

THE DISCOVERY OF A SINISTRAL OBELISCINAE (EUPULMONATA, SUBULININAE) IN BRAZIL, FOUND IN AMAZON ARCHAEOLOGICAL SHELL MOUNDS OF RONDONIA

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Abstract *Rectobelus levogyrus*, a new species of subulinid, is described found in archaeological surveys in Amazon shell mounds (*sambaquis*) from Costa Marques, Rondônia, Brazil. It is the first sinistral subulinid species recorded in Brazil, and that is its main distinguishing character. A brief taxonomical treatment of the other congener species, *R. rectus* (Baker, 1927) (the type species, from Venezuela) and *R. birabeni* (Hylton Scott, 1946) (from Argentina) is included, with figures, as well as a discussion on the validity of the genus. urn:lsid:zoobank.org:pub:0EC43E61-CFB0-497A-AA26-F94D1A32DAAA.

Key words *Rectobelus levogyrus* n. sp., *Subulinidae*, Amazon Region, zooarchaeology, morphology, shellmounds.

INTRODUCTION

Samples of animal remains collected during archaeological excavations are frequently deposited in Museu de Zoologia-USP (MZSP). They are carefully sent by archaeological teams for analysis, identification and maintenance in the museum collection and studies on these specimens are important for understanding the ancient environment and habitats. The analysis on this archaeo-malacofauna frequently reveals new species, some of them now extinct. A recent example is the strophocheilid *Megalobulimus jaguarunensis* Fontenelle, Cavallari & Simone, 2014, found in Santa Catarina shell-mounds (“*sambaquis*” in Portuguese).

This paper relates to samples collected by the team of archaeologists lead by Eduardo Góes Neves, Museu de Arqueologia e Etnologia – Universidade de São Paulo, in the Monte Castelo Shell Mound, Rondônia, SW Amazon region, about 4,000–4,500 years old. Amongst several shells of land and freshwater snails and mussels, specimens of a small subulinid came to our attention in being sinistral shelled (left-handed), a rarely found in South American subulinids. Analysis revealed a new species of a genus not previously reported in this region. More information on the archaeological site, including associated fauna, can be found in Carvalho *et al.* (2017) and Pugliese Jr. (2018).

The subfamily Subulininae includes 81 genera and about 820 species (Schileyko, 1999), mostly known based on shells. The data available on the internal anatomy of subulinids is restricted to about 31 genera and no more than 33 species (Schileyko, 1999; Medeiros *et al.*, 2013). The last extensive systematic review of this family was performed by Pilsbry (1906), with some modifications by Zilch (1960) and Schileyko (1999) and thus a deeper analysis of the Brazilian subulinids to include anatomical data in the coming years will likely add to the diversity of this group.

The genus *Rectobelus* Baker, 1927 [type species *Obeliscus (Rectobelus) rectus* Baker, 1927, by original designation and monotypy; from Venezuela] is mainly characterised by remarkably large and obtuse apex, a small columellar callus, growth sculpture not so developed, and not so oblique aperture, lacking parietal and palatal teeth (Baker, 1927: 6). The present discovery will shed some light on the genus' validity and stability. In the current taxonomy (e.g., Schileyko, 1999), beyond the type species, the genus also includes *Rectobelus birabeni* (Hylton Scott, 1946). In order to organise the genus' taxonomy, a taxonomical treatment and illustration of these species are also included herein.

MATERIAL AND METHODS

The sample herewith studied was collected from archaeological excavations carried out on Monte

Castelo Shell Mound (Rondônia, Brazil) (more details in Pugliese Jr, 2018). The shells were examined and photographed using stereomicroscopes, with most photos obtained by multifocus software Zeiss Axion Vision. The type specimens of the new species are now deposited in Museu de Zoologia da Universidade de São Paulo (MZSP).

