently working in Te Papa Tongarewa Museum in New Zealand, which I thank for the corrections, comments and ideas.

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