Revisiting *Drymaeus germaini* (Ancey, 1892) (Gastropoda, Bulimulidae): ecological niche and first anatomical description of a poorly known land snail species from Brazil (#103076)

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Revisiting *Drymaeus germaini* (Ancey, 1892) (Gastropoda, Bulimulidae): ecological niche and first anatomical description of a poorly known land snail species from Brazil

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Background. Terrestrial gastropods are one of the most imperiled animal groups in the world. However, ~~the~~ information ~~to attain the criteria based~~ on population size and structure, geographic range and their trends over time, necessary to assess species conservation status is unavailable or insufficient for most land snail taxa, making difficult to apply the IUCN criteria. Ecological niche modelling (ENM) has been used to predict species geographic distribution, allowing ~~to better characterize~~ the distribution ranges of endemic or rare species, offering the necessary information for stating their conservation status and planning for conservation measures. **Methods.** We compiled occurrence records of *Drymaeus germaini* associated with museum collections. A distribution map including geographic boundaries and Brazilian biomes was made with QGis version 3.10.14- La Coruña. For niche modelling, ten bioclimatic variables were used as predictors. The models were performed with MaxEnt version 3.4.3. **Results and Discussion**. We have redescribed *Drymaeus germaini* based on the inner anatomy and shell sculpture, also providing the first comparative conchological analysis with congeneric species. We also updated the current distribution of the species within the main Brazilian biomes and estimated its potential geographic distribution using the ENM approach. The results of the ENM analysis indicated that *D. germaini* may have a more restrict ecological niche breadth and limited geographical range within the Atlantic Forest and the Cerrado domains, the most degraded biomes in Brazil. One zone of high and mid-to-high environmental suitability was recovered in an area impacted by mining activities, with two recent disasters of great proportion and another impacted by a massive flooding recently. We found only one confirmed occurrence record of this species in an environmentally protected area. The federal and state conservation unities within the distribution range of *D. germaini* are in areas of mid suitability for this species. Together, these results may indicate that *D. germaini* is of conservation concern, evidencing the urgent need of

monitoring and obtaining the information necessary to stablish its conservation status.

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ABSTRACT

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Subjects Biodiversity, Biogeography, Ecology, Taxonomy, Zoology

Keywords Atlantic Forest, Cerrado, Pampas, Bulimulidae, Conservation

INTRODUCTION

Bulimulidae Tryon, 1867 (Orthalicoidea Martens, 1860) comprise a diverse group of land snails distributed in South and Central America, besides adjacent areas in USA and Caribbean (*Breure & Borrero, 2019*). The current taxonomy considers that Bulimulidae consists of three subfamilies: Bostrycinae Breure, 2012, Bulimulinae Tryon, 1867, and Peltelinae Gray, 1855 (*Bouchet et al., 2017; Salvador et al., 2023*) and 16 genera (*Salvador et al., 2023*). Bulimulidae is recognized as a family ~~remarkably rich,~~ with ~~circa of~~ 700 species, the greater diversity of species being concentrated within the area comprising northern South America and the Brazilian territory *(Solem, 1969; Breure, 1979*). About 120 bulimulid species allocated in 12 genera are currently known to occur in Brazil (*Simone, 2006; Salvador, 2019; MolluscaBase, 2024*).

Among the bulimulid genera, *Drymaeus* Albers,1850 is recorded in the ~~South~~ of North America, Caribbean islands, Central and South America, including the Andes and all mainland forests (*Breure, 1979; Simone, 2006*). This genus was previously ascribed to the subfamily

Bulimulinae Tryon, 1867 (*Breure, 1979; Schileyko, 1999*), but molecular evidence provided by *Breure & Romero (2012)* have justified its ~~allocation~~ in the subfamily Peltelinae. The number of species within this genus have changed over the time. Until the late 1960's, *Drymaeus* included about 552 species (*Breure, 1979*). Nowadays, 379 species of *Drymaeus* are recognized as valid (*MolluscaBase, 2024*). Despite the ~~expressive~~ number of *Drymaeus* species, data on internal anatomy, distribution, and life history of these species are scarce for most of the taxa (*Macedo et al., 2023*).

The original diagnosis of *Drymaeus* was established by *Albers (1850)* and it was based solely on shell morphology. Lately, the importance of the anatomical characters for species delimitation was shown by *Pilsbry (1897)*, encouraging the inclusion of information on anatomical traits in species diagnosis by subsequent authors (*Breure, 1979; Schileyko, 1999; Simone & Salvador, 2016; Simone & Amaral, 2018*). *Pilsbry (1897)* retained two subgenera, ie.: *Drymaeus* for species with outer lip expanded or reflected and *Mesembrinus* for species with outer lip unexpanded or simple. *Drymaeus* is characterized by peristome ~~usually expanded;~~ mandibula with 13 to 18 plates, which are 4 to 5 times as long as wide; ~~transverse rows of radula straight,~~ with relatively large, mono- to tricuspid teeth and bi- to tricuspid latero-marginal teeth (*Breure, 1979*). *Mesembrinus* is characterized by peristome ~~simple;~~ mandibula with 20 plates, which are 8 times as long as wide; transverse rows of radula V- or W-shaped with relatively small tri- to multicuspid central and latero-marginal teeth. In addition to *Drymaeus* and *Mesembrinus*, Germain (1907) proposed the subgenus *Antidrymaeus* to allocate species with ~~sinister~~ shells previously ascribed to *Drymaeus*. Recently, *Salvador et al. (2023)* have elevated *Mesembrinus* and *Antidrymaeus* to genus level.

In Brazil, 40 species of *Drymaeus*, 13 of *Mesembrinus* and two of *Antidrymaeus* were recorded (*Simone, 2006; Macedo et al., 2023; Salvador et al., 2023*), most of them characterized only on the basis of shell morphology; a better resolution of species numbers depending on the clarification of potential synonyms, besides the definition of the taxonomic status of varieties and subspecies and elucidation of complexes of species morphologically cryptic, by using molecular approaches (*Breure & Borrero, 2019*).

Drymaeus germaini Ancey, 1892 is a species originally ascribed to the genus *Bulimulus* Leach, 1814, based on a single dry shell, collected in Mato Grosso state, Brazil. In the original description, no exact collection locality was given. *Ancey (1892)* compared *D. germaine* with only one species of *Drymaeus*, i.e.: "It is in somewhat like a small, thin *B. felix,* but otherwise quite distinct from the New Granada shell". *Pilsbry (1898)*, based on shell morphology (aperture shape, expanded lip, and protoconch sculpture), reallocated *D. germaini* within the genus *Drymaeus*. *Morretes (1949)* ascribed it to the subgenus *Mormus* Martens, 1860. Later, the presence of shell aperture with expanded lip justified the inclusion of *D. germaine* in the subgenus *Drymaeus* (*Breure, 1979*). So far, no anatomical characterization of *D. germaine* was provided.

The current knowledge on the distribution of *D. germaini* is based on few occurrence records taken from the original description and former literature *(Pilsbry, 1897; Ancey, 1901; Morretes, 1949, Simone, 2006*). The distribution of several bulimulid species in Brazil, particularly species of *Drymaeus* and *Mesembrinus*, is poorly know (*Dutra-Clarcke & Souza, 1991; Simone, 2006; Macedo et al., 2023*). The lack of knowledge regarding the distribution of native bulimulid species constitutes an impediment to evaluate their conservation status and, consequently, to advocate for protective laws for vulnerable species.

Ecological niche modelling (ENM) has been used to predict species geographic distribution, allowing researchers to collect species whose occurrences have been unnoticed for great periods of time and thus better characterize their distribution ranges, offering the necessary information for stating their conservation status and planning for conservation measures (*Sillero et al., 2021*). Another important application of ENM is related to the potential effects of climate change on biodiversity conservation (*Beltramino et al., 2015*), enabling the evaluation of the potential impacts over species distributions. This approach allows the development of conservation strategies by revealing areas of critical concern, which is especially useful for species with ~~restrict~~ distributions, i.e.: endemic or rare species (*Beltramino et al., 2015*), as may be the case for *D. germaini*. Despite the possibility of using modelling tools to assess the potential distribution of species and favorable areas for species recollection, this approach has been rarely used (*Macedo et al., 2023*) and fieldwork to specifically assess the current distributional range of bulimulid species has not been conducted recently in Brazil. One reason for the scarcity of ENM studies on bulimulids may be the insufficiency of occurrence records for the species in the literature. In this context, malacological collections constitute an important source of unpublished distributional information for ecological niche modelling with the aim of

~~estimate suitability~~ areas and ~~species~~ potential distribution *(Pearson et al., 2006; Ball-Damerow et al., 2019*).

