Rediscovery of *Obeliscus agassizi* Pilsbry, 1906 (Gastropoda, Subulinidae, Obeliscinae), annotated checklist of species of *Obeliscus* Beck, 1837 and first description of the anatomy for the genus

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ABSTRACT

*Obeliscus agassizi* Pilsbry, 1906 was described from specimens collected in Brazil, by J. G. Anthony, during the Agassiz expedition, in 1865. The type locality of the species was given simply as Brazil, without further information. More than a century after its description, this species was rediscovered during an expedition to the Biological Reserve of Pedra Talhada, Alagoas/Pernambuco states, Brazil. In the present study we provide detailed description of the anatomy of the soft parts of *O. agassizi* specimens, collected during this expedition, besides more precise data concerning the species occurrence. This work presents the first anatomical description for the genus. An annotated checklist of *Obeliscus* Beck, 1837 species is also provided. The species of *Obeliscus* have been traditionally distinguished by shell characteristics, mainly the general shell shape, number of whorls proportionally to the shell size, shell ornamentation, the shape of the protoconch and aperture size and shape. The distinction between
species is often subtle. Considering that shell traits may be not sufficient as single taxonomic characters, other evidence for species boundaries, especially anatomical characters, is needed. Presently, it is not possible to discuss the taxonomic meaning of the set of anatomical characters described for O. agassizi, at the intra-genus level, as there is no information on the anatomy of the soft parts of other species of Obeliscus. The comparative analysis of the genital system of O. agassizi, Neobeliscus calcareaus (Born, 1780), Stenogyna terebrestrat (Lamarck, 1822) and Rectobelus birabeni (Hyloin-Scott, 1946) pointed out anatomical characters with potential diagnostic significance for the genus Obeliscus. However, the establishment of a definitive differential diagnosis for this genus, based in both conchological and anatomical traits, depends on the analysis of a greater number of species of Obeliscus, as well as species of other genera of Obeliscinace Thiele, 1931.

INTRODUCTION

Subulinidae Fischer & Crosse, 1877 is a near pan-tropical family of land snails, including nine subfamilies, 81 genera and about 820 species (Pilsbry 1906; Schileyko 1999). The systematics of this family has been entirely based on shell characteristics and the attempts to add new data about this family have been very scarce throughout the last century. Hence, Subulinidae figures as a neglected group of land snails, contrasting with its diversity.

Species delimitation based only on shell characters has been proved to be inadequate for several families of pulmonate snails, e.g. Lymnaeidae Rafinesque, 1815 (Penninger et al. 2006), Bradybaenidae Pilsbry, 1934 (Chiba & Davison 2008), Helicidae Rafinesque 1815 (Eleyalde et al. 2008), Hygromiidae Tryon, 1866 (Depraz et al. 2009), Camaenidae Pilsbry, 1895 (Köhler & Burghardt 2015), Enidae Pilsbry, 1895 (Modica et al. 2016), and Pyramidulidae Kennard & Woodward, 1914 (Razkin et al. 2017); since it leads to some taxonomic issues as the difficult detection of cryptic species or, on the other hand, the overestimation of species diversity. This observation pinpoints the need of revisiting the anatomy of soft parts, which has been often associated to molecular data, for a more precise delimitation of the species.

Considering the lack of other criteria of discrimination besides the shell (available data on the internal anatomy of Subulinidae concern 30 genera and no more than 32 species [Schileyko 1999; Medeiros et al. 2013]), and taking into account that no full systematic revision of the family has been provided during more than a century, the description of the anatomy of the soft parts as well as the characterization of life history traits of subulinid species is a necessary challenge.

Without these two sources of information, studies on ecology, evolution, phylogeny and conservation of subulinid species will remain in a state of impediment.

Obeliscinace Thiele, 1931 comprises 12 American, one Asian and three Pacific genera (Schileyko 1999). Among the 12 American genera, five were recorded in Brazil, including at least 13 endemic species (Pilsbry 1906; Simone 2006). Only Neobeliscus calcareaus (Born, 1780) (Pilsbry 1899, 1906), Stenogyna terebrestrat (Lamarck, 1822) (Schileyko 1999) and Rectobelus birabeni (Hyloin-Scott, 1946) were characterized from an anatomical perspective. So far, all other species included in this subfamily are known only from their shells. More than a century ago, Pilsbry (1906) stated that besides the information on the anatomy of N. calcareaus given by him, nothing was known of the soft parts of the other genera.
The more recent revision of the family Subulinidae was performed by Schileyko (1999), who has provided new information on the anatomy of the soft parts for several genera. Schileyko (1999) illustrated the anatomy of the genital system of S. terebraster (new data) and of N. calcareus after Pilsbry (1906). However, the author did not describe the anatomy of the other genera, including Obeliscus Beck, 1837, the type genus. Schileyko (1999) argued that the characters previously used to define Obeliscinae are not sufficient, proposing the maintenance of this subfamily until information on the anatomy of the soft parts of their representatives is available.