To provide information on the other known species of the genus *Rectobelus* searches were performed at the collections databases of the following institutions or from the data portals of GBIF or 'Global Biodiversity Information Facility', 'InvertEBase' Data Portal, 'SysTax – Zoological Collections' and 'SpeciesLink':

Academy of Natural Sciences of Philadelphia (Pennsylvania, USA; ANSP),
Bailey-Matthews National Shell Museum (Florida, USA),
California Academy of Science (San Francisco, USA),
Carnegie Museum of Natural History (Pennsylvania, USA; CMNH),
Field Museum of Natural History (Chicago, USA, FMNH),
Florida Museum of Natural History (Gainesville, USA),
Illinois Natural History Survey (Champaign, USA),
Löbbecke Museum Dusseldorf (Düsseldorf, Germany),
Museu Nacional do Rio de Janeiro (Brazil),
Muséum National de Histoire Naturelle (Paris, France),
Museum of Comparative Zoology (Cambridge, Massachusetts, USA, MCZ),
Naturalis Center of Biodiversity (Leiden, Netherlands),
Ohio State Museum of Biological Diversity (Columbus, USA),
Royal Belgian Institute of Natural Sciences (Brussels, Belgium),
South African National Biodiversity Institute (Brussels, Belgium),
United States National Museum – Smithsonian Institution (Washington DC, USA),
University of Michigan Museum of Zoology (Ann Arbor, USA),
Zoologische Staatssammlung München – Mollusca (Munich, Germany),
Museo Argentino de Ciencias Naturales (Buenos Aires, Argentina, MAC),

Museo de La Plata (La Plata, Argentina; MLP),
Senckenberg Museum Frankfurt (Germany; SMF),
Museu de Zoologia da Universidade de São Paulo MZSP (Brazil).

SYSTEMATICS

Rectobelus Baker, 1927

Rectobelus rectus (Baker, 1927)

(Fig. 11–13)

Obeliscus (Rectobelus) rectus Baker, 1927: 6 (pl. 23, fig.15).

Rectobelus rectus: Schileyko, 1999: 449 (fig. 643).

Material examined ANSP 140935 – syntype.

Type locality La Fria, Venezuela.

Other localities Species known only from the type locality.

Rectobelus birabeni (Hylton Scott, 1946)

(Fig. 10)

Obeliscus (Rectobelus) birabeni Hylton Scott, 1946: 364 (figs 1–6).

Material examined MLP s/n, Holotype (Fig. 10); ANSP 322187; CM-Mollusks 43122 – paratype; CM-Mollusks 59–1; CM-Mollusks 62–155; FMNH 216299; MACN 26639; MACN36936; MACN 39941; MACN 6593; MCZ 182057 – paratype; SMF171803 – paratype; SMF 220917 – paratype.

Type locality ARGENTINA: Banda de los Perales, Jujuy.

Further occurrences ARGENTINA: Las Capillas, Jujuy.

Rectobelus levogyrus sp. nov.