In the present study, the bulimulid species *D. germaini* was revisited. We have redescribed this species based on the inner anatomy and shell sculpture, also providing the first comparative analysis with congeneric species. We also updated the current distribution of the species within the main Brazilian biomes and estimated its potential geographic distribution using the ENM approach.

MATERIAL AND METHODS

Study area

Brazil has the fifth largest territory of the world being considered as a mega biodiverse country concentrating approximately 20% of the total number of known species on the planet (*Mittermeier et al., 2002*). Geographically it consists of five regions: North, Northeast, Southeast, South and Central-West. North Brazil corresponds almost entirely to the Amazon Forest domain, which occupies almost half of the country (*IBGE, 2019*). The equatorial climate, hot and humid, is predominant, with irregular average annual rainfall ranging from 1,500 mm/year to 2,500 mm/year. ~~The~~ Northeast Brazil includes the semi-arid domain, which ~~have~~ an irregularly distributed average annual rainfall ranging from 250 mm/year to less than 750 mm/year. The Southeast includes tropical areas, receiving most of the annual rainfall during the summer, with the annual average rainfall varying from 1,500 mm/year to 2,000 mm/year (*IBGE, 2019*). South Brazil comprises a temperate zone with cool and relatively dry winters and warm and relatively humid summers. The annual distribution of rainfall over southern Brazil is relatively uniform, the average annual rainfall varying from 1,250 mm/year to 2,000 mm/year (IBGE, 2019). The Central-West Region stretches from the fringes of the Amazon basin in the west to the state of Goiás in the east. At its westerly extreme it has a relatively well-distributed average annual rainfall of up to 2,500 mm/year. Further to the east, rainfall decreases to about 1,000 mm/year (*IBGE, 2019*). The Southern region corresponds to the Brazilian Pampas. It is characterized by a rainy climate, with the annual average of rainfall ranging from 1,250 mm/year to 2,000 mm/ year, without a systematic dry period, but marked by the influence of polar fronts and negative temperatures in the winter (*IBGE, 2019*).

Geographic distribution

Occurrence records of *D. germaine* were obtained from the biodiversity databases Global Biodiversity Facilities - GBIF (https://www.gbif.org) and *Sistema de Informação sobre a Biodiversidade Brasileira* (https://www.sibbr.gov.br), besides published papers and records associated to specimens deposited in the malacological collection of the *Museu de Malacologia Prof. Maury Pinto de Oliveira*. We validated species attribution associated with the occurrence records, by requesting images of the specimens to the curators of the malacological collections consulted online and by performing ~~the~~ morphological study of the specimens deposited in the CMMPO. We could not validate species attribution associated to the specimens from MNRJ, as they were lost during the fire of September 2018. However, the records of these specimens in GBIF show that they were previously identified by Dr Norma Campos Salgado, a Brazilian malacologist who ~~have~~ dedicated her life to the study bulimulid land snails, so we considered that these records are trustworthy. From the total number of occurrence records, four had only "São Paulo" as the collection site. These records were excluded from the analysis, as it was not possible to discriminate if the locality referred to the state of São Paulo, or the city of São Paulo. We also removed all the duplicated records, and thus the remaining eight unique sites with trustable geographic information were used during the ecological niche modeling. We used the application Gazetteers (https://www.geo-locate.org) for the georeferentiation of the localities for which geographic coordinates were lacking. When necessary, the coordinates were converted to decimal degree format using *Instituto Nacional de Pesquisas espaciais* - INPE geographic calculator (http://www.dpi.inpe.br/calcula/). We plotted and overlapped the occurrence records of *D. germaini* with the layers of biomes and administrative boundaries obtained from *Instituto Brasileiro de Geografia e Estatística* - IBGE (https://www.ibge.gov.br). The data was analyzed using QGis version 3.10.14- La Coruña (*QGIS Development Team, 2021*).

Ecological niche modeling

To delineate the abiotic components of the model, we used 19 bioclimatic variables obtained from the WorldClim database (http://www.worldclim.org) at a spatial resolution of 30 arc seconds (~1 km^2), besides two topographic variables, elevation (in meters) and soil type, also with the spatial resolution of 30 arc seconds (~1 km^2), obtained from IBGE (https://downloads.ibge.gov.br). We clipped the environmental data layers to the mask defined as the Brazilian territory. Correlation analysis using the abiotic variables previously selected was performed by using the "ntbox" package (Osorio-Olvera et al., 2020) in R environment version

4.2.0 (*R Core Team, 2021*). One variable per pair of highly correlated variables [$r \geq 0.85$] was eliminated resulting in ten bioclimatic variables for the analyses: BIO2 = Mean diurnal range [Mean of monthly (max temp–min temp)], BIO 3= Isothermality [(BIO2/BIO7) (*100)], BIO 4= Temperature seasonality [standard deviation *100], BIO 7= Temperature Annual Range [BIO5-BIO6], BIO 10 = Mean Temperature of Warmest Quarter BIO 11= Mean Temperature of Coldest Quarter, BIO12 = Annual precipitation, BIO14 = Precipitation of Driest Month, BIO17 = Precipitation of Driest Quarter, and elevation. The ENMs were performed with the software package MaxEnt version 3.4.3 (Phillips et al., 2021). Default parameters of MaxEnt algorithm were used, including a maximum of 500 iterations with a convergence threshold of 0.00001 and 10,000 randomly chosen background localities. Considering the small size of our sample, we followed the methodology proposed by *Pearson et al. (2007)* for samples with few records. The model ran eight replicates, with 75% of presence records randomly selected to generate the models, while the remaining 25% was used as test. The model was computed as "logistic" as the output returned a continuous map with an estimated probability of presence between 0 (no probability of the species presence) and 1 (high probability of presence), which permits fine distinctions between the suitability of different areas modeled. Jackknife tests were used to identify the variables that most influenced the model predictions. To evaluate the variable that most influence the model, a strong correlation test was performed. The resulted model was evaluated based on significance, i.e.: partial ROC, with 500 interactions and 50 percent of data for bootstrapping.

Morphological study

The specimens used for the morphological analyses came from the malacological collection of the *Museu de Malacologia Prof. Maury Pinto de Oliveira*, *Universidade Federal de Juiz de Fora* – Brazil. For the conchological characterization, only intact adult shells were selected. Sixteen shells were photographed with a Digital camera Nikon D5300 and measured according to the methodology proposed by *Miranda (2015)*. The obtained images were used to construct Tps files with the software TpsUtil version 1.81 (*Rohlf, 2021*) and the shell measurements were carried out with TpsDig2 version 2.32 (*Rohlf, 2018*) directly on the image with the "Make Linear Measures" tool on apertural and lateral views of the shells. The following linear measurements were taken: total shell height (tsh), body whorl height (bwh), spire height (sh), major shell diameter (masd), minor shell diameter (misd), apertural height (ah), apertural diameter (ad), parietal space length (psl), penultimate whorl height (pwh), and penultimate whorl diameter (pwd). For the anatomical characterization of the reproductive and pallial systems, adult snails were dissected immersed in ethanol, under an Olympus® stereoscopy microscope, model SZX7. The anatomical structures were ~~draw~~ with the aid of a camera lucida. Radulae and shells from two adult specimens were prepared for scanning electron microscopy, following the methodology proposed by *Ploeger & Breure (1977)*. The radulae were separated from the buccal mass, cleaned by immersion in sodium hypochlorite solution and dried. The shells and radulae were mounted on stubs covered with carbon tape, metalized with 50 nm of gold, and observed under a scanning electron microscope FEI Quanta 250 at the laboratory of Electron Microscopy, Federal University of Juiz de Fora.