The genus Obeliscus Beck, 1837 includes about 16 species, distributed throughout Tropical South America and Greater Antilles. So far, none of these species was anatomically characterized. The diagnosis of the genus reviewed by Pilsbry (1906) includes only shell characteristics and some fragmentary information on the radula of O. obeliscus, taken from the remains washed from a dry shell. After the work of Pilsbry (1906), other additional five species of Obeliscus were described based on shells only (Vanatta 1918; Pilsbry 1944; Simone & Salvador 2016; Thach 2017).

Obeliscus agassizi Pilsbry, 1906 was described from specimens collected in Brazil by J. G. Anthony, during the Agassiz expedition. The type locality of the species was given simply as Brazil, without further information. More than a century after its description, this species was rediscovered by Maestri et al. (2015) during an expedition to the Biological Reserve of Pedra Talhada, Alagoas/Pernambuco states, Brazil. In the present study we provided detailed description of the anatomy of O. agassizi, based on specimens collected during that expedition. An annotated checklist of Obeliscus species is also provided.

MATERIALS AND METHODS

The material consists of four specimens of Obeliscus agassizi, preserved in ethanol 70% (MZSP 133507; MZSP 133635), and deposited in the malacological collection of the Museu de Zoologia da Universidade de São Paulo (MZSP). All specimens were collected in the Pedra Talhada Biological Reserve, located in the municipalities of Quebrangulo in the state of Alagoas and of Lagoa do Ouro in the state of Pernambuco. Pedra Talhada is a federally administered biological reserve in North East Brazil, which contains a representative sample of the remaining Atlantic Rainforest ecosystem in the Serras of Guarábas, Pedra Talhada and Serra do Cavaleiro.

The snails were dissected immerse in ethanol and drawn under an Olympus stereo microscope, model SZX7As, equipped with camera lucida. Details of the shell were acquired through table top scanning electron microscope EDS. Shell specimens were analyzed without any preparation.

Identification was conducted based on the species original description provided by Pilsbry (1906) as well as on the revision of the family Subulinidae provided by Schileyko (1999), images of the shells of type specimens available in the online collection database of the ANSP, and the catalogue by Simone (2006).

The terminology employed to designate the structures of the reproductive system is mostly in accordance to recent papers (Gómez 2001; Bojat et al. 2001; Koene & Schulenburg 2005; Beese et al. 2006; Garefalaki et al. 2010; Simone 2011; Schmera et al. 2016).

To provide an annotated checklist of the species of the genus Obeliscus an intensive research was performed using both the literature and collections databases of the Academy of Natural Sciences of Philadelphia, Bailey-Matthews National Shell Museum, California Academy of Science, Carnegie Museum of Natural History, Field Museum of Natural History, Florida Museum of Natural History, Illinois Natural History Survey, Löbbecke Museum Düsseldorf, Museu Nacional do Rio de Janeiro, Muséum national de Histoire naturelle, Museum of Comparative Zoology, Naturalis Center of Biodiversity, Ohio State Museum of Biological Diversity, Royal Belgian Institute of Natural Sciences, South African National Biodiversity Institute, United States National Museum – Smithsonian Institution, University of Michigan Museum of Zoology and Zoologische Staatssammlung München – Mollusca, and MZSP. The data were obtained from the Institutions websites or from data portals as Global Biodiversity Information Facility, Invertebase Data Portal, Sys Tax – Zoological Collections and SpeciesLink (Pimenta 2017; Grant & Jones 2017; Academy of Natural Sciences 2018; Morris 2018; Orrell & Hollowell 2018; Paulay & Brown 2018; Royal Belgian Institute of Natural Sciences 2017; Systax 2018). The search in these online databases allowed us to update the geographical distribution of some species. All museum depositit numbers were provided in the checklist, including information on type specimens. Museum deposit numbers were also referenced in the topic “other localities” when occurrence data were obtained from the databases consulted online. We also provided the website links for the species original descriptions, illustrations, museum deposits and bibliographic references cited in the checklist.

