

Land snail diversity in Brazil

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Abstract: Brazil is a megadiverse country for many (if not most) animal taxa, harboring a significant portion of Earth's biodiversity. Still, the Brazilian land snail fauna is not that diverse at first sight, comprising around 700 native species. Most of these species were described by European and North American naturalists based on material obtained during 19th-century expeditions. Early 20th century malacologists, like Philadelphia-based Henry A. Pilsbry (1862–1957), also made remarkable contributions to the study of land snails in the country. From that point onwards, however, there was relatively little interest in Brazilian land snails until very recently. The last decade sparked a renewed enthusiasm in this branch of malacology, and over 50 new Brazilian species were revealed. An astounding portion of the known species (circa 45%) presently belongs to the superfamily Orthalicoidea, a group of mostly tree snails with typically large and colorful shells. It has thus been argued that the missing majority would be comprised of inconspicuous microgastropods that live in the undergrowth. In fact, several of the species discovered in the last decade belong to these "low-profile" groups and many come from scarcely studied regions or environments, such as caverns and islands. These places still undoubtedly hide many surprises for malacologists and there is still a long way to go until we have a good understanding of the terrestrial gastropod fauna in Brazil. The science behind this venture, however, is still underfunded and moving at a snail's pace. This is especially unsettling, as land snails are deemed one of the animal groups most vulnerable to extinction, and the overly-exploited natural environments in Brazil might not last long, especially considering the country's recent environmentally harmful policies.

Key-Words: Caenogastropoda, Eupulmonata, Neritimorpha, Stylommatophora.

INTRODUCTION

The term "land snails" does not refer to a natural group in evolutionary terms. Rather, it includes lineages belonging to distinct gastropod subclasses that colonized the terrestrial environment independently from one another. The vast majority of land snails, though, belongs to a single larger group, known colloquially as "pulmonates" (superorder Eupulmonata; Bouchet *et al.* 2017). In most cases worldwide, the bulk of gastropod diversity lies within pulmonates, but some other lineages, like the helicinids (subclass Neritimorpha), can also be remarkably diverse.

The number of known species of terrestrial gastropods worldwide sits around 25,000 (Rosenberg 2014), but it is widely expected that this number will increase as new species are discovered (Scheffers *et al.* 2012). Researchers consider that there is a certain urgency in discovering and describing new land snail species because they (and their freshwater counterparts) likely have the highest extinction rate of all animal groups (Lydeard *et al.* 2004; Régnier *et al.* 2009, 2015).

Brazil is a prime megadiverse country for many (if not most) animal taxa, harboring a significant portion of Earth's biodiversity, especially invertebrates (Lewinsohn *et al.* 2005). Its distinctive biomes such as the Atlantic Forest and the Cerrado have, besides the overall biodiversity, high degrees of endemicity (Mittermeier *et al.* 2004). Nevertheless, the Brazilian land snail fauna might not seem that diverse at first sight, including "only" 700 native species. There is a series of reasons why this statement is simultaneously true and inaccurate, and the present chapter will explore them. Herein, the diversity of land snails in Brazil is analyzed from historical, taxonomic, methodological and ecological perspectives; furthermore, the current state of the

knowledge and the biases in research are addressed, with indications of the areas that would most benefit from future research.

MALACOLOGY IN BRAZIL

A large portion of the terrestrial gastropods in Brazil (and South America in general) were described by European and North American naturalists based on material obtained from 19th-century expeditions. Several articles and books from that century discussed the country's land snails, such as Spix (1827), d'Orbigny (1835), Moricand (1836, 1846), Pfeiffer (1845, 1853), Albers (1860), and Martens (1868), to name a few.

Early 20th century malacologists also made remarkable contributions to the study of land snails in the country, but they were still mostly from Europe and the USA (*e.g.*, Gude 1902; Wagner 1907–1911; Baker 1914; Thiele 1927). One Brazilian naturalist, however, deserves a spotlight during this period: Hermann F. A. von Ihering. Born in Germany, he moved to Brazil in 1880 and eventually became the director of the Zoology Museum of São Paulo in 1894 (Lopes & Podgorny 2014). He published articles on recent and fossil animals, mollusks and vertebrates alike (*e.g.*, Ihering 1900, 1912), and had contact with many malacologists and paleontologists worldwide, such as Florentino Ameghino in Argentina, Henry Suter in New Zealand, and Henry A. Pilsbry in Philadelphia, USA, to whom he often sent specimens. The later researcher in particular deserves further notice

Pilsbry thoroughly explored South American snails in the second series of George W. Tyron's Manual of Conchology. He described many new species and revised most of the then-known species, assembling a vast collection of specimens in the Academy of Natural Science in Philadelphia (Baker 1958). The multi-volume Manual of Conchology ran from the late 19th century until the mid-1930s.

After Pilsbry, efforts in terrestrial malacology were few. Brazilian researcher Frederico L. de Morretes published some new land snail species (Morretes 1937, 1940) and had already made remarks about the lack of studies on mollusks in the country (Gernet *et al.* 2018). The first large effort to deal with Brazilian land snails, however, was Bequaert's monograph (1948) revising the Strophocheilidae, one of the most diverse families in South America. Shortly afterward, there was the publication of the first comprehensive inventory of Brazilian mollusks Morretes (1949), which was quickly followed by an expansion (Morretes 1953).

In the next years, Brazilian malacologists started to conduct more research on land snails. Nevertheless, publications were still relatively scarce (e.g., Oliveira & Castro 1979; Marcus & Marcus 1968; Vaz 1991), with some exceptions such as the several works authored by J. Leme mainly about the Strophocheilidae (e.g., Leme 1973), by J. Thomé on the Veronicellidae slugs (e.g., Thomé 1975), and by Dutch malacologist A. Breure on the Orthalicoidea (e.g., Breure 1979).

Salgado & Coelho (2003) published an extensive checklist of land snails (excluding slugs) in Brazil, and shortly after, Simone (2006) published his catalog book of Brazilian terrestrial and freshwater mollusks. That book was the first to offer colored photographs, including several type specimens. Not many Brazilian land snails were described in the period from the 1950s until Simone's (2006) catalog. In fact, that catalog might have sparked a new interest in these animals: in the 2010s the number of works increased dramatically, as reported by Birckolz *et al.* (2016), who updated said catalog.

METHODOLOGY

For the present chapter, the works of Simone (2006, and its corrigenda of 2008) and Brickolz *et al.* (2016) were used as basis for number of species in each family and their geographical occurrence (only mentions of specific localities, like cities and states, were considered, not vague regions such as "northern Brazil"). To those were added all the works published in the scientific literature since 2016. These later works comprise three sorts of data. (1) Works describing new species: Cuezzo & Pena (2017: 1 new species), Salvador *et al.* (2017: 1 species; 2018b: 1 species), Salvador (2018: 2 species), Simone (2016: 1 species; 2018a: 1 species; 2018b: 1 species; 2019: 2 species), and Simone & Amaral (2018: 3 species). (2) Works updating the geographical distribution of known species: Arruda *et al.* (2016), Coscarelli *et al.* (2018), Cuezzo *et al.* (2018), Fontenelle *et al.* (2019), Salvador (2018, 2019), Salvador *et al.* (2017, 2018b, 2018c), and Silva *et al.* (2019). (3) Works synonymizing species: three species synonymized by Salvador *et al.* (2018c) and one by Fontenelle *et al.* (2019).

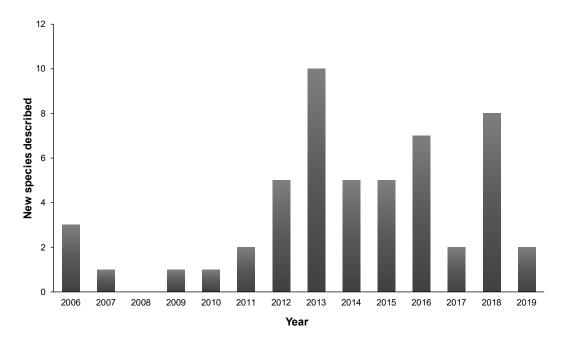


Figure 1. Chart showing the number of land snail species described from Brazil per year since the publication of the catalog of Simone (2006).