RESULTS

Taxonomic part and morphology

Systematic arrangement

Superfamily Orthalicoidea Martens, 1860

Family Bulimulidae Tryon, 1867

Subfamily Peltellinae Gray, 1855

Drymaeus Albers, 1850

Type species: Helix hygrohylaeus (d'Orbigny, 1835)

***Drymaeus germaini* Ancey, 1901**

Bulimulus germaini Ancey (1892): 91.

Drymaeus germaini —Pilsbry (1897): 206.

Drymaeus (Mormus) germaini —Morretes (1949): 150.

Drymaeus (Drymaeus) germaini —Breure (1979): 109.

Drymaeus germaini —Salgado & Coelho (2003): 162; —Simone (2006):137; —Salvador (2019b):86.

Type material:

Type locality: **Brazil** • Matto Grosso [Mato Grosso].

Material examined: **Brazil** • 1 shell; Minas Gerais, Ponte Nova, Jul. 1961; CMMPO 1865. • 2 shells; Minas Gerais, Ipaba, Fazenda da Macedônia, 06 Apr. 2011; CMMPO 8697. • 3 shells; Minas Gerais, Ipaba, Fazenda da Macedônia, 10 Nov. 2011; Junqueira, F. O. leg.; CMMPO11258. • 2 shells; Minas Gerais, Ipaba, Fazenda da Macedônia, 27 May 2011; Junqueira, F. O. leg.; CMMPO11260. • 2 shells; Minas Gerais, Ipaba, Fazenda da Macedônia, 18 Nov. 2012; Junqueira, F. O. leg.; CMMPO11261. • 8 shells; Minas Gerais, Ipaba, Fazenda da Macedônia, 05 Jul. 2011; Junqueira, F. O. leg.; CMMPO11262. • 1 specimen preserved in ethanol; Minas Gerais, Ipaba, Fazenda da Macedônia, 18 Nov. 2012; Junqueira, F. O. leg.; CMMPO11263. • 3 shells; Minas Gerais, Ipaba, Fazenda da Macedônia, 27 May 2011; Junqueira, F. O. leg.; CMMPO11264. • 1 shell; Minas Gerais, Ipaba, Fazenda da Macedônia, 12 Jul. 2012; Junqueira, F. O. leg.; CMMPO11265. • 3 shells; Minas Gerais, Ipaba, Fazenda da Macedônia, 11 Apr. 2012; Junqueira, F. O. leg.; CMMPO11266. • 6 shells; Minas Gerais, Ipaba, Fazenda da Macedônia, 17 May 2012; Junqueira, F. O. leg.; CMMPO11267. • Minas Gerais, Ipaba, Fazenda da Macedônia, 17 May 2012; Junqueira, F. O. leg.; CMMPO11268. • 1 specimen preserved in ethanol; Minas Gerais, Ipaba, Fazenda da Macedônia, 05 Jul. 2011; Junqueira, F. O. leg.; CMMPO 11269. • 2 specimens preserved in ethanol; Minas Gerais, Ipaba, Fazenda da Macedônia, 28 Apr. 2011; Junqueira, F. O. leg.; CMMPO 11270. • 3 shells; Minas Gerais, Ipaba, Fazenda da Macedônia, 06 Apr. 2011; Junqueira, F. O. leg.; CMMPO 11379. • 2 specimen preserved in ethanol; Minas Gerais, Ipaba, Fazenda da Macedônia, 03 Jul. 2005; Junqueira, F. O. leg.; CMMPO11394. • 1 shell; Minas Gerais, Ipaba, Fazenda da Macedônia, 28 Dec. 2011; Junqueira, F. O. leg.; CMMPO11405. • 1 shell; Minas Gerais, Ipaba, Fazenda da Macedônia, 11 Apr. 2012; Junqueira, F. O. leg.; CMMPO11406. • 1 shell; Minas Gerais, Ipaba, Fazenda da Macedônia, 17 May 2012; Junqueira, F. O. leg.; CMMPO11407.

Information from collections assessed online. **Brazil** • 5 shells; Minas Gerais, Ponte Nova; 42W53’47.612”, 20S25’0.041”; 20 Jan. 2009; Junqueira, F.O. and Salgado, N.C. leg.; MNRJ 13475. • 2 shells; Minas Gerais, Viçosa, Recanto das Cigarra; 42W51’50.011”, 20S45’30.917”; 20 Jan. 2009; Junqueira, F.O. and Salgado, N.C. leg.; MNRJ 13476. • 3 shells; Minas Gerais, Ponte Nova, Amparo da Serra; May 1961; Costa, C.J.F. leg.; MNRJ 18942. 2 shells; São Paulo, São Paulo; 06 Jul. 1905; Sowerby & Fulton legs. ANSP 89838. • São Paulo, São Paulo; UF 109243. • São Paulo, São Paulo; UF 161247. • 3 shells; São Paulo; NHMUK 1905.4.14.5-7. • 1 shell; São Paulo; FMNH 31322. • 2 shells; Paraná, Casiro; NHMUK 1920.10.19.9-10. • 1 shell; Fazenda Santa Rita de Cássia, Paraná, São João do Caiuá; Salvador, R. B. leg.; MZSP 108007. • 2 shells; • São Paulo; Sowerby and Fulton leg.; RMNH 266069. • 6 shells; São Paulo, São Paulo; UMMZ 124282.

Morphology

Shell (Figs 1 and 2, Table 1)

Shell perforate, oblong-attenuated, shining, very narrowly rimate. Shell height 25.5 to 29.7 mm (Table 1); whorls $6^{1/4}$, convex, separated by well-marked sutures, the last whorl attenuated, oblong, making a short, sudden ascent at the aperture (Fig. 1). Spire rather obtuse, ~ 1/3 of the shell length. Transition between protoconch to teleoconch well marked. Aperture a little oblique, oblong, slightly lunate, angular above, patulous; interior with the parietal wall and columella purple colored. Outer lip broadly reflected, columella slightly curved, dilated at the top. Sutures well marked, simple, sightly oblique. Body whorl bluish white to pale purple with irregularly flexuous or lightning-zigzagged streaks of tawny-bluish, with small punctuations above the suture. Peristome expanded in adult specimens. Body whorl ~ 2/3 of the shell length, rounded; umbilicus narrow, partially covered by peristome reflection; periumbilical area purplish. Protoconch with 1 ½ whorl, bluish white to lilac in color; well-marked with a grating sculpture with axial riblets and spiral striae (Fig. 2 A, B, C.).

Jaw (Fig. 2)

Jaw simple, beige arched; above 10 to14 pairs of uniform subvertical overlapping plates sold at the inner face, free at their outer edges, shallow horizontal striae; central plate trapezoidal, larger than lateral plates. The plates gradually decrease in size from the center to the border of the jaw (Fig. 2 D, E, F).

Radula (Fig. 2)

Radula with approximately 82 teeth per row. Mean number of teeth per half row (except for central tooth) 41. Rachidian tooth triangular, slightly smaller than lateral teeth (~9/10 of the length of laterals), symmetric, without cusps (Fig. 2 G, H); basal plate trapezoidal, tapered, with cutting edge. First lateral teeth triangular, oblique, less tapered than central tooth (Fig. 2 G, H). A basal-lateral cusp gradually appears in lateral teeth and becomes more distinct in marginal teeth (Fig. 2I). Marginal teeth tricuspid; mesocone well developed with a bicuspid cutting edge; exocone relatively reduced (Fig. 2I). Each radular row is disposed in a shallow V-inverted shape, with rounded borders.

Pallial Cavity

Mantle border simple, thick. Rectum narrow, walls thick. Primary ureter along the rectal side of the kidney up to the top of the pallial cavity. Secondary ureter, long and slender, running along the entire left side of the rectum. Mantle cavity short, ~1/4 of the body whorl. Kidney elongate, narrowly triangular, occupying ~1/3 of pallial cavity length. Pericardial cavity on the left side of the kidney, at the columellar margin of the posterior end of the pallial cavity, with approximately the same length as the kidney. Ventricle triangular. Auricle elongate, ~1/3 of the triangular ventricle. Pulmonary vein converging to pneumostome region, oblique in anterior half of the pallial cavity, running along right edge in the posterior half, and presenting a bifurcation in the last 1/7 of the pallial cavity. Vessels well marked in the right edge of the pallial cavity, in the space between the pulmonary vein and the ureter. Vessels imperceptible in the left edge of the pallial cavity.