All the species are listed according to their current taxonomic status. The citations of the specimens from the collections databases are in accordance with the format proposed by Chester et al. (2019). Some information were sometimes not available in the databases, such as the number or the kind of available specimens (dry shell or ethanol preserved shell and soft parts).

ABBREVIATIONS

In figures

| Abbreviation | Description |
|--------------|-------------|
| ac           | albumen chamber; |
| ag           | albumen gland; |
| al           | allospermoduct; |
| at           | autospermoduct; |
| au           | auricle; |
| bc           | bursa copulatrix; |
| cm           | columellar muscle; |
| cv           | pulmonary vein; |
| da           | anterior lobe of digestive gland; |
| dg           | posterior lobe of digestive gland; |
| di           | diaphragm; |
| es           | esophagus; |
| ey           | eye; |
Morphological description

Shell (Fig. 1A-H)

Shell turritiform-conic, minutely perforate, not decollated, dextral, tapering; periostracum thin, yellowish, opaque in fully developed individuals, glossy in young individuals. Columella nearly straight, slightly concave (Fig. 1C). Embryonic whorls smooth, shining (Fig. 1A). Protoconch with c. 3 whorls. Boundary between protoconch and teleoconch well defined. Last whorls plicate below suture, nearly smooth elsewhere (Fig. 1B). Spire of c. 12 whorls, convex, very regularly increasing (Fig. 2A). Sutures well marked, a little inclined (Fig. 1B, E). Teleoconch of c. 10 whorls, smooth, except for growth lines (Fig. 2D). Aperture somewhat oblique, ovate (Fig. 1C); inner lip simple, outer lip thin.

Head-foot (Figs 1D-F; 2B, C)

Head protruded. Head-foot almost transparent in living animals, color pale cream, with fine tessellation (Figs 1D-F, 2B). Foot broad, sole oval, edges rounded in fixed animals. Genital opening visible as a rounded area, without tessellation in fixed animals, and as a small fissure near head in living animals (Fig. 2B).

Mantle organs (Fig. 2C)

Mantle edge simple, thick. Rectum narrow, walls thick, running along right edge of pulmonary cavity. Ureter running parallel to rectum, both structures covered by fine membrane. Pulmonary cavity very long and narrow, occupying the two last whorls. Kidney and pericardium restricted to middle and left sides, occupying c. ½ of pallial roof. Pulmonary vein running along entire pallial cavity, oblique in anterior ¼, running along left edge in remaining regions.

Circulatory and excretory systems (Fig. 2C)

Pericardium located at columellar margin of posterior end of pallial cavity, c. ⅓ of the kidney length. Auricle small, triangular, located in middle length of kidney left margin. Ventricle near same size of auricle. Kidney occupying c. ⅔ of pulmonary cavity length, located along middle and left regions of transition pallial cavity and visceral mass. Kidney rather bilobed, with smaller lobe just anterior to auricle. Pulmonary vein running along columellar margin of pallial cavity, straight in posterior ⅔ portion of the mantle, curved in anterior ¼ portion, converging to pneumostome region along with renal tube and rectum.

Visceral mass (Figs 2C, E)

Digestive gland brownish, located along inferior region of seventh visceral whorl, covering part of stomach at sixth whorl and filling entire visceral whorls posterior to stomach, including nepionic whorls (Fig. 2E). Rectum visible at eighth visceral whorl.

Genital system (Figs 3A-F)

Gonad located at the sixth visceral whorl, covered by the digestive gland (Fig. 3E; go). Albumen gland elongated, sheltering spermoduct under its columellar face. Carrefour lying at tran-
Rediscovery of Obeliscus agassizi