The family-level classification of all genera presented herein was updated to conform to the work of Bouchet *et al.* (2017), while the generic allocation of species follows MolluscaBase (2018), which compiles the latest revisionary taxonomic works.

TAXONOMY

Presently, there are circa 700 native species described from Brazil (Table 1). Simone (1999), however, estimated that only a third of land snail species in Brazil was then known and described, which would raise this number to around 2,000.

Since the publication of Simone's catalog in 2006, 52 new species of land snails have been described from Brazil (Figure 1). As argued above, this renewed interested was likely inspired by said catalog, which brought all the knowledge together in one place and became a handy starting point for any research on Brazilian land snails. Moreover, circa 85% of the new species were described since 2012 (Figure 1), showing that the study of the terrestrial molluscan fauna is seemingly picking up the pace. Even so, if the estimate of Simone (1999) that only one third of the species are presently known corresponds to reality, then it would take more than three centuries to describe everything in the current rate. A snail's pace indeed.

On the other hand, the slow rate of discovery could mean that the estimate of Simone (1999) is not accurate and that there are fewer species awaiting discovery than initially expected. For instance, a thorough expedition to Pedra Talhada Biological Reserve in NE Brazil recorded a total of 47 species (Salvador *et al.* 2018b), of which only two had never been reported from Brazil and only one was entirely new to science. That represents circa 6% of the records adding to the number of species in Brazil. Even though the molluscan fauna from this Reserve was only scarcely studied before, this number might not be a good representative for the country's undiscovered biodiversity, as other types of habitats and regions might hold more discoveries (see below).

Another interesting point is that almost all the species listed on Simone's (2006) catalog are still considered valid (apart from a few taxa noted as *nomina nuda*, *nomina dubia* or *species inquirendae*). This can at first be seen as a statement to the actual reality of those species and to a solid state of their taxonomy. However, a more down-to-earth assessment needs to consider the lack of revisionary studies that aimed to determine the taxonomic validity of all these species. Some families indeed have been revised since Pilsbry's Manual of Conchology, like Strophocheilidae (Bequaert 1948) and Bulimulidae (Breure 1979), but even these now need a new careful look. Furthermore, even revisions in the generic or species level were few (e.g., in the

last decade or so: Hausdorf 2007; Salvador & Cavallari 2013; Fontenelle *et al.* 2019) and only 4 species have been placed in synonymy of others.

In effect, taxonomically-inflated genera like *Drymaeus* Albers, 1850 (Bulimulidae) and *Megalobulimus* Miller, 1878 (Strophocheilidae), respectively with 54 and 55 species in Brazil, probably contain several taxa yet to be synonymized. According to Rosenberg (2014), revisions tend to "clean up" the taxonomy of a given group and "reduce" the apparent biodiversity due to synonymization. Consequently, it is possible that the present number of land snail species in Brazil will simultaneously shrink and grow, as old species are placed in synonymy and new ones are discovered.

BIODIVERSITY

The circa 700 native species in Brazil are unequally divided among taxonomic groups (Table 1). As usual, the "pulmonates" are extraordinarily more diverse than neritimorphs and caenogastropods, but inside Eupulmonata, just a small fraction of the 27 families present in Brazil concentrate the bulk of the diversity.

The Bulimulidae are by far the most diverse family (with 17.1% of all known species), followed by Odontostomidae (12.7%), Strophocheilidae (11.4%), Simpulopsidae (8.3%) and Streptaxidae (7.7%). Three of these families belong to the superfamily Orthalicoidea, which alone accounts for circa 45% of the land snail diversity in Brazil.

Table 1. Families of native land snails present in Brazil, with the number (and relative proportion) of valid species in each (total = 702). The asterisk indicates a species described from Rio de Janeiro state that was likely introduced from North America

Taxon	Species Nr	Species %	Taxon	Species Nr	Species %
NERITIMORPHA			Orthalicoidea		
Helicinoidea			Amphibulimidae	8	1.1
Helicinidae	37	5.3	Bulimulidae	120	17.1
CAENOGASTROPODA			Megaspiridae	25	3.6
Cyclophoroidea			Odowntostomidae	89	12.7
Diplommatinidae	9	1.3	Orthalicidae	20	2.8
Neocyclotidae	16	2.3	Simpulopsidae	58	8.3
EUPULMONATA			Pupilloidea		
Veronicelloidea			Gastrocoptidae	6	0.9
Veronicellidae	27	3.8	Strobilopsidae	1	0.1
Achatinoidea			Valloniidae	1	0.1
Achatinidae	33	4.7	Vertiginidae	2	0.3
Ferussaciidae	3	0.4	Clausilioidea		
Streptaxoidea			Clausiliidae	1	0.1
Streptaxidae	54	7.7	Gastrodontoidea		
Scolodontoidea		_	Gastrodontidae	1	0.1
Scolodontidae	36	5.1	Trochomorphoidea		
Punctoidea		_	Euconulidae	4	0.6
Charopidae	26	3.7	Oleacinoidea		
Helicodiscidae*	1	0.1	Spiraxidae	2	0.3
Succineoidea			Sagdoidea		
Succineidae	10	1.4	Solaropsidae	26	3.7
Rhytidoidea			Helicoidea		
Strophocheilidae	80	11.4	Labyrinthidae	3	0.4
			Xanthonychidae	3	0.4

Meanwhile, the so-called microgastropods (usually snails with shells smaller than 5 mm; Geiger et al. 2007) do not seem to be particularly diverse in Brazil. The Pupilloidea and Punctoidea are the most typical microgastropods and tend to be very diverse elsewhere (e.g., Powell 1979; Welter-Schultes 2012). Other families, such as Euconulidae, Scolodontidae, and Helicinidae, also have species that would fall into this category.

While the numbers from Table 1 might represent a good estimate of land snail diversity in Brazil, this is very likely not the case: there are still some biases at work that might be confusing these numbers. These biases arise from a mixture of historical, methodological and ecological issues and are explained in the following section.

RESEARCH BIASES

As shown above, the greater part of land snail diversity in Brazil is due to the Orthalicoidea, Strophocheilidae, and Streptaxidae. These are typically large snails, with colorful or otherwise attractive shells, which would have been primary targets for the 19th-century expeditions and shell collectors ever since. These snails are also easier to find and collect, typically requiring only a visual search and some close examination of plants and soil. Undoubtedly, these groups are very diverse, but their current proportion in relation to

other members of the Brazilian land snail fauna might be due to this biased collection effort. For instance, in the survey in Pedra Talhada Reserve mentioned above (Salvador et al. 2018b), other families were found to be more or as diverse as Orthalicoidea, Strophocheilidae and Streptaxidae; a similar scenario was observed in a survey in Alto Ribeira State Park, in São Paulo state (Salvador et al. 2016). These other families include microgastropods and groups that might represent cryptic species.

Microgastropods are known to be very diverse elsewhere in the world, but there are comparatively few of them known from Brazil (Table 1). Collecting them requires a different sort of sampling of leaf litter and soil and sorting under a stereomicroscope (Geiger et al. 2007). This activity is typically carried out in broader surveys and more ecologically-inclined studies, which are still uncommon in terrestrial malacology in South America. Furthermore, those ecological surveys typically to not leave voucher specimens behind for future research (Turney et al. 2015). Notably, several new microgastropods have been described or newly

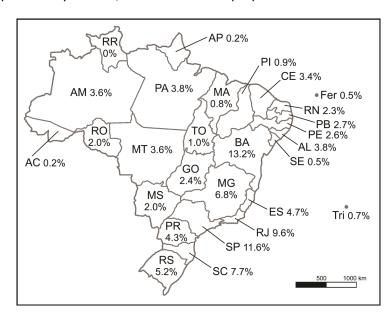


Figure 2. Proportion of species described from each of the 26 of the states in Brazil. Abbreviations: AC, Acre; AL, Alagoas; AM, Amazonas; AP, Amapá; BA, Bahia; CE, Ceará; ES, Espírito Santo; Fer, Fernando de Noronha archipelago (part of PE); GO, Goiás; MA, Maranhão; MG, Minas Gerais; MS, Mato Grosso do Sul; MT, Mato Grosso; PA, Pará; PB, Paraíba; PE, Pernambuco; PI, Piauí; PR, Paraná; RJ, Rio de Janeiro; RN, Rio Grande do Norte; RO, Rondônia; RR, Roraima; RS, Rio Grande do Sul; SC, Santa Catarina; SE, Sergipe; SP, São Paulo; TO, Tocantins; Tri, Trindade and Martin Vaz archipelago (part of ES).

reported from Brazil in the last decade (e.g., Martins & Simone 2014; Salvador et al. 2017, 2018b; Simone 2019); it is thus expected that these groups will represent a source of many new species in the years to come.

In fact, several new species could be cryptic species, waiting to be revealed. This is especially true for groups where shell characters are not enough to diagnose species, such as the Euconulidae, Scolodontidae, Subulininae, and Succineidae. As argued by Salvador *et al.* (2018b), such species complexes can be eventually solved by molecular analyses, still extremely rare in Brazil, and/or in-depth anatomical studies. A consequent increase in the number of known species can then be expected (Bickford *et al.* 2007).

Another bias in the research in Brazil becomes crystal clear if we assemble the known distributions of the species and analyze the number present in each of the country's states (Figure 2). One third of the biodiversity in Brazil is concentrated in only three of the 26 administrative states: Bahia (13.2%), São Paulo (11.6%) and Rio de Janeiro (9.6%). This disparity is due to two reasons. First, Bahia and Rio de Janeiro were historically

important regions and received the largest number of foreign naturalists during the 19th century; São Paulo grew in importance only later. Furthermore, Bahia remains a preferred destination for shell collectors up to this day, largely due to the attractive orthalicoid species that can be found there. Secondly, towards the end of the 19th century, São Paulo and Rio de Janeiro became the core area of scientific research in Brazil. Naturally, researchers would first explore their own region before venturing farther into the country.

Several states presently have less than 1% of the country's land snail biodiversity; more surprisingly, one of them (Roraima) has no specific land snail record whatsoever. Part of this is a result of few expeditions being conducted in those regions. However, there is a second geopolitical reason for this: some states and territories were not precisely defined during the time of the naturalist expeditions in the 19th century and Pilsbry's Manual of Conchology, so there are no records from them. Rondônia, Roraima, and Amapá were dismembered from neighboring areas in 1943; Mato Grosso do Sul was split from Mato Grosso in 1977, and Tocantins was split from Goiás in 1988. Thus, old records, which typically lack precise locality data, might belong to one of these "new" states, although we cannot know for certain now.

Those undersampled regions also represent diverse biomes, like the Amazon Forest and the Pantanal, which are known for a high level of biodiversity in other animal groups (Junk *et al.* 2006; Hoorn *et al.* 2010). A more thorough collection effort in these areas should result in novel discoveries, be it new records of species known from neighboring countries (*e.g.*, Salvador *et al.* 2018c) or entirely new species (*e.g.*, Simone 2010). Likewise, there are some types of habitats that are scarcely explored: islands, caves, mountaintops, forest enclaves and transition areas. For instance, the more meticulous exploration conducted in the last decade in cave environments has led to the discovery of several new, and likely highly endemic, species (Simone 2013, 2018b, 2019; Salvador *et al.* 2016, 2017). Likewise, the incipient study of insular species has resulted in the discovery of endemic species (Simone & Amaral 2018). Finally, Cavallari *et al.* (2016) drew renewed attention to Bahia state, which despite seemingly oversampled is still rife with new discoveries. Those authors hypothesized that the meeting of three of the main Brazilian biomes (Cerrado, Caatinga and Atlantic Forest) there generated diverse habitats in the contact areas which in turn could have resulted in increased diversification and hence, a large number of endemics.

In summary, there are still several regions and "unusual" habitats to be fully explored and surveyed and likely a good amount of "hidden" diversity in the form of microgastropods and cryptic species. By that, we should expect an increase in the number of land snail species described from Brazil. Meanwhile, taxonomic revisions should bring into synonymy several of the now-valid species in the taxa with larger and conspicuous shells, thus actually "reducing" the known diversity. Accordingly, rather than the tripling of biodiversity expected by Simone (1999), a more conservative estimate would imply in an increase of 50% to 100% in the number of snail species in Brazil.

FOSSIL RECORD

The fossil record of land snails in Brazil is very scarce, virtually counting only with Late Paleocene Itaboraí Basin (Salvador *et al.* 2018a). There are 11 families, all "pulmonates", with known fossil record in the country and as expected, the Orthalicoidea are the most diverse (Salvador *et al.* 2018a). Curiously, there are Paleocene records of the families Cerionidae and Urocoptidae from Rio de Janeiro, SE Brazil, two groups which today are mostly restricted to the Caribbean area (Salvador & Simone 2013).

With so few fossils, it is hard to uncover the biogeographical history of the recent fauna, although molecular analyses are starting to shed light on this matter. For instance, Orthalicoidea is deemed to have originated in South America, with subsequent radiations to Central America and Australasia (Breure & Romero 2012) and possibly southern Europe and northern Africa (Hammouda *et al.* 2017). The orthalicoid families Bulimulidae and Odontostomidae are known from the late Cretaceous of Uruguay (Cabrera *et al.* 2018) and were already very diverse in Rio de Janeiro during the Paleocene (Salvador & Simone 2013)

On the other hand, other common and conspicuous families in Brazil, such as the Streptaxidae, have originated elsewhere (in this case Africa), radiating to South America afterward (Rowson *et al.* 2010). Finally, even though a Holarctic origin has been settled on for the Helicoidea, the relationships between its South American representatives (which might include Sagdoidea) are still in flux, even after much study (*e.g.*, Wade *et al.* 2007; Razkin *et al.* 2015).

Little is still known about the terrestrial molluscan fauna in Brazil and in South America as a whole, so their biogeography remains obscure for the most part. As remarked by Solem (1979), the first step is to revise

• 15 •

the species (fossil and recent alike) and to construct working phylogenies for each group; only then can biogeographical hypotheses be tested.

FUTURE PROSPECTS

As argued above, there are several areas that are of particular interest and need urgent attention: (1) revising the known species of land snails in Brazil and assessing their validity; (2) investigating phylogenetic relationships of the higher taxa occurring in Brazil and proposing biogeographic hypotheses; (3) conducting expeditions to poorly-sampled regions (e.g., Acre and Amapá states) and habitats (e.g., caves, mixed-biomes areas), and cataloguing new records and new species; (4) conducting regular expeditions to better assess the distribution of known species and hence, their conservation status; (5) excavating outcrops of continental settings (especially of Paleogene and Neogene ages) that can harbor fossil land snails.

The bright side to all of this is that there is still much work to be done and plenty of room to accommodate several researchers. Fortunately, it seems clear that the study of terrestrial gastropods in Brazil is now picking up the pace, but there is still reason to worry. Even if we accept a more conservative estimate of the unknown fauna in 50–100% of the present number (compared to the 200% increase predicted by Simone 1999), there is still a long way to go. In the current pace, we would need roughly one to two centuries to describe everything, not to mention the time required to revise the already described species and investigate their phylogenetic relationships. This problem, though, is not exclusive to land snails; rather, it is faced by virtually all major invertebrate groups, which remain poorly known. When grouped together, these invertebrate phyla comprise almost all animal diversity (the typical estimate is 97%; May 1988) and are the groups most affected by extinction and the so-called taxonomic impediment (Casagrande 2003; Cardoso *et al.* 2011).

Furthermore, given the new and grim turn Brazilian policies have taken, largely considering environmental concerns as obstacles to development (Nature Editorials 2018), the current situation seems dire for land snails. Terrestrial (and freshwater) gastropods are considered some of the most threatened and extinction-prone groups (Lydeard *et al.* 2004; Régnier *et al.* 2009), but only eight species are considered protected in Brazil (MMA, 2014). In fact, we are starting to see cases of species being formally described from Brazil after they have become extinct (Simone & Salvador 2016), something that also happens in other diversity hotspots across the world (*e.g.*, Richling & Bouchet 2013). A better understanding of the country's fauna would go a long way towards action, but besides dealing with the lack of interest in environmental matters, scientists in Brazil are now faced by a lack of funding (Tollefson 2018). Thus, the future of the country's land snails and all fauna is not looking good at the moment.

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