Reproductive system (Fig. 3)

Albumen gland slightly elongated, connected to the fertilization complex in the distal portion (Fig. 3 A, B). Free oviduct short and narrow. Spermoviduct long and glandular (Fig. 3 A, B). Bursa copulatrix elongated, poorly differentiated ~~of~~ the distal portion of the duct (Fig. 3 C). Prostate long, juxtaposed to the uterus, containing numerous tubular acini (Fig. 3 B, C). Penial complex elongated, with approximately the same length as the spermoviduct when stretched, ~~pallus~~ subcylindrical, penial sheath present (Fig. 3 A, B, C). Phallus-epiphallus transition undifferentiated externally. Insertion of the vas deferens into the epiphallus subterminal. Flagellum present, subcylindrical, short, ~1/6 of the penial complex length (Fig. 3 B, C). Insertion of the bursa copulatrix and penial complex at different levels. Genital atrium very short, ~1/8 of spermoviduct length. Spermatheca complex well differentiated, sinuous, lying in superior third of the albumen gland (Fig. 3 A, B).

Distribution: BRAZIL, Mato Grosso, Minas Gerais, Paraná, and São Paulo states. Cerrado and Atlantic Forest biomes (Fig. 4).

Differential diagnose

Shell oblong-attenuated, aperture oblique, slightly lunate. Outer lip broadly reflected. Color bluish white to pale purple with irregularly flexuous or lightning-zigzagged streaks of tawny-bluish. Penis with a sheath, flagellum short, subcylindrical. Genital atrium very short.

Remarks

Considering the congeneric species occurring in Brazil, *D. germaini* is very similar to *Drymaeus suprapunctatus* F. Baker, 1914 in shell shape, dimensions and pigmentation pattern. The images provided by *Simone (2006)* for both species show that the holotype of *D. suprapunctatus* (ANSP 109307) present, as also observed for *D. germaini*, a pigmentation pattern characterized by the presence of vertical sinuous stripes and dots. In the image of the *D. suprapunctatus* ANSP 109307 specimen, a spiral roll of dots is observed from the penultimate whorl up to the shell apex, the stripes being absent. In the image of *D. germaini* ANSP 89838 specimen, the dots are less evident as they merge with the vertical stripes. The shells of both species imaged by *Simone (2006)* seem to be identical, except for this subtle difference in pigmentation pattern. Herein, shells of *D. germaini* collected at the same locality in Minas Gerais state evidence the presence of intraspecific variation in shell pigmentation, with a graduation in pigmentation pattern from shells presenting mainly stripes to shells bearing dots predominantly (Supplementary Fig. 1 C-F; Fig. 6). The shells also may be more elongate or more rounded. This find indicates that there is no clear hiatus between the patterns presented by the holotype of *D. suprapunctatus* and the specimen of *D. germaini* imaged by *Simone (2006)*. We also found images of live specimens in GBIF/iNaturalist, corresponding to *D. germaini* (Suplemmentary Figure 1 A and B) showing such variation in pigmentation pattern. From these observations, we are inclined to consider that *D. germaini* and *D. suprapunctatus* correspond to a single species. This matter, however, must be addressed in a more comprehensive study including the molecular analysis of a geographically representative set of specimens.

At the time of its description, *D. germaini* was compared with just one species, *D. felix*, which was never recorded in Brazil. The shell of *D. germaini*, as characterized by *Ancey (1892)*, is smaller and thinner than that of *D. felix*. The observation of the lectotype and paralectotypes of *D. felix* confirm that ~~this last species present greater size~~ ~~and~~ a very distinct pigmentation pattern, with wide bands, reddish brown, and apex blackish (Supplementary Fig. 1 G). *Drymaeus linostoma* (d'Orbigny, 1835) is ~~somehow~~ similar to *D. germaini*, but it ~~presents~~ a bigger shell with a more oval aperture (Supplementary Fig. 1 H). Anatomical data of both species is unavailable. In addition, the distribution of these species ~~doesn't seem to~~ overlap, at least considering the present knowledge on their geographical ranges.

Ecological Niche Modelling

Evaluations of the model

Our model presented a good performance, with mean AUC values of 0.826, with standard deviation of 0.06. The mean value of partial ROC test was 0.93, and $p < 0$, showing that the model was statistically significant. The Jacknife test of variable importance indicated that the distribution of *D. germaini* was mainly influenced by Temperature seasonality (BIO 4) (63.9% of contribution), followed by elevation (11.4%), Mean Temperature of Coldest Quarter (BIO 11) (6.2%), and Precipitation of Driest Quarter (BIO 17) (5.9 %) (Table 2). Response curves also gave an indication of the range under which the variable reaches its optimum suitability. The responses of Temperature seasonality (BIO 4), elevation, and Mean Temperature of the Coldest Quarter (BIO 11) are ascendent curves reaching the asymptote with highest values, while the response curve of the variable Precipitation of Driest Quarter (BIO 17) is a descendent curve near zero. The optimum suitability of this variable is around 4000-4500. Considering the other variables that significantly contributed to the model, the maximum suitability corresponded to elevation values between 1600–1660 meters; Mean Temperature of the Coldest Quarter (BIO 11) above 0^{o}C, and Precipitation of Driest Quarter (BIO 17) above 500 mm.

Estimations of potential geographic distribution

The consensus map with the projection of environmental suitability areas resulting from the ecological niche model obtained herein is shown in Figure 5. The results showed the presence of two major areas of high and mid-to-high environmental suitability for *D. germaini*, i.e.: one continuous area in the mid-southern Minas Gerais state, extending southwards to the frontier with São Paulo state, and eastward to Rio de Janeiro and Espírito Santo states, including five vegetational formations (Tropical Savana, Tropical Rain Forest, Altitudinal fields, Rupestrian fields, Semideciduous Dry Forest), most of them contained in the Atlantic Forest domain; and another continuous area comprising southern and mid-northeastern Rio Grande do Sul state with two vegetational formations in the Atlantic Forest domain (Subtropical Forest) and Pampas domain (South Brazilian Grasslands). In addition, smaller areas of mid-to-high suitability were recovered in ~~the~~ mid-western Rio de Janeiro, and southeastern São Paulo, Paraná, and Santa Catarina states, including three vegetational types contained in the Atlantic Forest domain (Semideciduous Dry Forest, Tropical Rain Forest) and Pampas domain (South Brazilian Grasslands). Four areas of highest environmental suitability are in northeast Minas Gerais, Centre west of Rio de Janeiro, between São Paulo and Paraná states, and southeast of Rio Grande do Sul. Additionally, areas of mid-to-low environmental suitability were recovered in Southwestern, Central, and Southern Bahia; Southern Mato Grosso state; Southwestern Mato Grosso do Sul state; Western and Northern Minas Gerais state; Eastern Rio de Janeiro and Espírito Santo states; most of the area of São Paulo and Paraná states; Western, Southern and Eastern Santa Catarina states, besides Northern Rio Grande do Sul state. Isolated areas of mid-to-low suitability were also recovered in Mato Grosso, Pará, and Pernambuco states. Areas of low suitability were recovered mainly in Northern and Northeastern Brazil.

DISCUSSION

In the present study, using records from malacological collections, we have updated the geographic distribution of *D. germaini*, providing, for the first time, specific localities where this species occurs, which also allowed us to estimate its potential distribution. *Drymaeus germaini* was described from a single dry shell and since its description, occurrence records of this species in the literature are outdated, scarce, and refer only to Brazilian states, with no mention to specific localities. The analysis of the data associated to museum specimens, revealed that *D. germaini* was collected and then incorporated to a collection for the last time in January 2011. In a recent effort to recollect this species in this same locality, i.e.: Ipaba, Minas Gerais state, no specimen was recovered (Macedo, *M.I.P.F., personal communication*). Accordingly, there have been no recent records of this species in the literature. Nonetheless, we found records of *D. germaini*, and confirmed the species taxonomic identity, in iNaturalist for the following years: 1982; 2015, 2016, 2020, 2022, 2023, and 2024, evidencing that this gap in the entrance of specimens in malacological collections is mainly due to the shortage in collection efforts. We also attempt to find museum occurrence records of *D. germaini* in Mato Grosso state, where the type locality is enclosed, but we only found records of human observation for localities in Mato Grosso (Alta Floresta, Sinop, and Novo Mundo) and Mato Grosso do Sul (Dourados) (*GBIF, 2024*). These results indicate the need for collecting *D. germaini* in these localities, improving its ~~representativity~~ in malacological collections, and proving a geographically representative set of specimens for molecular studies on species delimitation, population genetics, molecular taxonomy, and phylogeny. Such studies are greatly necessary to better resolve species limits within this genus and their conservation status.

Among the ten environmental variables used in ENM of *D. germaini*, the main variables that influenced the model were the Temperature seasonality (BIO 4), elevation, Mean Temperature of Coldest Quarter (BIO 11), and Precipitation of Driest Quarter (BIO 17). Temperature seasonality was the variable with greater influence and Precipitation of Driest Quarter was the variable that less influenced the model. Temperature in known to have a significant impact on the reproductive strategies adopted by various species or populations of land snails, influencing the reproductive success of individuals *(Resende et al., 2020*). The risk of desiccation is also an important factor with influence on their life history traits and survival, as land snails depend on environmental moisture for breathing, reproduction, and locomotion (*Arad, 1993; Cook, 2001; Storey, 2002*). The fact that the Precipitation of Driest Quarter was the variable that less influenced the model may be explained by the humid, relatively stable environment provided in the Atlantic Forest domain, as well as the Pampas domain (IBGE, 2019), where the occurrence records and areas with greater environmental suitability for *D. germaini* are contained.

We found occurrence records for *D. germaini* in localities contained in the Cerrado (human observation) and the Atlantic Forest (preserved specimens in museum collections). As discussed above, the ENM results revealed that the most environmentally suitable areas for *D. germaini* are in the Atlantic Forest and Pampas biomes. The Atlantic Forest is considered as a biodiversity hotspot with high levels of endemism in both fauna and flora (*Myers et al., 2000*). It is also the most degraded biome in Brazil, enclosing most of threatened invertebrate species. Cerrado is the second most degraded biome in Brazil. The main threats to biodiversity conservation in these biomes are ~~the~~ habitat fragmentation, fire, and habitat loss as consequence of urbanization pressure, large scale agriculture, and cattle raising (*Zaú, 1998; Santana et al., 2020*). These facts highlight the need of monitoring *D. germaini* and obtaining the information necessary to stablish its conservation status. In a previous study on *Mesembrinus interpunctus* (*Martens, 1887*) (Bulimulidae, Peltelinae), we observed that this species is present in all six Brazilian biomes, the results of the niche modeling, however, showed only a thin area of high suitability to this species within the Atlantic Forest Biome, indicating that *M. interpunctus* may be a generalist species, with a niche breadth that might favor its presence in a range of different ecoregions (*Macedo et al., 2023*). The results herein obtained for *D. gemaini* show an opposite pattern for this species. The known records are restricted to only two biomes (Atlantic Forest and Cerrado) and the areas of high and mid-to-high environmental suitability herein recovered are restricted to only two geographic areas, one of them with no confirmed record of the species. These results seem to indicate that *D. germaini* may rather have a more restrict ecological niche breadth and limited geographical range within the Atlantic Forest and the Cerrado domain.

Herein, *D. germaini* is reported for the first time for Minas Gerais state, in Ipaba, Ponte Nova, and Viçosa municipalities. The continuous area of high and mid-to-high suitability for *D. germaini* in Minas Gerais comprises two large ferruginous geosystems, i.e.: *Serra da Serpentina-Morro do Pilar* and *Quadrilátero Ferrífero*, this last one concentrating major mining companies. In recent years, this area was the scenario of two environmental disasters caused by the collapse of two dams, i.e.: Fundão (2015) from Vale Mining Company and Córrego do Feijão (2019) from Samarco Mining Company. These disasters had profound environmental and social effects, with the loss of many human lives, contamination of water bodies and soil with toxic substances, and devastation of forested areas, with severe impacts on the fauna and flora (*Carmo et al., 2017; Rotta et al., 2020*). Herein, the fact that this main area of high suitability for *D. germaini* is in such impacted area, pose some concerns about its conservation status. Mining is a relevant threat to species conservation, as it can causes habitat loss and fragmentation, resulting in increased extinction risk, specially to habitat specialists and species with dispersal limitations such as terrestrial gastropods (*Pena et al., 2017; Mallett et al., 2021; Macêdo et al., 2024*). The other continuous area of high and mid-to-high suitability for *D. germaini* in Rio Grande do Sul state was affected by a massive flooding, recently, which had a devastating impact, leaving hundreds of towns under water. The impact of this event on the fauna is still unknown, nonetheless, this flooding may have a huge impact on land snail fauna.

We observed that most of Brazilian conservation unities are situated in areas of medium suitability for this species. In northeast of Minas Gerais state, there is only one National Park (Sempre Vivas State Park) and four State Park (Biribiri, Rio Preto, and Itambé Pic) contained in areas of high environmental suitability for *D. germaini*. A similar situation is observed in Rio de Janeiro state, with only one National Park (*Serra dos Órgãos*), Paraná and São Paulo states, one state park (*Escarpa Devoniana Stadual Protect Area* and *Vale do Códo State Park*), Rio Grande do Sul with one state park (*Espinilho State Park*). None of the occurrence records recovered from malacological collections overlap with federal, state, or private Conservation Unities. Only the records from the municipality of Ipaba, Minas Gerais, correspond to a Private Natural Reserve.

Terrestrial gastropods are one of the most imperiled animal groups in the world (*Régnier et al., 2015*). In Brazil, 62 land snail species ~~were~~ classified as endangered, this number being probably underestimated. The International Union for Conservation of Nature Red List of Threatened Species relies on several criteria, based on population size, and structure, geographic range and their trends over time to assess species conservation status. Nonetheless, the necessary information is unavailable or insufficient for most land snail taxa, making difficult to apply the IUCN criteria (*Régnier et al., 2015*). Only two species of *Drymaeus*, i.e.: *Drymaeus acervatus* (L. Pfeiffer, 1857) and *Drymaeus henseli* (E. von Martens, 1868), were classified, both considered vulnerable (*IUCN, 2024*); the poor classification of *Drymaeus* species with regard to its conservation status being primarily due to the lack of data on their abundance and distribution range.

Our analyzes also allowed us to critically explore the data associated with museum specimens. Dry specimens made up the majority (86%) of the material contained in malacological collections. Our finds showed the presence of specimens of *D. germaini* preserved in ethanol in only one malacological collection, i.e.: *Coleção Malacológica Prof. Maury Pinto de Oliveira*, evidencing the significance of small regional collections for our knowledge on Biodiversity. Small Natural History collections contribute with fewer specimens than larger, renowned ones, but they offer distinctive knowledge on local biodiversity, filling critical gaps in taxonomy, geographic distribution, and temporal variation of species (*Monfils et al., 2020*).

Herein, we observed the presence of intraspecific variation in shell pigmentation of *D. germaini*, with a graduation in pigmentation pattern from shells presenting mainly stripes to shells bearing dots predominantly. Such variation evidence the absence of a clear hiatus between the shell traits of *D. germaini* and *D. suprapunctatus*, which may possibly indicate that *D. suprapunctatus* is a junior synonym of *D. germaini*. This hypothesis, however, must be addressed in the future, from the recollection of specimens of *D. suprapunctatus* and *D. germaini* and an integrative approach including molecular and anatomical sources of evidence to delimitate or synonymize these species. Subtle differences in shell characteristics, including the pigmentation pattern, have long been used as operational criteria for the delimitation of *Drymaeus* species, without considering intraspecific variation in these traits (*Macedo et al., 2023*). Intraspecific variations in color patterns have already been documented for *Drymaeus* (*Breure & Borrero, 2019*), however, most of the nominal species within this genus are known only from their shells, the limit between intra- and interspecific variation in shell morphology and pigmentation being unknown. This evidences the need to incorporate other diagnostic criteria in addition to shell traits for the delimitation of *Drymaeus* species.

CONCLUSIONS

Considering the results of the ecological niche modeling analysis indicating that *D. germaini* may have a more restrict ecological niche breadth and limited geographical range within the Atlantic Forest and the Cerrado domains, the most degraded biomes in Brazil; the presence of one zone of high and mid-to-high environmental suitability in an area impacted by mining activities, with two recent disasters of great proportion and another zone impacted by a massive flooding recently; the scarcity of confirmed occurrence records of this species in environmentally protected areas (only one record); and the presence of conservation unities only in areas of mid suitability may indicate that *D. germaini* is of conservation concern. Our results evidence the need of monitoring *D. germaini* and obtaining the information necessary to stablish its conservation status.

Institutions Acronyms

ANSP Academy of Natural Science of Philadelphia

CMMPO Coleção Malacológica Maury Pinto de Oliveira

FMNH Field Museum of Natural History

IBGE Instituto Brasileiro de Geografia e Estatística

MNRJ Museu Nacional do Rio de Janeiro

MZSP Museu de Zoologia da Universidade do Estado de São Paulo
NHMUK Natural History Museum
UF Florida Museum of Natural History
RMNH Rijksmuseum voor Natuurlijke Historie
UMMZ University of Michigan Museum of Zoology

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Table 1 (on next page)

Table 1. Shell linear measurements perimeter and surface area of shells of *Drymaeus germaini* Ancey, 1892. Alues given in millimeters.

Legend: **ad**: shell apertural diameter; **ah**: shell apertural height; **bwh**: body whorl height; **masd**, major diameter of the shell; **misd**: minor diameter; **psl**: parietal space length; **pwd**: penultimate whorl major diameter; **pwh**: penultimate whorl height; **sh**: spire height; **tsh**: shell height; **sp**: shell perimeter; **ssa**: shell surface area; **spp**: spire perimeter; **spsa**: spire surface area; **bwp**: body whorl perimeter; **bwsa**: body whorl surface area; **ap**: aperture perimeter; **asa**: aperture surface area.

Table 1. Shell linear measurements perimeter and surface area of shells of *Drymaeus germaini* Ancey, 1892. Alues given in millimeters.

Measurements	Min-Max (SD) Mean
tsh	29.7- 25.5 (±1.57) 27.3
bwd	21.0-17.6 (±1.11) 19.5
sh	8.8-6.6 (±0.62) 7.8
masd	10.7 -9.1 (±0.49) 10.1
misd	10.3-7.5 (±0.73) 8.38
ah	12.84-9.1 (±0.89) 13.6
ad	9.63-7.0 (±0.68) 8.5
psl	8.6-6.5 (±0.68) 7.8
pwh	4.2-3.2 (±0.23) 3.8
pwd	7.4-6.4 (±0.3) 7.0

Legend: **ad**: shell apertural diameter; **ah**: shell apertural height; **bwh**: body whorl height; **masd**, major diameter of the shell; **misd**: minor diameter; **psl**: parietal space length; **pwd**: penultimate whorl major diameter; **pwh**: penultimate whorl height; **sh**: spire height; **tsh**: shell height; **sp**: shell perimeter; **ssa**: shell surface area; **spp**: spire perimeter; **spsa**: spire surface area; **bwp**: body whorl perimeter; **bwsa**: body whorl surface area; **ap**: aperture perimeter; **asa**: aperture surface area.

Table 2(on next page)

Table 2. Relative contribution and permutation importance of environmental variables to the Ecological niche model generated for *Drymaeus germaini* Ancey, 1892, in Brazil.

Table 2. Relative contribution and permutation importance of environmental variables to the Ecological niche model generated for *Drymaeus germaini* Ancey, 1892, in Brazil.

Variable	**Percent contribution**	**Permutation importance**
BIO 4	63.9%	43.2
Elevation	11.4%	1.9
BIO 11	6.2%	9.3
BIO 17	5.9%	5.9
BIO 3	5%	24.2
BIO 7	4.6%	0.5
BIO 10	2.2%	13.4
BIO 14	0.8%	1.5
BIO 12	-	0
BIO 2	-	0

Figure 1

Shell of *Drymaeus germaini* Ancey, 1892.

Material examined: Brasil • 1 shell; Fazenda Macedônia, Ipaba, Minas Gerais; 28 Oct 2011; MIPS Macedo & S. D'ávila leg.; F.O. Junqueira col.; CMMPO 11405. **A**. ventral view. **B**. Dorsal view. **C**. Lateral view. Shell height 29 mm.

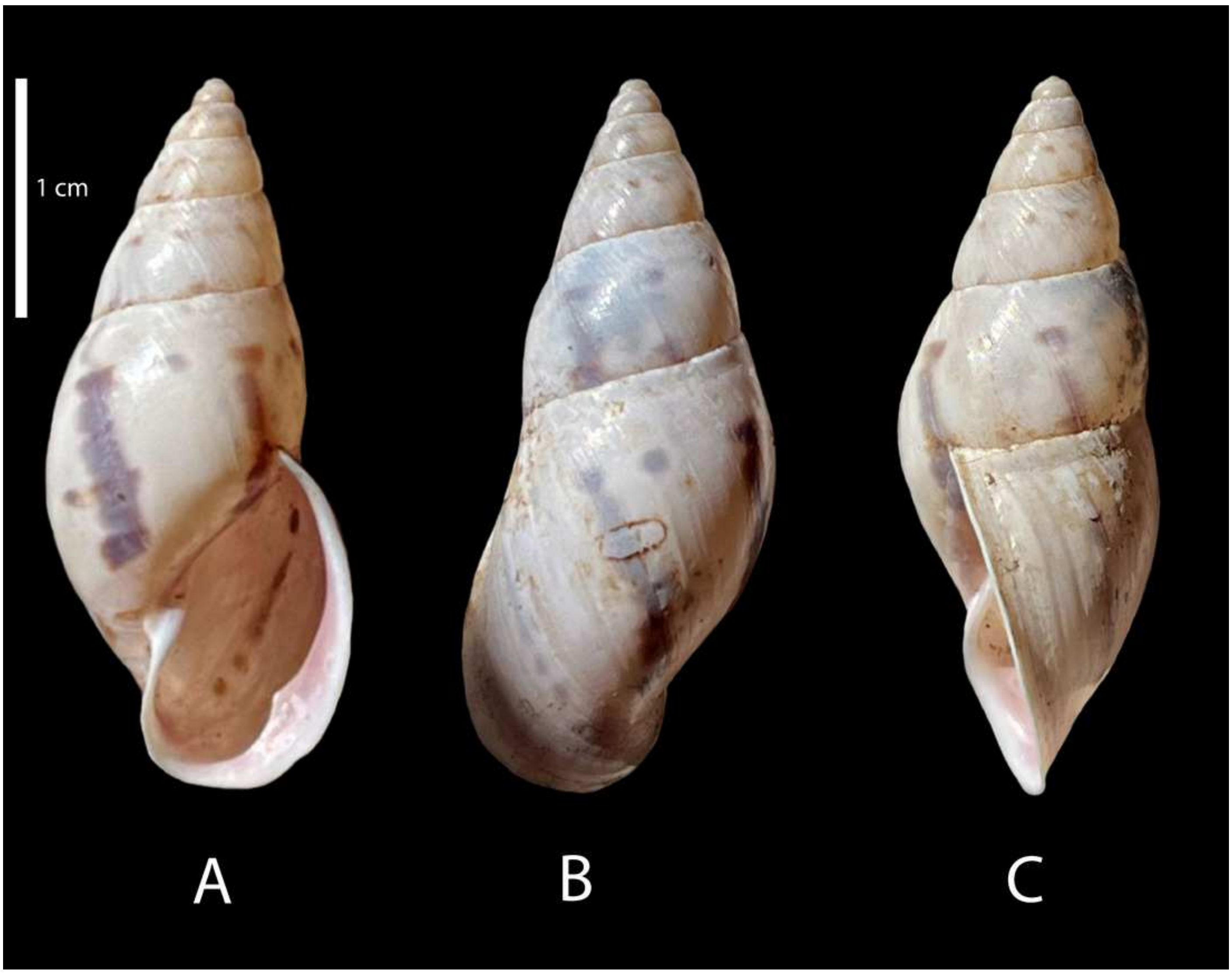

Figure 2

Sccaning electron Microscopy images of the shell, radula, and jaw of *Drymaeus germaini* Ancey, 1892.

material examined: Brasil • 2 shells; Fazenda Macedonia, Ipiaba, Minas Gerais; 27 may 2011; MIPS Macedo & S. D'ávila leg.; F.O. Junqueira col.; CMMPO 11260. **A-C**. Protoconch. **D-F**. jaw. **G-I.** radula.

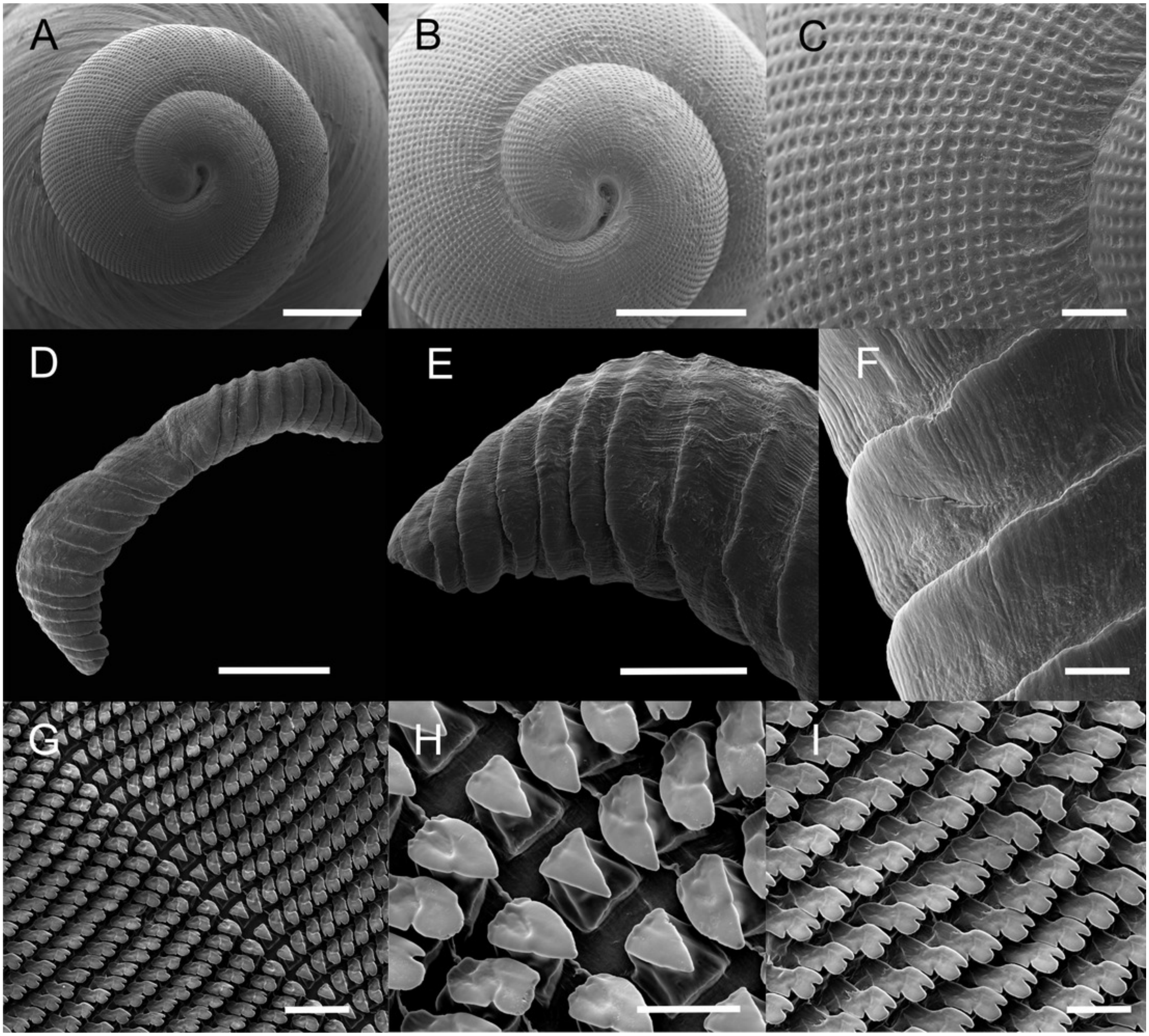
A
B
C
D
E
F
G
H
I

Figure 3

Anatomy of the reproductive system of *Drymaeus germaini* Ancey, 1892.

ag: albumen gland; **atg**: genital atrium; **bcd**: bursa copulatrix duct; **ep**: epiphallus; **fl**: flagellum; **ot**: ovariotestis; **ph**: phallus; **pr**: prostate; **sc**: spermatheca complex; **spo**: spermoviduct; **vd**: vas deferens.

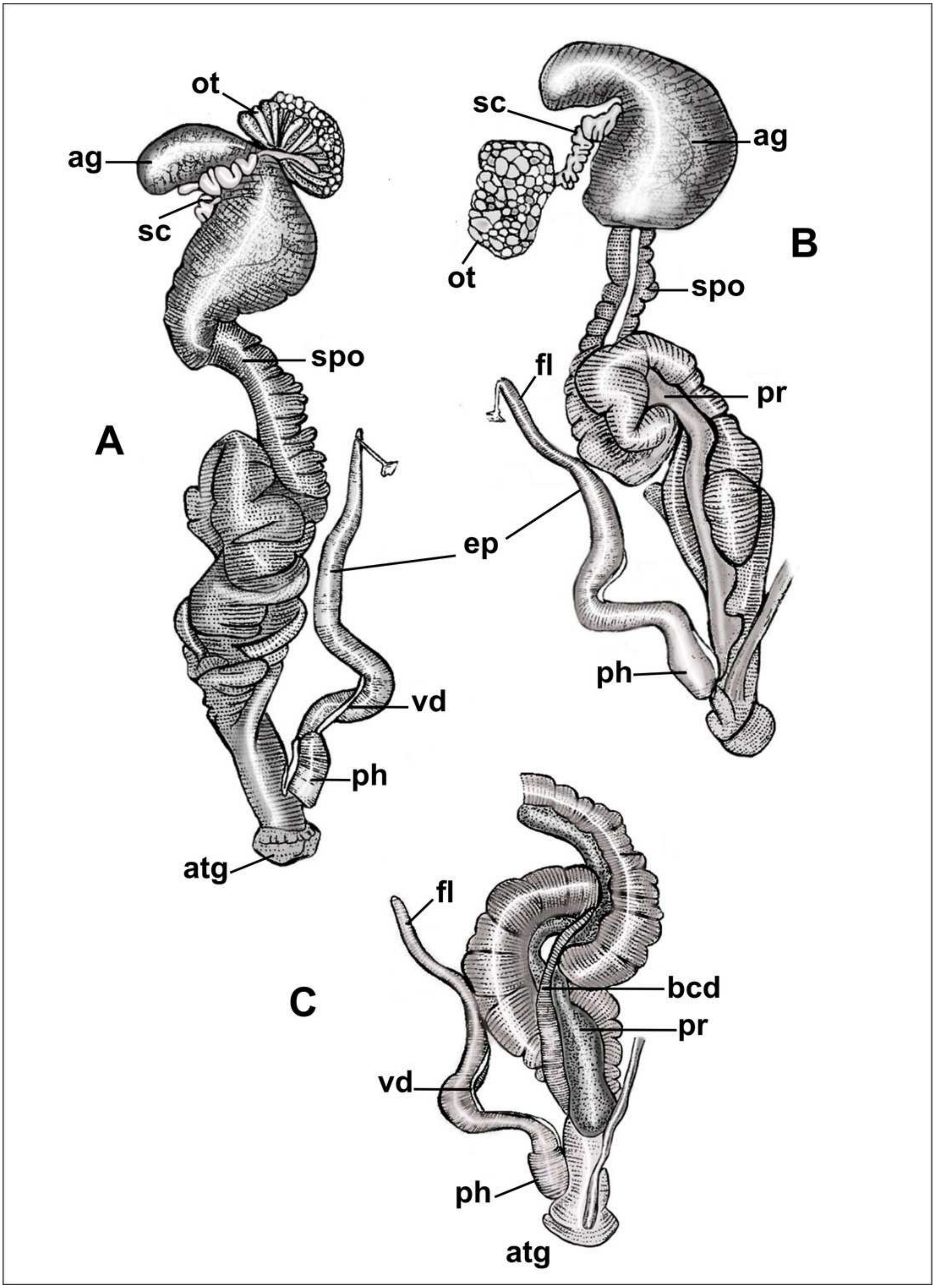
ot
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Figure 4

Occurrence records of *Drymaeus germaini* Ancey, 1892 in the Brazilian biomes.