Fig. 1. — Obeliscus agassizi Pilsbry, 1906 shell and living specimen: A, SEM of apex in profile; B, same, middle region of teleoconch; C, same, last whorl, frontal view, asterisk showing epiphragm; D-F, living crawling specimen, shell length c. 6 mm; G, detail of suture of protoconch, SEM; H, detail of epiphragm insertion on body whorl. Scale bars: A–C, 1 mm; G, 0.15 mm; H, 0.1 mm.
Fig. 2. — Obeliscus agassizi Pilsbry, 1906 anatomical drawings: A, outline of adult shell, part of read-foot also shown; B, soft parts last whorls, specimen just extracted from shell; C, whole specimen view, pallial cavity extracted and extended to right; D, detail of shell first whorls showing delicate sculpture; E, detail of visceral mass. Abbreviations: see Material and methods. Scale bars: 2 mm.
FIG. 3. — Obeliscus agassizi Pilsbry, 1906 anatomical drawings: A, outline of adult shell, part of read-foot also shown; B, soft parts last whorls, specimen just extracted from shell; C, whole specimen view, pallial cavity extracted and extended to right; D, detail of shell first whorls showing delicate sculpture; E, detail of visceral mass. Abbreviations: see Material and methods. Scale bars: 2 mm.
sition between spermoviduct and albumen gland (Fig. 3B). Seminal receptacle as spermovioduct, lying at superior half of albumen gland (Fig. 3B: sr). Spermovioduct long, occupying first three shell whorls, running along columellar muscle (Fig. 3A, E). Autospermoduct situated at columellar face of spermovioduct (Fig. 3A: at). Allospermoduct situated at the opposite face, visible as a separated duct until reach the free-oviduct (Fig. 3A, E: al). Prostate with well defined acini, occupying columellar surface of spermovioduct (Fig. 3A, E: pt). Bursa copulatrix about as wide as its duct (Fig. 3E: bc), lying in transition between spermovioduct and free oviduct; length c. ½ of that of spermovioduct. Free oviduct c. ½ length of bursa copulatrix duct. Vagina c. ½ free oviduct length. Atrial retractor muscle well developed. Vas deferens with greater diameter at level of free oviduct, adhered to free oviduct wall at its more convoluted and thicker portion through fine muscle bundles. Vas deferens meeting gland with unidentified function after leaving prostate, running along entire free oviduct; vas deferens convoluted in median portion of free oviduct, showing greater diameter until basis of free oviduct, joining to penis. Penis long, club-shaped (Fig. 3D: pm) originated in diaphragm region close to right ommatophore and under esophagus. Penial retractor muscle (Fig. 3D: pm) originated in diaphragm region close to columellar muscle, inserted terminally in the epiphallus.

**ANNOTATED CHECKLIST OF SPECIES OF *OBELISCUS* BECK, 1837**

**Family SUBULINIDAE** Fischer & Crosse, 1877
Subfamily OBELISCINAE Thiele, 1931
Genus *Obeliscus* Beck, 1837

**Obeliscus abbotti** Vanatta, 1918

*Obeliscus abbotti* Vanatta, 1918: 238, fig. 3.

**Museum deposits.** — **Lectotype.** Haiti • 1 shell; near The Generals Cave, 1 mile west of Jeremie; 1918; Abbott W. L. leg.; ANSP 118244. Puerto Rico • 2 shells; USNM 252558.

**Type locality.** — Haiti: General’s Cave, west of Jeremie. Found in debris.

**Other localities.** — Puerto Rico.

**Illustration.** — Vanatta (1918: fig. 3).

**References.** — The only bibliographic reference is the original description of the species.

**Obeliscus agassizi** Pilsbry, 1906

*Obeliscus agassizi* Pilsbry, 1906: 249, pl. 36, fig. 76. — Clench & Turner 1962: 7. — Salgado & Coelho 2003: 155. — Simone 2006: 187, fig. 686.

**Museum deposits.** — **Lectotype.** Brazil • 1 shell; Anthony J. G. leg.; Agassiz expedition; ANSP 59334.

**Obeliscus boitata** Simone & Salvador, 2016

*Obeliscus boitata* Simone & Salvador, 2016: 25, 29 (figs 77-79).

**Museum deposits.** — **Holotype.** Brazil • 1; Minas Gerais, Nanuque, 17°51’S, 40°23’W; 120 m a.s.l.; very close to the borders with the states of Bahia and Espirito Santo, very small fragment of Atlantic Forest; MZSP 106169.

**Paralectotypes.** Brazil • 4 shells; Anthony J. G. leg.; Agassiz expedition; ANSP 465075. Peru • 4 shells; Chosica, North side of valley; Dept. Lima; X.1964; Hocking P. leg.; FMNH 140941.

**Type locality.** — Brazil (collected by J. G. Anthony, during the Agassiz exped.), no specific locality.

**Other localities.** — Brazil: Alagoas and Pernambuco states, Biological Reserve of Pedra Talhada (present study). Peru: Chosica, N side of valley, Dept Lima.

**Illustration.** — Pilsbry (1906: pl. 36; fig. 76)

**References.** — Clench & Turner (1962): Salgado & Coelho (2003); Simone & Salvador (2016).

**Obeliscus bacterionides** (d’Orbigny, 1835)

*Helix bacterionides* Orbigny, 1835: 9.

*Balimus bacterionides* — Pfeiffer 1852: 117, pl. 35, figs 15, 16.

**Obeliscus bacterionides** — Pilsbry 1906: 250, pl. 36, figs 71, 72.

**Museum deposits.** — **Syntypes.** Bolivia • 6 shells; Rio Grande; collection d’Orbigny 1818-1838; MNHN-IM-2000-28012 • 2 shells; USNM 117487 • Beni Dept., Cercado Province, 6 km South Trini- dad; 28.XII.1982; Thompson F. leg.; FLMNH 040622 • same data as for preceding; FLMNH 040623 • Santa Cruz Dept., Chiquitos Province, 20 km ENE of Santiago de los Chiquitos; 30.XI.1982; Thompson F. leg.; FLMNH 210580.

**Type locality.** — Bolivia: Rio Grande.

**Other localities.** — Bolivia: no specific locality (Pfeiffer, 1852); Beni Department, Cercado Province, 6 km South Trinidad (FLMNH 040622; 040623); Santa Cruz, Chiquitos Province, 20 km North East of Santiago de los Chiquitos (FLMNH 210580).

**Illustration.** — Pfeiffer (1906: pl. 35, figs 15, 16); Pilsbry (1906: pl. 36; fig. 71, 72).

**Imaging.** — MNHN-IM-2000-28012, syntypes.

**References.** — Pfeiffer (1906); Pilsbry (1906); Haas (1949).

**Obeliscus blandi** (Pfeiffer, 1852)

*Balimus blandi* Pfeiffer, 1852: 85.

**Obeliscus blandi** — Pilsbry 1906: 257, pl. 36, figs 83, 84.

**Type locality.** — Colombia: Baranquilla, in the Andes.

**Other localities.** — Colombia: Baranquilla, in the Andes.

**References.** — Pilsbry (1906).

**Obeliscus boitata** Simone & Salvador, 2016

*Obeliscus boitata* Simone & Salvador, 2016: 25, 29 (figs 77-79).

**Museum deposits.** — **Holotype.** Brazil • 1; Minas Gerais, Nanuque, 17°51’S, 40°23’W; 120 m a.s.l.; very close to the borders with the states of Bahia and Espirito Santo, very small fragment of Atlantic Forest; MZSP 106169.
Paratypes. Brazil • 39 shells; same collection data as for holotype; MZSP 106170.

Type locality. — Brazil: Minas Gerais, Nanuque.

Other localities. — Species known only from the type locality.

References. — The only bibliographic reference is the original description of the species.

Obeliscus carphodes (Pfeiffer, 1852)

* Bulimus carphodes * Pfeiffer, 1852: 108, pl. 34, fig. 2.

* Obeliscus carphodes * — Pilshby 1906: 246, pl. 34, fig. 53. — Salgado & Coelho 2003: 155. — Simone 2006: 187, fig. 687.

Museum deposits. — Brazil • 1 shell; A. D. Brown Collection; ANSP 59330 • 2 shells; 1872; Heukelon F. van leg.; ZMA.MOLL 32528 • 1 shell; RBINS 539204 • 1 shell; RBINS 499929 • 1 shell; Rio Grande do “Sal” [Rio Grande do Sul], Albuquerque; Thayer Exp. to Brazil; MCZ:Mala:119453.

Type locality. — Brazil: no specific locality.

Other localities. — Brazil (ANSP 59330; ZMA.MOLL 32528; RBINS 539204; RBINS 499929; MCZ:Mala:119453); Rio Grande do “Sal” [Rio Grande do Sul], Albuquerque (MCZ- 119453).

Imaging. — ZMA.MOLL 32528.

Illustration. — Pfeiffer (1852: pl. 34, fig. 2); Pilshby (1906: pl. 34., fig. 53).

Obeliscus columella (Philippi, 1844)

* Bulimus columella * Philippi, 1844: 158 (pl. 2, fig.7).

* Obeliscus columella * — Pilshby 1906: 248, pl. 34., figs 49-50. — Simone 2006: 187, fig. 688.

Museum deposits. — Brazil • 1 shell; USNM 20276.

Type locality. — Brazil.

Other localities. — Species known only from the type locality.

Illustration. — Pilshby (1906: pl. 34., figs 49, 50).

References. — Pilshby (1906).

Obeliscus latissipra Pilshby, 1944

* Obeliscus latissipra * Pilshby, 1944: 127, pl. 11, fig. 18. — Clench & Turner 1962: 84.

Museum deposits. — Paratypes. Peru • 1 shell; Junin Dept., Huacaipistana: 1800 m; 1942; Weyrauch W. leg.; ANSP 451843 • Junin Dept., