ZOOLOGIA 39: e21033
ISSN 1984-4689 (online)
scielo.br/zool

RESEARCH ARTICLE

Cave-dwelling gastropods (Mollusca: Gastropoda) of Brazil: state of the art and conservation

Rodrigo B. Salvador[1], Fernanda S. Silva[2], Daniel C. Cavallari[3], Carlo M. Cunha[4], Maria E. Bichuette[5]

[1]*Museum of New Zealand Te Papa Tongarewa. 169 Tory Street, 6011 Wellington, New Zealand.*
[2]*Museu de Zoologia da Universidade de São Paulo. Avenida Nazaré 481, 04263-000 São Paulo, SP, Brazil. (fernanda06@alumni.usp.br)*
[3]*Departamento de Biologia, Faculdade de Filosofia, Ciências e Letras de Ribeirão Preto, Universidade de São Paulo. Avenida Bandeirantes 3900, 14049-900 Ribeirão Preto, SP, Brazil. (dccavallari@usp.br)*
[4]*Programa de Pós-Graduação em Ciência e Tecnologia Ambiental, Universidade Santa Cecília. Rua Oswaldo Cruz 277, 11045-907 Santos, SP, Brazil. (carlomagenta@gmail.com)*
[5]*Laboratório de Estudos Subterrâneos, Universidade Federal de São Carlos. Rodovia Washington Luís km 235, Caixa Postal 676, 13565-905 São Carlos, SP, Brazil. (lina.cave@gmail.com)*
Corresponding author: Rodrigo B. Salvador (salvador.rodrigo.b@gmail.com)

https://zoobank.org/9A7A0DF1-B878-47B7-9A8D-D62F1B92419E

ABSTRACT. An up-to-date list of exclusively cave-dwelling gastropod species recorded in Brazil is presented including updated taxonomy, detailed geographic information, and illustration of types. The list includes 18 cave-exclusive (troglobitic) gastropods encompassing 15 land and three freshwater species, with the status of further species pending additional studies. Their unusual morphology and diversity are discussed, as well as their conservation status and prospects in the current Brazilian environmental and political scenario.

KEY WORDS. Caenogastropoda, cave fauna, endemism, Stylommatophora, troglobitic species.

INTRODUCTION

There are circa 700 terrestrial and around 260 freshwater gastropod species reported from Brazil (Simone 2006, Birckolz et al. 2016, Salvador 2019). Most are endemic, naturally, as would be expected from a country with continental proportions and very diverse biomes, but many also inhabit neighboring countries in South America, with a few even extending to Central America (Simone 2006, Birckolz et al. 2016). Even so, knowledge about land and freshwater gastropod species is still incipient in Brazil (Salvador 2019) and that problem is even more pronounced for the cave-dwelling molluscan fauna (Cavallari et al. 2021).

The lists of cave-dwelling (exclusively troglobitic and other categories) invertebrates in Brazil historically had shortcomings regarding gastropods. Most checklists presented identifications reaching family or genus level only, and species-level identifications were in many cases indicated in open nomenclature (cf.) due to uncertainties about those species' identities (Gnaspini and Trajano 1994, Pinto-da-Rocha 1995, Trajano and Bichuette 2009). Although there have been records of more widespread species also inhabiting caves, the first exclusive troglobitic gastropod in Brazil was only described in the 1990s: *Potamolithus troglobius* Simone & Moracchioli, 1994 – but see the discussion of *Zilchogyra paulistana* (Hylton Scott, 1973) below.

We hope to start addressing this shortfall in the literature by providing a more complete checklist of exclusive cave-dwelling (troglobites sensu Schiner-Racovitza, 1907) land and freshwater gastropods known from Brazil. We also update the taxonomy of some species, present detailed information on geographic distribution, and illustrate the type specimens. Finally, we propose a discussion about the morphology and diversity of cave-dwelling gastropods in Brazil, the threats they are exposed to, and prospects for conservation and follow-up studies.

MATERIAL AND METHODS

To produce the present list, we conducted a literature survey of the main checklists and catalogues of Brazilian mollusks (Morretes 1949, 1953, Salgado and Coelho 2003, Simone 2006, Birckolz et al. 2016) and troglobitic invertebrates (Gnaspini

and Trajano 1994, Pinto-da-Rocha 1995, Trajano and Bichuette 2009, Gallão and Bichuette 2018), as well as more recent species descriptions and regional checklists (see below). We present here an up-to-date inventory of cave-dwelling gastropods in Brazil, excluding troglophilic species (i.e., that also live outside caves).

The list is organized in systematic order, with the classification updated according to Bouchet et al. (2017), Lydeard and Cummings (2019), and more specific revisionary works (Salvador et al. 2020, Simone and Salvador 2021). We also provide information on each species' type locality and distribution, as well as photographs of their type specimens. Additional remarks are provided as needed.

Cave maps were produced using the software QGIS (version 3.6.0; QGIS Development Team 2019), considering the coordinates in the original descriptions and also from MEB expeditions for collections. Besides the occurrences of gastropods, geomorphological information is also detailed in the maps.

The following abbreviations are used throughout this study: H, shell height (measured parallel to the columellar axis of the shell); MACN, Museo Argentino de Ciencias Naturales Bernardino Rivadavia (Buenos Aires, Argentina); MCN, Museu de Ciências Naturais da Fundação Zoobotânica do Rio Grande do Sul (Porto Alegre, Brazil); MZSP, Museu de Zoologia da Universidade de São Paulo (São Paulo, Brazil).

TAXONOMY

Caenogastropoda
Cyclophoroidea
Diplommatinidae
Habeas Simone, 2013
Habeas corpus Simone, 2013

Fig. 1

Type locality: Bahia state; Carinhanha municipality, Serra do Ramalho region, Gruna das Três Cobras cave (14°19″S, 43°47′W).

Distribution: Also known from the nearby Gruna do Cesário cave (13°31′06″S, 43°38′26″W), on the same outcrop.

Habeas data Simone, 2013

Fig. 2

Type locality: Bahia state, Carinhanha municipality, Serra do Ramalho region, Gruna do Cesário cave (13°31′06″S, 43°38′26″W).

Distribution: Also known from the nearby Gruna Vila Nova cave (13°33′14″S, 43°52′40″W), on the same outcrop.

Habeastrum Simone, 2019
Habeastrum parafusum Simone, 2019

Fig. 3

Type locality: Mato Grosso do Sul state, Bonito municipality, Gruta Pitangueiras cave (21°06′37″S, 56°34′52″W).

Distribution: Known only from the type locality.

Habeastrum omphalium Simone, 2019

Fig. 4

Type locality: Mato Grosso do Sul state, Bonito municipality, Gruta Pitangueiras cave (21°06′37″S, 56°34′52″W).

Distribution: Known only from the type locality.

Habeastrum strangei Simone, Cavallari & Salvador, 2020

Figs 5, 6

Type locality: Minas Gerais state, Presidente Olegário municipality, Lapa da Fazenda São Bernardo cave (18°16′37″S, 46°06′46″W).

Distribution: Minas Gerais state, Pains municipality, Gruta dos Coralóides cave (20°20′33″S, 45°46′46″W), CBA cave (20°17′44″S, 45°47′18″W); Pedro Leopoldo municipality (unnamed cave, 19°37′50″S, 44°00′25″W); Piumhi municipality (unnamed caves, 20°20′45″S, 45°50′55″W, 20°20′46″S, 45°50′56″W, 20°20′51″S, 45°50′54″W, 20°20′57″S, 45°50′45″W, 20°20′59″S, 45°50′45″W, 20°21′05″S, 45°50′28″W, 20°21′06″S, 45°50′21″W); Presidente Olegário municipality: Gruta da Juruva cave (18°19′19″S, 46°04′53″W), Lapa do Moacir cave (18°11′10″S 46°09′34″W), Lapa Vereda da Palha cave (18°15′19″S, 46°07′34″W), Lapa Zé de Sidinei cave (18°18′06″S 46°05′41″W).

Remarks: Given its ample distribution, this species is probably troglophilic and not strictly troglobitic, but specimens have not been recovered on surface environments as of writing.

Truncatelloidea
Cochliopidae
Spiripockia Simone, 2012
Spiripockia punctata Simone, 2012

Fig. 7

Type locality: Bahia state, Carinhanha municipality, Serra do Ramalho region, Lapa dos Peixes cave (13°49′22″S, 43°57′24″W).

Distribution: Known only from type locality.

Remarks: The genus was recently reassigned to Cochliopidae (Simone and Salvador 2021).

Spiripockia umbraticola Simone & Salvador, 2021

Figs 8, 9

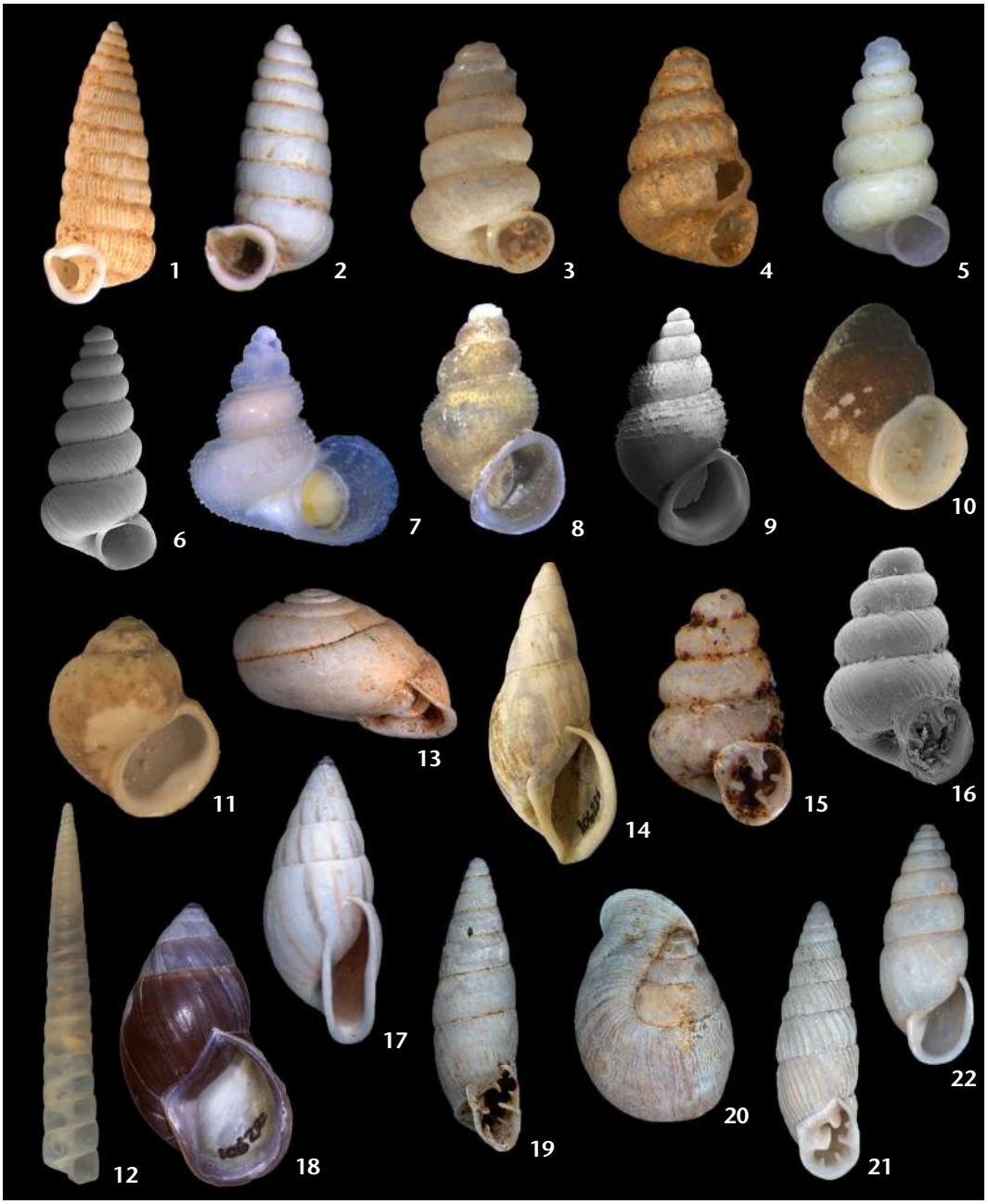
Type locality: Bahia state, Carinhanha municipality, Serra do Ramalho region, Gruna do Domingão cave (13°44′41″S, 43°50′00″W).

Distribution: Known only from type locality.

Tateidae
Potamolithus Pilsbry, 1896
Potamolithus troglobius Simone & Moracchioli, 1994

Fig. 11

Type locality: São Paulo state, Iporanga municipality, Are-



Figures 1–22. (1) *Habeas corpus*, holotype MZSP 110000, shell height H = 10.3 mm; (2) *Habeas data*, holotype MZSP 106810, H = 5.7 mm; (3) *Habeastrum parafusum*, holotype MZSP 134301, H = 1.4 mm; (4) *Habeastrum omphalium*, holotype MZSP 135583, H = 1.7 mm; (5) *Habeastrum strangei*, paratype MZSP 137432, H = 1.6 mm; (6) *Habeastrum strangei*, SEM image of holotype MZSP 151626, H = 2.8 mm; (7) *Spiripockia puncata*, holotype MZSP 105000, H = 4.6 mm; (8) *Spiripockia umbraticola*, paratype MZSP 151100, H = 4.8 mm; (9) *Spiripockia umbraticola*, SEM image of holotype MZSP 151099, H = 5.2 mm; (10) *Potamolithus karsticus*, paratype MZSP 27946, H = 1.2 mm; (11) *Potamolithus troglobius*, paratype MZSP 27948, H = 2.3 mm; (12) *Lavajatus moroi*, holotype MZSP 131060, H = 35.4 mm; (13) *Streptartemon molaris*, holotype MZSP 112451, H = 8.7 mm; (14) *Gonyostomus elinae*, holotype MZSP 106226, H = 48.0 mm; (15) *Gastrocopta sharae*, holotype MZSP 122725, H = 1.9 mm; (16) *Gastrocopta sharae*, SEM image of holotype; (17) *Anctus prolatus*, holotype MZSP 112450, H = 25.2 mm; (18) *Kora nigra*, holotype MZSP 106232, H = 30.1 mm; (19) *Bahiensis ribeirensis*, holotype MZSP 120774, H = 21.3 mm; (20) *Clinispira insolita*, holotype MZSP 111847, H = 14.6 mm; (21) *Cyclodontina capivara*, holotype MZSP 112448, H = 19.2 mm; (22) *Rhinus gilbertus*, holotype MZSP 112449, H = 21.9 mm.

ias I and Areias II caves (23°35'20"S, 48°42'05"W), Ressurgência das Areias de Água Quente cave (23°35'20"S, 48°42'05"W).

Distribution: Known only from type localities (Areias System).

Potamolithus spp.

Distribution: São Paulo state, Eldorado municipality, Tapagem cave ("Diabo cave", 24°38'12.2"S, 48°24'06.1"W); Iporanga and Apiaí municipalities, Água Suja cave (24° 31'26.4"S, 48°42' 28.4"W), Água Sumida cave (24°28'43.7"S, 48°37'45.5"W), Alambari de Baixo cave (24°33'26"S, 48°39'52"W), Alambari de Cima cave (24°33'15.0"S, 48°39'55.0"W), Betari de Baixo cave (24°34'34.0"S, 48° 37' 39.0"W), Chapéu cave (24°26'06.1"S, 48°35'25.9"W), Córrego Seco cave (24°33'06.8"S, 48°40'59.7"W), Desmoronada cave (24°24'16.2"S, 48°32' 44.2"W), Gruta do Chapéu Mirim I and II caves (24°25'52"S, 48°35'07"W), Gurutuva cave (24°32'03.3"S, 48°39'13.4"W), Jeremias cave (24°38'16.7"S, 48°42'03.8"W), Morro Preto-Couto cave system (24°32'00.5"S, 48°41'57.0"W), Ouro Grosso cave (24°32'31.9"S, 48°40'36.8"W), Pérolas cave (24°33'52.7"S, 48°44'34.7"W), Pescaria cave (24°24'16.6"S, 48°33'02.5"W), Santana cave (24°32'02.3"S, 48°42'09.5"W), Teminina II cave (24°23'05.0"S, 48°34'08.0"W), Aranhas cave (24°26'04.0"S, 48°35'20.6"W); border of Iporanga and Ribeirão Grande municipalities, Colorida cave (24°16'25.6"S, 48°25'11.1"W), Fendão cave (24°16'24.0"S, 48°26'32.0"W), Jane Mansfield cave (24°15'50.0"S, 48°26'42.0"W), Minotauro cave (24°16'22.0"S, 48°27'22.0"W), Paiva cave (24°16'22.4"S, 48°26'44.2"W).

Remarks: Bichuette and Trajano (2018) list 12 morphospecies of *Potamolithus* in the same overall area in the Upper Ribeira Valley as *P. troglobius* above and the related troglophilic *P. karsticus* Simone & Moracchioli, 1994 (known from Calcário Branco cave, including epigean; Fig. 10). Of those 12 morphs, five are deemed to be troglobites, six troglophiles, and one epigean. *Potamolithus* spp. are restricted to micro-basins and/or caves, showing small areas of distribution and probably a high degree of endemism. Whether they are indeed new species remains to be fully investigated.

Eupulmonata
Stylommatophora
Achatinoidea
Achatinidae
Lavajatus Simone, 2018
Lavajatus moroi Simone, 2018

Fig. 12

Type locality: Ceará state, Santa Quitéria municipality, undetermined cave (4°33'51"S, 39°46'44"W).

Distribution: Known only from type locality.

Streptaxoidea
Streptaxidae
Streptartemon Kobelt, 1905
Streptartemon molaris Simone & Casati, 2013

Fig. 13

Type locality: Piauí state; Serra da Capivara, Coronel José Dias municipality, Toca de Cima dos Pilão cave (8°51'47"S, 42°33'27"W).

Distribution: Known only from type locality.

Punctoidea
Cystopeltidae
Zilchogyra Weyrauch, 1965
Zilchogyra paulistana (Hylton Scott, 1973)

Type locality: São Paulo state.

Distribution: The original work of Hylton Scott (1973) did not provide precise locality data for the species and there was scarce additional information accompanying the type specimens (holotype and 2 paratypes MCN 1054; and paratype MACN 27622). Further literature, however, indicates that the species is found in caverns (e.g., Gnaspini and Trajano 1994) in São Paulo state, more specifically in Iporanga municipality, which is part of the Upper Ribeira Valley, famous for its multiple caves (e.g., Salvador et al. 2016). Nevertheless, further specimens have imprecise locality data: Fonseca and Thomé (1993) referred to shells from Cerro Azul municipality in Paraná state (erroneously listed as paratypes by those authors), but no additional information was given. Considering that Cerro Azul is also part of the Upper Ribeira Valley (and just 70 km SW of Iporanga), it is impossible to exclude the possibility that the specimens were collected in one of the many caves in the region. As such, the status of this species as a troglobitic remains uncertain.

Remarks: The placement of this species in Cystopeltidae follows the molecular phylogeny of Salvador et al. (2020), which removed the members of genera *Zilchogyra* and *Lilloiconcha* Weyrauch, 1965 from Charopidae and included them in Cystopeltidae. Those authors raised the possibility that a smooth protoconch could be a diagnostic character for South American cystopeltids.

Rhytidoidea
Strophocheilidae
Gonyostomus H. Beck, 1837
Gonyostomus elinae Simone, 2016

Fig. 14

Type locality: São Paulo state, Iporanga municipality, Parque Estadual Turístico do Alto Ribeira (PETAR), Gruta do Chapéu Mirim cave (24°25'52"S, 48°35'07"W).

Distribution: Known only from type locality.

Pupilloidea

Gastrocoptidae

Gastrocopta Wollaston, 1878

Gastrocopta sharae Salvador, Cavallari & Simone, 2017

Figs 15, 16

Type locality: Goiás state, Posse municipality, Gruta Revolucionários cave (14°14'03"S, 46°20'42"W).

Distribution: Known only from type locality.

Remarks: Incorrectly assigned to *Gastrocopta geminidens* (Pilsbry, 1917) by Wendebourg and Hausdorf (2019).

Orthalicoidea

Bulimulidae

Anctus E. von Martens, 1860

Anctus prolatus Simone & Casati, 2013

Fig. 17

Type locality: Piauí state; Serra da Capivara, Coronel José Dias municipality, Toca de Cima dos Pilão cave (8°51'47"S, 42°33'27"W).

Distribution: Known only from type locality.

Kora Simone, 2012

Kora nigra Simone, 2015

Fig. 18

Type locality: Bahia state, Carinhanha municipality, Serra do Ramalho region, Gruna do Cesário cave (13°31'06"S, 43°38'26"W).

Distribution: Carinhanha municipality in Bahia state (type locality), and the National Park Cavernas do Peruaçu in Minas Gerais state (Lapa dos Brancos cave; Salvador and Simone 2021).

Odontostomidae

Bahiensis Jousseaume, 1877

Bahiensis ribeirensis Salvador, Cavallari & Simone, 2016

Fig. 19

Type locality: São Paulo state, Iporanga municipality, Parque Estadual Turístico do Alto Ribeira (PETAR), Alambari de Baixo cave (24°33'26"S, 48°39'52"W).

Distribution: Known only from type locality.

Clinispira Simone & Casati, 2013

Clinispira insolita Simone & Casati, 2013

Fig. 20

Type locality: Piauí state; Serra da Capivara, Coronel José Dias municipality, Toca de Cima dos Pilão cave (8°51'47"S, 42°33'27"W).

Distribution: Known only from type locality.

Cyclodontina Beck, 1837

Cyclodontina capivara Simone & Casati, 2013

Fig. 21

Type locality: Piauí state; Serra da Capivara, Coronel José Dias municipality, Toca de Cima dos Pilão cave (8°51'47"S, 42°33'27"W).

Distribution: Known only from type locality.

Simpulopsidae

Rhinus Martens in Albers, 1860

Rhinus gilbertus Simone & Casati, 2013

Fig. 22

Type locality: Piauí state; Serra da Capivara, Coronel José Dias municipality, Toca de Cima dos Pilão cave (8°51'47"S, 42°33'27"W).

Distribution: Known only from type locality.

DISCUSSION

Morphology

There are a variety of reasons that can lead individual animals and populations to inhabit caves, such as exploitation of alternative resources (e.g., food sources, mating sites), usage of caves as temporary or seasonal refugia, and chance (Weigand 2014). Speciation of troglobitic lineages can establish morphological traits that are considered typical of cave environments.

Several of the species listed here show some of those classical troglomorphisms, such as reduction/absence of eyes and lack of body/periostracum pigmentation (i.e., white body and typically translucent shell), well exemplified by *H. strangei* and *S. punctata* (Figs 5, 7). Such morphological features are common in virtually all terrestrial and freshwater cave-dwelling snail lineages worldwide (e.g., Boeters 1979, Weigand 2013, Delicado 2018), but not mandatory, as not all troglobitic species develop troglomorphisms (Romero 2009, Christiansen 2012, Trontelj et al. 2012). Case in point, many of the troglobitic species listed here (more than half of which are stylommatophorans; Figs 12–22) do not present obvious troglomorphisms; however, we should caution that most are known only from their shells. Besides, physiological and "unconventional" anatomical troglomorphisms (e.g., specializations in sensory organs, elongation of tentacles) have not been investigated yet, so some of these may be identified as new live specimens and additional data become available.

Miniaturization and morphological simplification are also common in troglobitic species (Romero 2009, Christiansen

2012, Gladstone et al. 2021) and can be seen in some Brazilian species in the form of unsculptured and unornamented shells (Figs 10–12). *Potamolithus troglobius* (Fig. 11) is an example of miniaturization, where some organs (e.g., intestine, ctenidium) are simplified or absent (Bichuette and Trajano 2018).

However, a few species listed here exhibit "extreme" morphologies when compared to their close relatives, like the twisted body whorl of *Clinispira insolita* (Fig. 20), the teleoconch sculpture of *Spiripockia* spp. (Figs 7, 8), and the dextral shells of the diplommatinids (unusual in this typically sinistrally-coiled family; Figs 3–6). Similar unusual sculptures and shapes, though uncommon, are also known from troglobitic snails worldwide (e.g., Khalik et al. 2018). Nevertheless, these features may be related to other factors in the snails' life histories that are not exclusive to cave environments. For instance, the shell shape of *Clinispira insolita* is possibly related to a better attachment to rock surfaces when retracted, as reported from unrelated species with similar morphology (Páll-Gergely and Neubauer 2020).

Diversity

While there are many gastropod species known to inhabit caves in Brazil, most are not restricted to cave environments. Typically, those species are widespread in surface environments, but are also able to inhabit caves – some even down to the aphotic zone (e.g., Salvador and Simone 2016, 2021, Salvador et al. 2016, 2017, 2021a, Bichuette and Trajano 2018). There are relatively few (around 1.5%) exclusively subterranean species known from Brazil, as our results show.

Despite that reduced number, there are five exclusively subterranean genera, distributed among five families. Those genera are: *Clinispira*, *Habeas*, *Habeastrum*, *Lavajatus*, and *Spiripockia*. Only the latter inhabits freshwater habitats; all other genera are terrestrial. This does not reflect a high diversity, however, as these genera (except for *Habeas*) are either monotypic or include very few species. Effectively, this apparent high number of troglobitic genera simply indicates that the differences in morphology and anatomy found in those animals have been deemed large enough to justify the creation of new genera (Simone 2012, 2013, 2018, 2019, Simone and Casati 2013).

In total, there are 15 land and three freshwater exclusively troglobitic snail species known from Brazil; no slug or semi-slug has ever been reported as troglobitic in the country. These numbers are potentially larger, pending the assessment of *Zilchogyra paulistana* and the undescribed morphs *Potamolithus* spp., excluded from the total above. Nevertheless, this is a small number in comparison to circa 950 known species of continental gastropods in Brazil (Simone 2006, Salvador 2019). Moreover, given the extension of the Brazilian territory and a large number of caves (circa 20,000, over half of which are calcareous; CECAV 2020; Figs 23–28), this number is certainly a gross underestimation. As alluded to by Salvador (2019), caves are among the least explored habitats in malacological studies in Brazil, a bias that is also present in other countries (e.g., Gladstone et al. 2018, Czaja et al. 2020). In Brazil, our knowledge is biased toward a relatively low number of caves in the eastern portion of the country (44 caves, Fig. 29). When that number is considered taking the total number of caves and the sheer territoral extension of the country into account (Fig. 29), the lack of malacological works focused on cave environments in Brazil becomes immediately evident. As such, it can be surmised that many species remain undiscovered (e.g., Bichuette and Trajano 2018, Salvador 2019). Still, there is a vast quantity of material (both recently-collected or already in museum collections and not fully processed yet) to be studied in more detail.

Caves are potential hotspots for molluscan diversity, especially of freshwater snails (Culver and Sket 2000, Sket 2006, Grego et al. 2000, Gladstone et al. 2021), and there have been studies pointing toward cryptic species in cave systems in Brazil. For instance, in caves in the Upper Ribeira Valley in southeastern Brazil (Figs 23, 25, 28), Bichuette and Trajano (2003, 2018) have identified several morphotypes of *Potamolithus* sp., though species limits need to be investigated further to assess their validity, preferably using molecular data. As cave environments are being better explored, the rate of description of troglobitic species is also picking up, as seen by the description dates of most species listed here (largely, from the past decade). Hopefully, this trend will continue to improve.

An interesting feature of cave molluscan fauna in Brazil is that the most diverse and abundant taxa are Subulininae and Scolodontidae (Salvador et al. 2016, 2021a), contrary to the "regular" fauna of the country, which is dominated by Orthalicoidea (Salvador 2019). Nevertheless, all the subulinine and scolodontid species reported so far from caves are widespread species; not a single one is exclusively cavernicolous. Meanwhile, the present list counts six orthalicoid species that so far are known only from caves.

Threats and conservation prospects

As alluded to above, there likely are many new troglobitic gastropod species awaiting discovery and formal description. A similar scenario has been proven true for other troglobitic taxa such as isopods, spiders, and fishes (Gallão and Bichuette 2018). Cave species typically have a narrow geographic distribution, with many being endemic to one or very few caves or aquifers, which makes them immediately prone to extinction. Given that cave environments can be fragile ecosystems and that they are being progressively explored in Brazil (Gallão and Bichuette 2018, Cavallari et al. 2021), troglobitic species throughout the country might be facing several threats and require protection. Some impacts are widespread in Brazil (see Gallão and Bichuette 2018), such as pollution of waters due to agriculture and mining activities, poorly controlled tourism, deforestation, changes in local hydrology, etc. Another important but often overlooked threat to the subterranean fauna is over-collection (Bichuette and Trajano 2010), which must be avoided given that population sizes of these species are typically small.

Figures 23–28. Examples of caves where some of the species listed here inhabit: (23) Tapagem cave (Eldorado, São Paulo); (24) Gruna das Três Cobras cave (Carinhanha, Bahia; photo: Adriano Gambarini); (25) Aranhas cave (Apiaí, São Paulo); (26) Lapa Zé de Sidinei cave (Presidente Olegário, Minas Gerais); (27) Lapa da Fazenda São Bernardo cave (Presidente Olegário, Minas Gerais); (28) Teminina II cave (Apiaí, São Paulo cave; photo: Adriano Gambarini).

Presently, there are only three cave-dwelling gastropod species listed on the Brazilian Red List (Gallão and Bichuette 2018, ICMBio 2018), categorized (according to the guidelines of IUCN 2012) as follows: *Spiripockia punctata* (a troglobitic species), endangered (EN); and *Potamolithus karsticus* (troglophilic) and *P. troglobius* (troglobitic), critically endangered (CR). Even though other troglobitic gastropod species (and other invertebrates) are not on the list of threatened fauna, they certainly face several threats (see Gallão and Bichuette 2018 for details). For example, the region of Serra do Ramalho in Bahia state (Fig. 24) has threats mainly related to agricultural expansion and mining; the genus *Spiripockia* is endemic to caves of that region, as well as *Kora nigra* and some species of *Habeas*. Another region with a high diversity of gastropods is Presidente Olegário in Minas Gerais state (Figs 26, 27; Salvador et al. 2021a), for which several impacts have been observed, such as pollution by pesticides and large-scale deforestation for plantations (e.g., *Eucalyptus*, sugar cane; M.E. Bichuette, pers. obs.). The Upper Ribeira Valley, home of *Gonyostomus elinae* and *Bahiensis ribeirensis*, is threatened by poor use of natural resources and uncontrolled ecotourism (Salvador et al. 2016). Very recently, a new government decree allows the destruction of any cave in Brazil for "public utility enterprises" (e.g., mining, energy, transport), which is in line with the destructive policies of the current far-right Brazilian administration (Luiz 2022).

To enforce the protection of this particular and fragile cave-dwelling fauna, systematic collection, taxonomic works, and long-term monitoring projects are fundamental (Cavallari et al. 2021), such as has been done for *P. troglobius* (Bichuette and Trajano 2003). Those projects also must be allied to outreach and educational initiatives aiming to develop public awareness, since science communication about invertebrates can play a critical role in their conservation (Salvador et al. 2021b).

ACKNOWLEDGEMENTS

We are grateful to Janine O. Arruda (MCN) for information about the type specimens of *Zilchogyra paulistana*; to L. Assis for the confection of the map; to A. Gambarini for the photographs of Figs 24, 28; to the LES team (Laboratório de Estudos Subterrâneos, Universidade Federal de São Carlos), for all support in

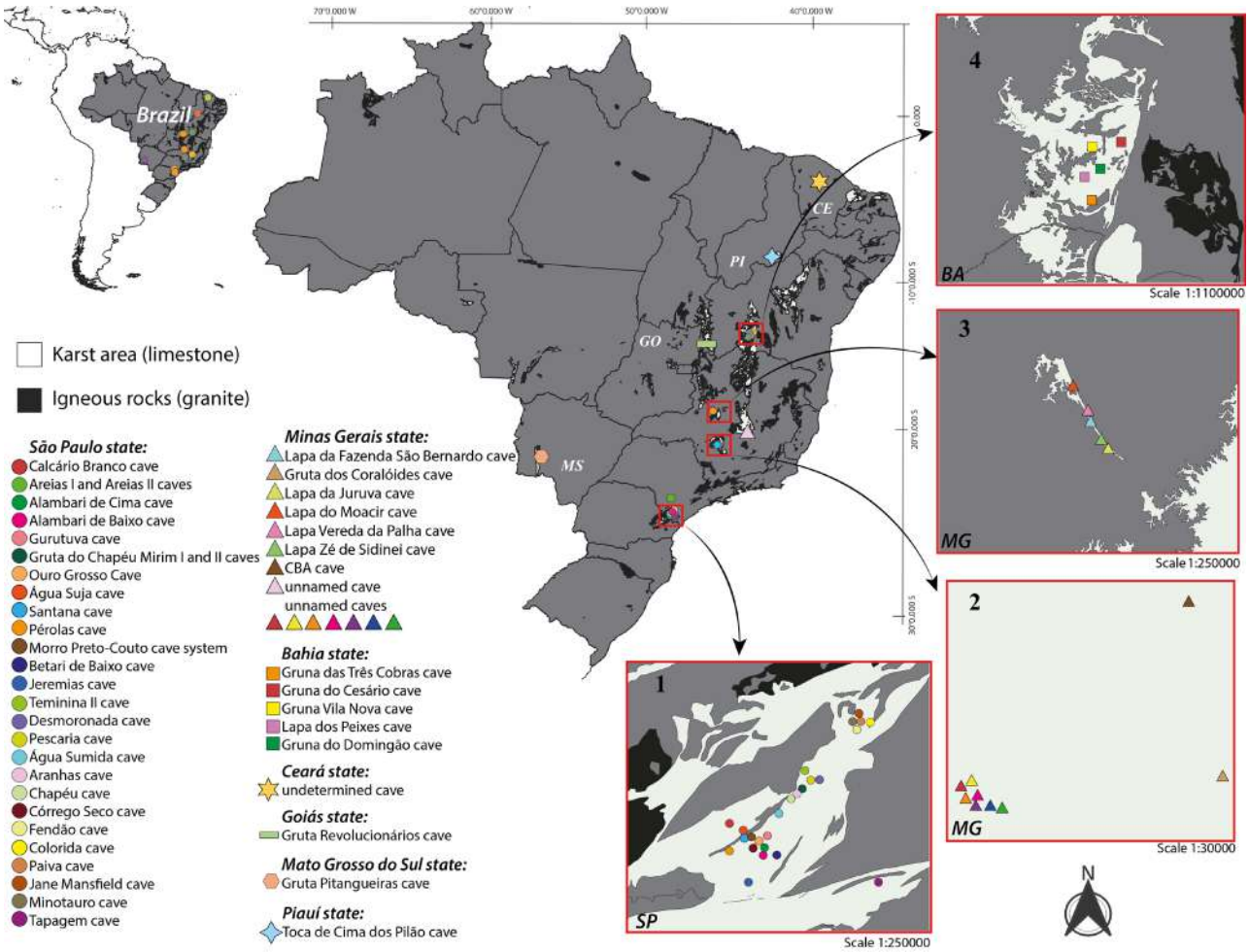


Figure 29. Map of Brazil highlighting the caves where the species listed here occur: (SP) São Paulo, square 1 shows caves located in the Upper Ribeira karst area; (MG) Minas Gerais, square 2 corresponds to caves in the municipalities of Pains and Pedro Leopoldo, and square 3 to caves in Presidente Olegário municipality; (BA) Bahia, square 4 shows caves in the Serra do Ramalho region. Other state abbreviations: (CE) Ceará, (GO) Goiás, (MS) Mato Grosso do Sul, (PI) Piauí.

the collections and discoveries in the Brazilian caves, namely: J.E. Gallão, D.F. Torres, J.S. Gallo, T. Zepon, D.M. von Schimonsky, P.P. Rizzato, D.R. Pedroso, C.S. Fernandes, L.B. Simões, and T.L.C. Scatolini; to Grupo Bambuí de Pesquisas Espeleológicas (GBPE) for the support and information regarding the Serra do Ramalho region; to Grupo Pierre Martin de Espeleologia (GPME) for information from Presidente Olegário region; and to Alex Weigand and an anonymous reviewer for the helpful comments to the manuscript. MEB received funding from the Brazilian agencies CNPq, FAPESP, and CAPES.

LITERATURE CITED

Bichuette ME, Trajano E (2003) A population study of epigean and subterranean *Potamolithus* snails from southeast Brazil (Mollusca: Gastropoda: Hydrobiidae). Hydrobiologia 505: 107–117. https://doi.org/10.1023/B:HYDR.0000007299.26220.b8

Bichuette ME, Trajano E (2010) Conservation of subterranean fishes. In: Trajano E, Bichuette ME, Kapoor BG (Eds) Biology of Subterranean Fishes. CRC Press, Boca Raton, 65–80.

Bichuette ME, Trajano E (2018) Diversity of *Potamolithus* (Littorinimorpha, Truncatelloidea) in a high-diversity spot for troglobites in southeastern Brazil: role of habitat fragmentation in the origin of subterranean fauna, and conservation status. Subterranean Biology 25: 61–88. https://doi.org/10.3897/subtbiol.25.23778

Birckolz CJ, Salvador RB, Cavallari DC, Simone LRL (2016) Illustrated checklist of newly described (2006–2016) land and freshwater Gastropoda from Brazil. Archiv für Molluskenkunde 145: 133–150. https://doi.org/10.1127/arch.moll/145/133-150

Boeters HD (1979) Species concept of prosobranch freshwater molluscs in Western Europe, I. Malacologia 18: 57–60.

Bouchet P, Rocroi JP, Hausdorf B, Kaim A, Kano Y, Nützel A, Parkhaev P, Schrödl M, Strong EE (2017) Revised classification, nomenclator and typification of gastropod and monoplacophoran families. Malacologia 61: 1–527.

Cavallari DC, Silva FS, Cunha CM, Bichuette ME, Salvador RB (2021) Brasilian troglobitic snails begin to emerge – and are already in danger. Tentacle 29: 32–34.

CECAV (2020) Anuário Estatístico do Patrimônio Espeleológico Brasileiro 2019. Centro Nacional de Pesquisa e Conservação de Cavernas, ICMBio, Brasília, 20 pp.

Christiansen K (2012) Morphological adaptations. In: Culver DC, White WB (Eds) Encyclopedia of Caves. Elsevier Academic Press, Asmterdam, 2nd ed., 517–528.

Culver DC, Sket B (2000) Hotspots of subterranean biodiversity in caves and wells. Journal of Cave and Karst Studies 62: 11–17.

Czaja A, Meza-Sánchez IG, Estrada-Rodríguez JL, Romero-Méndez U, Sáenz-Mata J, Ávila-Rodríguez V, Becerra-López JL, Estrada-Arellano JR, Cardoza-Martínez GF, Aguillón-Gutiérrez DR, Cordero-Torres DG, Covich AP (2020) The freshwater snails (Mollusca: Gastropoda) of Mexico: updated checklist, endemicity hotspots, threats and conservation status. Revista Mexicana de Biodiversidad 91: e912909. https://doi.org/10.22201/ib.20078706e.2020.91.2909

Delicado D (2018) A rare case of stygophily in the Hydrobiidae (Gastropoda: Sadleriana). Journal of Molluscan Studies 84: 480–485.

Fonseca ÁLM, Thomé JW (1993) Descrição de *Glabrogyra* subgen. n., recaracterização de *Austrodiscus twomeyi* (Parodiz, 1954) e reclassificação das espécies sulamericanas dos géneros *Austrodiscus* Parodiz, 1957, *Radioconus* Baker, 1927, *Radiodomus* Baker, 1930e, *Trochogyra* Weyrauch, 1965 (Charopidae) e *Zilchogyra* Weyrauch, 1965 (Helicodiscidae) (Gastropoda, Stylommatophora, Endodontoidea). Iheringia, Série Zoologia 75: 97–105.

Gallão JE, Bichuette ME (2018) Brazilian obligatory subterranean fauna and threats to the hypogean environment. ZooKeys 746: 1–23. https://doi.org/10.3897/zookeys.746.15140

Gladstone NS, Carter ET, McKinney ML, Niemiller ML (2018) Status and distribution of the cave-obligate land snails in the Appalachians and interior Low Plateau of the eastern United States. American Malacological Bulletin 36: 62–78.

Gladstone NS, Niemiller ML, Hutchins B, Schwartz B, Czaja A, Slay ME, Whelan NV (2021) Subterranean freshwater gastropod biodiversity and conservation in the United States and Mexico. Conservation Biology 36(1): e13722. https://doi.org/10.1111/cobi.13722

Gnaspini P, Trajano L (1994) Brazilian cave invertebrates, with a checklist of troglomorphic taxa. Revista Brasileira de Entomologia 38: 549–584.

Grego J, Mumladze L, Falniowski A, Osikowski A, Rysiewska A, Palatov DM, Hofman S (2020) Revealing the stygobiotic and crenobiotic molluscan biodiversity hotspot in Caucasus: Part I. The phylogeny of stygobiotic Sadlerianinae Szarowska, 2006 (Mollusca, Gastropoda, Hydrobiidae) from Georgia with descriptions of five new genera and twenty-one new species. ZooKeys 955: 1–77. https://doi.org/10.3897/zookeys.955.51983

Hylton Scott MI (1973) Endodontidos neotropicales IV (Gastropoda – Pulmonata). Neotropica 19: 104–109.

ICMBio (2018) Livro Vermelho da Fauna Brasileira Ameaçada de Extinção. ICMBio, Brasília, vol. 7, 492 pp.

IUCN (2012) IUCN Red List Categories and Criteria. International Union for Conservation of Nature, Gland, v. 3.1, 2nd ed.

Khalik MZ, Hendriks K, Vermeulen JJ, Schilthuizen M (2018) A molecular and conchological dissection of the "scaly" *Georissa* of Malaysian Borneo (Gastropoda, Neritimorpha, Hydrocenidae). ZooKeys 773: 1–55. https://doi.org/10.3897/zookeys.773.24878

Luiz W (2022) Decreto de Bolsonaro libera destruir caverna para construir empreendimento. Folha de São Paulo. https://www1.folha.uol.com.br/ambiente/2022/01/decreto-de-bolsonaro-libera-destruir-caverna-para-construir-empreendimento.shtml [Accessed: 28/05/2022]

Lydeard C, Cummings KS (2019) Freshwater mollusks of the world: a distribution atlas. Johns Hopkins University Press, Baltimore, 242 pp.

Morretes FL (1949) Ensaio de catálogo dos moluscos do Brasil. Arquivos do Museu Paranaense 7: 5–216.

Morretes FL (1953) Adenda e corrigenda ao ensaio de catálogo dos moluscos do Brasil. Arquivos do Museu Paranaense 10: 37–76.

Páll-Gergely B, Neubauer TA (2020) The value of a single character: the Paleogene European land snail *Ferussina* Grateloup, 1827 is likely a cyclophorid (Gastropoda, Caenogastropoda). ZooKeys 918: 29–40. https://doi.org/10.3897/zookeys.918.50135

Pinto-da-Rocha R (1995) Sinopse da fauna cavernícola do Brasil (1907-1994). Papéis Avulsos de Zoologia 39: 61–173.

QGIS Development Team (2019) QGIS Geographic Information System. Open Source Geospatial Foundation Project. http://qgis.osgeo.org

Racovitza EG (1907) Essai sur les problèmes biospéologiques. Archives de Zoologie Expérimentale et Générale 6: 371–488.

Romero A (2009) Cave Biology: Life in Darkness. Cambridge University Press, Cambridge, 306 pp.

Salgado NC, Coelho ACS (2003) Moluscos terrestres do Brasil (Gastrópodes operculados ou não, exclusive Veronicellidae, Milacidae e Limacidae). Revista de Biología Tropical 51(Suppl. 3): 149–189.

Salvador RB (2019) Land snail diversity in Brazil. Strombus 25: 10–20.

Salvador RB, Simone LRL (2016) A new species of *Kora* from Bahia, Brazil (Gastropoda: Pulmonata: Orthalicoidea), with an emended diagnosis of the genus. Stuttgarter Beiträge zur Naturkunde A, Neue Serie 9: 1–7. https://doi.org/10.18476/sbna.v9.a1

Salvador RB, Simone LRL (2021) New records of Orthalicoidea land snail species for the state of Minas Gerais, southeastern Brazil (Gastropoda, Stylommatophora). Check List 17: 395–399. https://doi.org/10.15560/17.2.395

Salvador RB, Brook FJ, Shepherd LD, Kennedy M (2020) Molecular phylogenetic analysis of Punctoidea (Gastropoda, Stylommatophora). Zoosystematics and Evolution 96: 397–410. https://doi.org/10.3897/zse.96.53660

Salvador RB, Cavallari DC, Simone LRL (2016) Taxonomical study on a sample of land snails from Alto Ribeira State Park (São Paulo, Brazil), with description of a new species. Archiv für Molluskenkunde 145: 59–68. https://doi.org/10.1127/arch.moll/1869-0963/145/059-068

Salvador RB, Cavallari DC, Simone LRL (2017) Taxonomical study on a sample of land and freshwater snails from caves in central Brazil, with description of a new species. Zoosystematics and Evolution 93: 135–141. https://doi.org/10.3897/zse.93.10995

Salvador RB, Silva FS, Cavallari DC, Simone LRL (2021a) Terrestrial Gastropoda from the caves of Presidente Olegário, southeastern Brazil. Biota Neotropica 21: e20201169. https://doi.org/10.1590/1676-0611-BN-2020-1169

Salvador RB, Tomotani BM, O'Donnell KL, Cavallari DC, Tomotani JV, Salmon RA, Kasper J (2021b) Invertebrates in science communication: confronting scientists' practices and the public's expectations. Frontiers in Environmental Science 9: 606416. https://doi.org/10.3389/fenvs.2021.606416

Simone LRL (2006) Land and Freshwater Molluscs from Brazil. EGB/Fapesp, São Paulo, 390 pp.

Simone LRL (2012) A new genus and species of cavernicolous Pomatiopsidae (Mollusca, Caenogastropoda) in Bahia, Brazil. Papéis Avulsos de Zoologia 52: 515–524.

Simone LRL (2013) *Habeas*, a new genus of Diplommatinidae from central Bahia, Brazil (Caenogastropoda), with description of three new species. Journal of Conchology 41: 519–525.

Simone LRL (2015) Three new species of *Kora* (Pulmonata, Orthalicidae) from Bahia and Minas Gerais, Brazil. Journal of Conchology 42: 51–56.

Simone LRL (2016) A new species of the genus *Gonyostomus* from Brazil (Gastropoda, Stylommatophora, Strophocheilidae). Spixiana 39: 11–13.

Simone LRL (2018) *Lavajatus moroi*, new cavernicolous Subulininae from Ceará, Brazil (Gastropoda, Eupulmonata, Achatinidae). Spixiana 41: 173–187.

Simone LRL (2019) The new genus *Habeastrum*, with two new species (Gastropoda, Diplommatinidae) in Mato Grosso do Sul caves, Brazil. Zootaxa 4543: 287–290. https://doi.org/10.11646/zootaxa.4543.2.7

Simone LRL, Casati R (2013) New land mollusk fauna from Serra da Capivara, Piauí, Brazil, with a new genus and five new species (Gastropoda: Orthalicoidea, Streptaxidae, Subulinidae). Zootaxa 3683: 145–158. https://doi.org/10.11646/zootaxa.3683.2.4

Simone LRL, Moracchioli N (1994) Hydrobiidae (Gastropoda: Hydrobioidea) from the Ribeira Valley, S.E. Brazil, with descriptions of two new cavernicolous species. Journal of Molluscan Studies 60: 445–459.

Simone LRL, Salvador RB (2021) A new species of *Spiripockia* from eastern Brazil and reassignment to Cochliopidae (Gastropoda, Truncatelloidea). Journal of Natural History 54: 3121–3130. https://doi.org/10.1080/00222933.2021.1890850

Simone LRL, Cavallari DC, Salvador RB (2020) A new troglobite species of *Habeastrum* Simone, 2019 from Brazil, and support for classification in Diplommatinidae (Mollusca, Caenogastropoda). Zoosystematics and Evolution 96: 639–647. https://doi.org/10.3897/zse.96.53880

Sket B (2016) Subterranean (hypogean) habitats in karst and their fauna. In: Finlayson C, Milton G, Prentice R, Davidson N (Eds) The Wetland Book. Springer, Dordrecht, 1–14.

Trajano E, Bichuette ME (2009) Diversity of Brazilian subterranean invertebrates, with a list of troglomorphic taxa. Subterranean Biology 7: 1–16.

Trontelj P, Blejec A, Fišer C (2012) Ecomorphological convergence of cave communities. Evolution 66: 3852–3865.

Weigand AM (2013) New *Zospeum* species (Gastropoda, Ellobioidea, Carychiidae) from 980 m depth in the Lukina Jama – Trojama cave system (Velebit Mts., Croatia). Subterranean Biology 11: 45–53.

Weigand AM (2014) Next stop: underground. Variable degrees and variety of reasons for cave penetration in terrestrial gastropods. Acta Carsologica 43: 175–183.

Wendebourg B, Hausdorf B (2019) The land snail fauna of a South American rainforest biodiversity hotspot: the Panguana conservation area in the Peruvian Amazon. Journal of Molluscan Studies 85: 311–318.

Submitted: October 21, 2021
Accepted: March 28, 2022
Editorial responsibility: Carlos Eduardo Belz

Author Contributions

RBS conceptualized the article; RBS and FSS conducted the investigation and wrote the original draft; all authors contributed equally to analysis, interpretation, and final writing.

Competing Interests

The authors have declared that no competing interests exist.

How to cite this article

Salvador RB, Silva FS, Cavallari DC, Cunha CM, Bichuette ME (2022) Cave-dwelling gastropods (Mollusca: Gastropoda) of Brazil: state of the art and conservation. Zoologia (Curitiba) 39: e21033, https://doi.org/10.1590/S1984-4689.v39.e21033

Published by

Sociedade Brasileira de Zoologia at Scientific Electronic Library Online (https://www.scielo.br/zool)