The data was obtained from malacological collections.

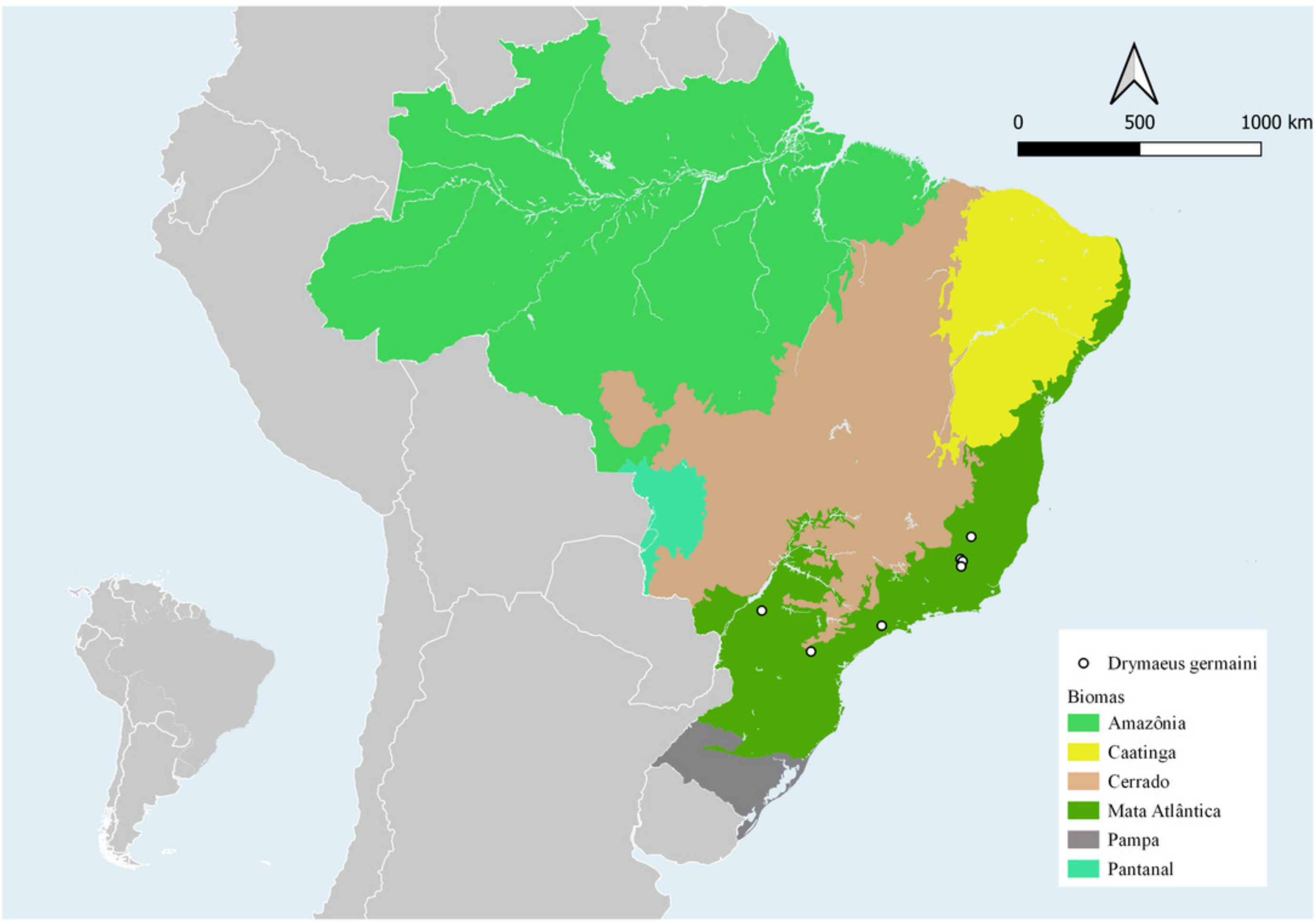

Figure 5

Ecological niche modeling for *Drymaeus germaini* Ancey, 1892, in Brazil.

A. Environmental suitability for *Drymaeus germaini* Ancey, 1892, in Brazil. The ecological niche models were generated by using nine bioclimatic and one topographic variable, at a spatial resolution of 30 arc seconds (~1 km^2), (2012) , with the software package MaxEnt version 3.4.3 and default parameters, including a maximum of 500 iterations with a convergence threshold of 0.00001 and 10,000 randomly chosen background localities. **B**. Contribution of the variables to the model.

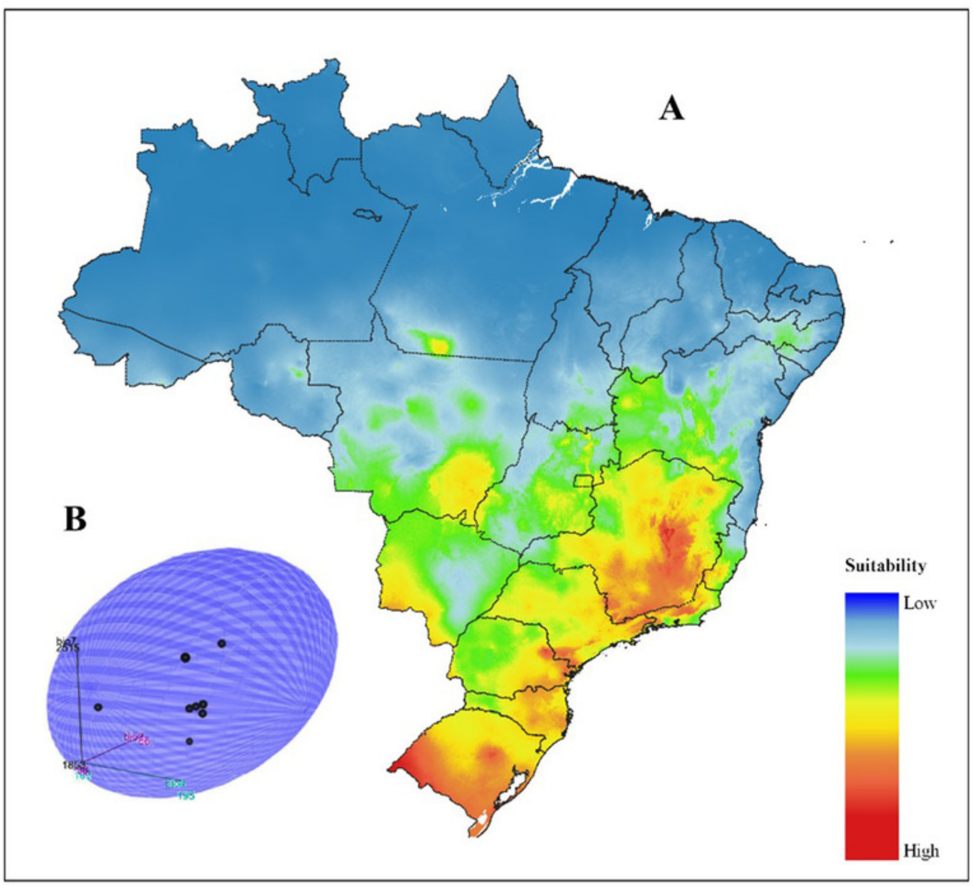

Figure 6

Intraspecific variation in pigmentation pattern of shells of *Drymaeus germaini* Ancey, 1892.

A-**E** penultimate whorl (**PW**) showing only dots (**A**), dots and incomplete stripes (**B** and **C**), dots and stripes (**D**) and dots merged with stripes (**E**). **F**-**I.** Body whorl (**BW**) showing dots and stripes **(F)**, dots and dots merged with stripes **(G),** and dots merged with stripes (**H** and **I**). One specimen may present different combinations of dots, stripes, and dots merged with stripes throughout the shell.