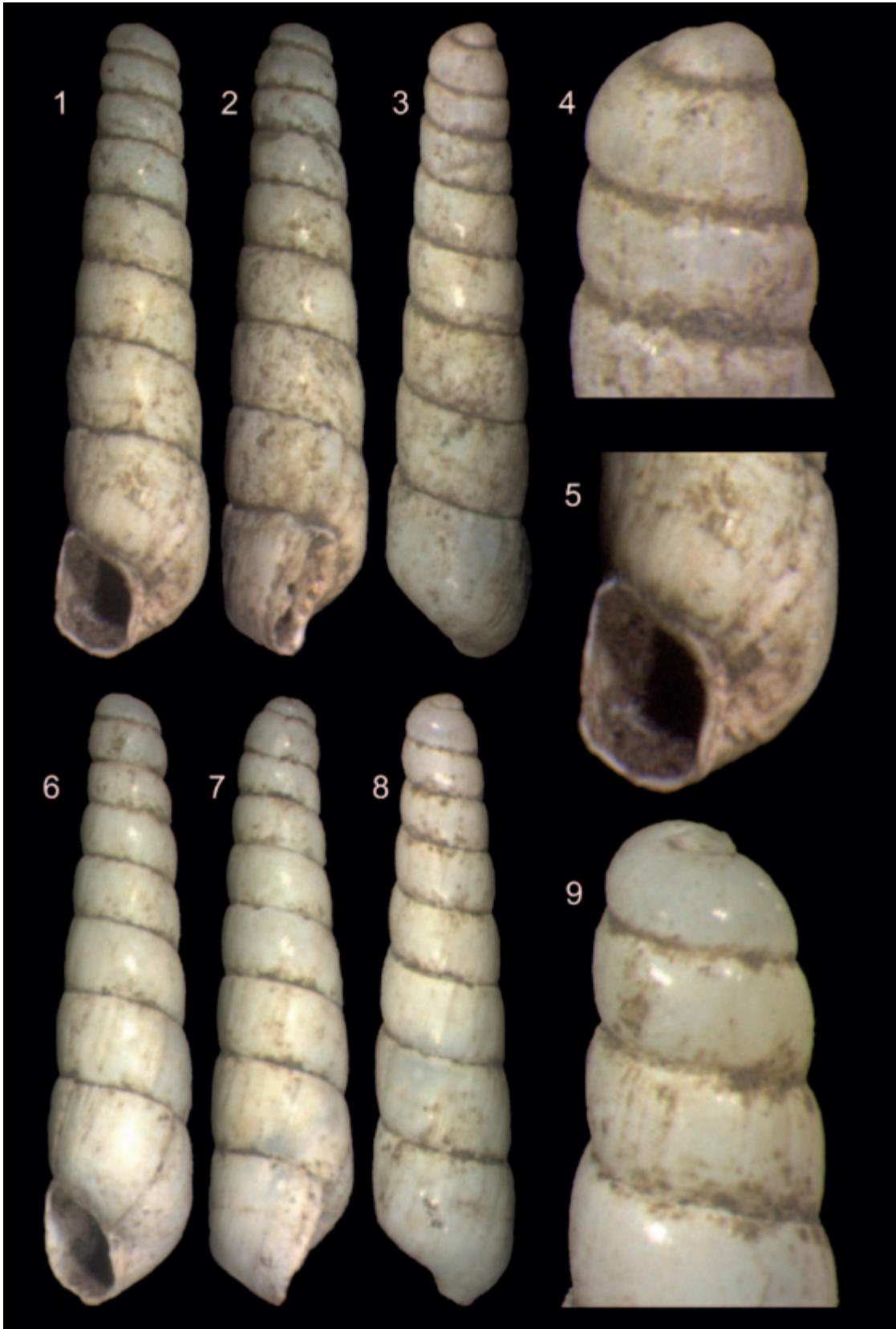
(Figs 1–9, 14)

urn:lsid:zoobank.org:act:6D53DF66-606E-44C4-9417-AD7E45EF1A1E

Holotype MZSP 133359.

Paratypes MZSP 122681, 14 shells, MZSP 122679, 2 shells, from type locality.

Type locality BRAZIL. **Rondônia**; Costa Marquels, Monte Castelo Shell Mound, alluvial floodplain of Guaporé River Basin, 12°33'12.41"S 63°05'45.00"W (Eduardo Neves col.; ii.2014).



Figures 1–9 *Rectobelus levogyrus*, new species, types: 1–5) holotype MZSP 133359 (L 11.0mm): 1) frontal view; 2) left view; 3) dorsal view; 4) detail of apex in profile (base 1.7mm); 5) detail of aperture, frontal view (base 2.6mm); 6–9) paratype MZSP 122681 (L 10.6mm): 6) frontal view; 7) left view; 8) dorsal view; 9) detail of apex in profile (base 1.8mm).



Figures 10–14 *Rectobelus* shells for comparative purposes: 10) *R. birabeni* holotype MLP s/n (L 16mm), frontal view; 11) *R. rectus* paratype ANSP 140935 (L 8.9mm), frontal view (courtesy Malacology Department, ANSP); 12) same, right view; 13) same, dorsal view; 14) *R. levogyrus* holotype, inverted image (L 11.0mm).

Additional material examined ~80 fragments in archaeological collection of Museu de Arqueologia e Etnologia, University of São Paulo.

Diagnosis Sinistral shell. Columella lacking distinct spiral thickening. Small umbilicus.

Description Shell turritiform, solid, opaque; sinistral-coiling, 8–10 whorls, about 12mm long; ~5 times longer than wide. Color uniform whitish-beige. Spire angle ~10°. Protoconch blunt, smooth, of one whorl; transition with teleoconch unclear; occupying ~10% of shell length, ~60% of shell width. Teleoconch with uniform growth along its length; last whorl as widest whorl. Suture shallow, but well-marked. Sculpture lacking, except for well-marked growth lines. Aperture oval, width ~60% of length; occupying ~15% of shell length and ~half of shell width.

Peristome simple, not reflected; outer lip arched, fragile edge; inner lip slightly more concave than outer lip, edge thin; callus lacking, slightly thicker in inferior half, flanking small umbilicus.

Habitat Unknown, found in shell mounds of about 4,500 years of age.

Measurements (respectively length and maximum width in mm) Holotype: 11.0 by 2.6; paratype MZSP 122681: 10.6 by 2.6.

Distribution Only known from the type locality.

Remarks *Rectobelus levogyrus* differs from the Venezuelan type species *R. rectus* (Baker, 1927: pl. 23, fig. 15) (Figs 11–13) in having whorls' profile slightly straighter, a more elongated aperture, in lacking a small tooth in the inferior half

of inner lip, and in lacking a so angulate inner lip in its middle level and absence of small notch in its base (Fig. 11). *Rectobelus levogyrus* differs from the Argentinean species *R. birabeni* (Scott, 1946: pl. 1, fig.1–4) (Fig. 10) by the absence of spiral thickening and the greater number of whorls. Additionally, *R. levogyrus* differs from both species in having a proportional wider protoconch, by a more uniform growth (the spire profile is rather straight), and by its aperture slightly more elongated antero-posteriorly, in an oblique position (Figs 1, 5, 6). The height of each whorl in the spire is also a distinctive feature, as that of *R. levogyrus* is ~30% higher (Figs 1–3, 6–8) than that of the two congeners (Figs 10–11). Numerically, the protoconch of *R. levogyrus* is ~60% of maximum width, while that of *R. pirabeni* is ~45%, and *R. rectus* is ~50%. In absolute measures, the protoconch of *R. levogyrus* has 1.4mm width, that of *R. pirabeni* has 1.7mm, and *R. rectus* has 1.2mm. The last whorl of *R. levogyrus* occupies ~35% of length, that of *R. pirabeni* occupies ~30%, and that of *R. rectus* ~34%. In order to facilitate comparison of species the holotype of *R. levogyrus* is shown inverted in Fig. 14. To demonstrate the differences in size of the three species they are shown at the same scale in Fig. 15.

DISCUSSION

In the present study we adopted the systematic arrangement proposed by Schileyko (1999), which represents the more recent revision of what was at that time the family Subulinidae. The previous comprehensive revision of subulinids was the work by Pilsbry (1906). Pilsbry (1906) did not use the name Subulininae, but Stenogyrinae, also as a subfamily of Achatinidae. Pilsbry (1906) compiled virtually all recognised species and genera incorporated in Stenogyrinae at that time, and proposed a systematic arrangement based on shell characteristics. The formal recognition of Subulinidae as a family occurred in 1955, when the name was included in the official list of families of the International Commission on Zoological Nomenclature (Direction 27, Opinions & Declarations rendered by the ICZN, vol. 10, PT 20, 1955: 484, name number 52). Since then, Subulinidae was widely accepted as a full taxon (Naggs, 1994; Schileyko, 1999, 2011; Lange & Maes, 2001; Tattersfield *et al.*, 2001; Grego *et al.*, 2007; Hayes *et al.*, 2012; Hausdorf *et al.*, 2012;



Figure 15 *Rectobelus* shells for comparative purposes all three species to scale **a** *R. birabeni* holotype, **b** *R. rectus* paratype and **c** *R. levogyrus* holotype. Scale bar = 2mm.

Pickford, 2018; Sang & Nhuong, 2014; Budha *et al.*, 2015; López *et al.*, 2015; Capinera, 2017; Budha *et al.*, 2017; Girod & Balzarini, 2017; Miguel & Jaime, 2018) although has since officially been reduced to a subfamily of Achatinidae (Wade *et al.*, 2006; Bouchet *et al.*, 2017; Fontanilla *et al.*, 2017).

Schileyko (1999) was the first author to systematically collect data on the anatomy of subulinine species, aiming at expanding the diagnoses at both genus and subfamily levels. The author also proposed relocation of the genera among the 6 previously established and 3 new subfamilies, besides the new family Glessulidae.

In respect to the generic attribution, *Rectobelus* and other subgenera of *Obeliscus sensu* Pilsbry, 1906, i.e., *Protobeliscus*, *Stenogyra*, *Pseudobalea* and *Lyobasis*, were recharacterised and raised to the genus level by Schileyko (1999). *Rectobelus* was originally described as a subgenus of *Obeliscus* Beck, 1837 probably because it presents similarities with some of the characteristics described for that genus, i.e. shell imperforate or nearly so, whorls 9 to 18, embryonic whorls smooth and globose, the summit obtuse, aperture ovate, the outer lip and columella simple (Pilsbry, 1906). However, *Obeliscus* species are characteristically much larger and have typically deeper shell sutures than *Rectobelus* (Baker, 1927; Hylton Scott, 1946).

Rectobelus, *Obeliscus* and other 17 genera were incorporated into the subfamily Obeliscinae Thiele, 1931 by Schileyko (1999), mainly on the basis of shell traits, i.e., shell turreted to subfusiform, not decollate, dextral, last whorl lacking internal sculpture, columella simple. Obeliscinae *sensu* Schileyko (1999) includes 7 of the 12 taxa considered by Pilsbry (1906) as closely related, and grouped them in the so-called "Phyllum" *Obeliscus*, i.e., *Neobeliscus*, *Obeliscus*, *Rhodea*, *Synapterpes*, *Chryserpes*, *Zoniferella*, and *Stenogyra*.

Anatomically, Obeliscinae was not fully characterised, but there is available data on the soft parts of *Neobeliscus calcareus* (Pilsbry, 1906; Schileyko, 1999), *Stenogyra terebraster* (Lamarck, 1822) (Schileyko, 1999), *Rectobelus birabeni* Hylton Scott, 1946 (in original description), and *Obeliscus agassizi* Pilsbry, 1906 (D'ávila *et al.*, 2019). These species show affinities related to the anatomy of the reproductive system, which may corroborate their placement in a same subfamily (D'ávila *et al.*, 2019).

Herein we consider *Rectobelus* as a genus of Obeliscinae (*sensu* Schileyko, 1999), instead of a synonym of *Ischnocion* Pilsbry, 1906 (*sensu* Hausdorf *et al.*, 2012), based on more consistent diagnosis by Schileyko (1999), who also dealt with the definition and affinities between these taxa. In addition, contrarily to the view of Hausdorf *et al.* (2012), *Rectobelus* and *Ischnocion* present significant differences in the shell morphology well explored by Schileyko (1999), and might not be synonymised. Thus, considering the diagnosis proposed by Schileyko (1999), *Rectobelus* and *Ischnocion* share some characters, i.e., shell dimension, apex widely rounded, embryonic

whorls smooth, aperture ovate with simple margins, and umbilicus absent. However, with the exception of shell dimension, these traits are also shared between *Rectobelus* and other subulinine taxa, such as *Obeliscus* for example. Moreover, *Rectobelus* and *Ischnocion* show important differences related to the columella and the internal sculpture of the last whorl, i.e., in *Rectobelus* the last whorl is lacking internal sculpture and the columella is subtruncate, while *Ischnocion* exhibits an internal sculpture of the last whorl, the columella is concave, notched by a large lamella, and palatal wall with lamellar folds. These are major differences, and have justified the placement of these genera into distinct taxa within Subulininae, i.e., Obeliscinae and Coleaxinae (*sensu* Schileyko, 1999). The two genera can be further differentiated by shell profile, as *Rectobelus* has flattened whorls, while *Ischnocion* presents convex whorls.

Internal sculpture in the last whorl appears in few subulinine species and genera, which were placed into the subfamily Coleaxinae Pilsbry, 1906, which also includes the genus *Ischnocion* (Schileyko, 1999). Internal sculpture seems to be consistent in all coleaxine genera, even when lamellae and folds are not visible in the aperture of the adult shell, as shown in the illustrations of the interior of the last whorls of coleaxine shells, provided by Schileyko (1999). This feature is absent in the species of all other subfamilies, i.e., Opeatinae Thiele, 1931; Obeliscinae Thiele, 1931; Subulininae Fisher and Crosse, 1877; Petriolinae Schileyko, 1999; Rishetiinae Schileyko, 1999; Tristaniinae Schileyko, 1999; Rumininae Wenz, 1923 and Perrieriinae Schileyko, 1999. All these taxa possibly can be changed to tribe rank, if previous Subulinidae is actually within Achatinidae.

The original diagnosis of *Ischnocion* proposed by Pilsbry (1906) was based on the sole species known at that time: *Ischnocion triptyx* (Pilsbry, 1908). This species presents a shell with very marked internal ornamentation in the last whorl, aperture with strong parietal and columellar lamellae and a palatal fold, and it was considered by Pilsbry (1906) as "remarkable" and "quite unlike any described form". This statement can show some significance of the internal and apertural ornamentation in subulinine taxonomy.

Both diagnoses provided by Pilsbry (1906) and Schileyko (1999) for the genus *Ischnocion* were fully based on *I. triptyx*. More recently, new

species of *Ischnocion* were described (Hausdorf *et al.*, 2012). Those species present less marked apertural ornamentation, compared to the type species, and the presence of lamellae and parietal folds may be visible only in juvenile stages. This fact, along with the opinion that other subulinine taxa without marked internal and apertural ornamentation, i.e., *Rectobelus* and *Microbeliscus*, should be integrated to the genus *Ischnocion*, lead Hausdorf *et al.* (2012) to amend the diagnosis of this genus, attenuating the weight of the apertural ornamentation, as follows: “usually a columellar lamella or a weak spiral thickening on the not truncated columella and a parietal lamella and/or palatal folds at least in some growth stages”.

The proposal of Hausdorf *et al.* (2012) of integrating *Rectobelus* into the genus *Ischnocion* was based on similarities between these two taxa, which can be superficial, as the presence of small subcylindrical shells. The various differences between *Rectobelus* and *Ischnocion* highlighted by Schileyko (1999), related to internal and apertural ornamentation, were considered of minor importance, arguing that parietal and palatal lamellae may be present in some growth stages, and absent in others. Hausdorf *et al.* (2012) based this argument on their own observations of the new species *Ischnocion conica* Hausdorf *et al.*, 2012, and the observation by Hylton Scott (1946), who found a palatal fold in juvenile specimens of *Rectobelus birabeni*.

Shifts in apertural characteristics during shell development are not uncommon in obeliscini taxa. As an example, *Protobeliscus cuneus* (Pfeiffer, 1852) and *Stenogyra terebraster* (Lamarck, 1822) present a truncate columella when young (Pilsbry, 1906), and juvenile *Rhodea californica* (Pfeiffer, 1846) presents a simple aperture, contrasting to the aperture of adult shells, which presents a strong columellar fold. Thus, in our opinion, the integration of *Rectobelus* taxa into the genus *Ischnocion* as proposed by Hausdorf *et al.* (2012) is unjustified, and both genera must be kept separate.

In the present study, we also included sinistrality as a component of the differential diagnosis proposed for the new species *R. levogyrus*, in relation to its two congeners. In order to provide a general view on the significance of sinistrality for the taxonomy of subulinids, we analysed the two revision works available for this group, specifically, the monographs of Pilsbry (1906)

and Schileyko (1999). Contrarily to the general perception that dimorphism in coiling direction is a common trait among eupulmonate snails, some studies have shown that, in reality, very few species are chirally dimorphic (Schilthuizen *et al.*, 2007; Gittenberger *et al.*, 2012; Schilthuizen *et al.*, 2012). The majority of snail species are monomorphic in respect to chirality, mostly dextral, and the stabilisation of this monomorphism occurs via selection against the chiral minority, resulting from sexual asymmetry (Asami *et al.*, 1998). These studies have also showed that the emergence of taxa with the opposite chiral phenotype may be the result of left-right reversal of asymmetry during speciation process (Asami *et al.*, 2008; Gittenberger *et al.*, 2012; Barna Páll-Gergely *et al.*, 2018, Simone, 2018). In some cases, enantiomorphs have been proven to be insipient species that have recently diverged in allopatry (Barna Páll-Gergely *et al.*, 2018). This can be the case of *R. levogyrus*, as all specimens are left-coiling, including many (~80) fragmented specimens not included in the type series.

Pilsbry (1906) systematically revised the presence of variations in shell traits between the so-called “varieties”, “forms” and “subspecies” of several subulinine species. The main features pointed out by the author when describing these intraspecific variations were the proportion of shell diameter to length, aperture dimension, shell size, number of whorls, flatness of the whorls, shell solidity and texture. Among these variations, the proportion of diameter to length is the trait most frequently mentioned by Pilsbry (1906), with slender and stouter forms usually occurring together.

Chirality was mentioned by Pilsbry (1906) as a source of variation only for *Perrieria canefriana* Sykes, 1904; *Rhodea aequatoria* Da Costa, 1899, whose descriptions were based on two syntypes, one sinistral and other dextral; and *Baculum orthoceras* (Godwin-Austen, 1875), with a single young sinistral specimen from a distinct locality. Despite being considered “dextral or sinistral” by Pilsbry (1906), these species might not be truly dimorphic for coiling direction. In a recent revision of the genus *Rhodea* Grego *et al.* (2007) stated that the two syntypes after which *R. aequatoria* was described, might not be conspecific. The authors argued that the sinistral specimen has a less conspicuous keel on the last three whorls and a finely striated surface, and it could be a

different species. Also, the fact that the sinistral specimen of *B. orthoceras* came from a distinct locality brings some doubt about the presence of chiral dimorphism in this species, in view of the possibility of allopatric speciation of enantiomorphs (Gittenberger *et al.*, 2012; Páll-Gergely *et al.*, 2018).

For other sinistral taxa mentioned by Pilsbry (1906), dextral forms were never reported. This is the case for *Euonyma laeocochlis* (Melvill & Ponsonby, 1896); *Tristania tristensis* (Gray, 1825); *Tristania ventricosa* (Gray, 1825); *Rhodea wallisiana* Dohrn, 1875; *Pseudobalea dominicensis* (Pfeiffer, 1851); *Pseudobalea latus* (Gundlach in Pilsbry, 1906) (genus *Pseudobalea*, *sensu* Schileyko, 1999); *Ochroderma pittieri* (Martens, 1898), and *Cryptelasmus canteroiana* (Gundlach in Pfeiffer, 1857).

From the 77 subulinine genera recognised by Schileyko (1999), sinistrality was included in the diagnoses of seven: *Pseudobalea* Shuttleworth, 1854; *Cryptelasmus* Pilsbry, 1906; *Rhodea* H. & A. Adams, 1855; *Ochroderma* Pilsbry, 1906; *Euonyma* Melvill & Ponsonby, 1896; *Orehomorus* Pilsbry, 1919; and *Tristania* Boettger, 1878. Among these genera, *Pseudobalea*; *Cryptelasmus* and *Tristania* include only sinistral species. Pilsbry (1906) included sinistrality as a character in the diagnosis of the genera *Tristania*, *Rhodea*, *Cryptelasmus*, and *Pseudobalea*. The author also considered chirality in differential diagnoses, when comparing species closely related as, for example, *Ochroderma martensi* and *O. pittieri*.

The analysis of the compiling monographs of Pilsbry (1906) and Schileyko (1999), along with further works on sinistral taxa (Grego *et al.*, 2007), showed that the presence of enantiomorphs is not a common feature among subulinines. It has also been shown that subulinines are predominantly directionally asymmetric, with the vast majority of the species consisting either of dextral or of sinistral individuals. These facts suggest that the reversal of chirality, linked to speciation process is a more likely explanation for sinistrality observed in subulinid species than chiral polymorphism. This also corroborates the taxonomic significance attributed by previous authors, as well as in the present study, to sinistrality, with the inclusion of this trait in the diagnoses of subfamilies, genera and subgenera, as well as in species differential diagnoses (Pilsbry, 1906; Schileyko, 1999; Grego *et al.*, 2007).

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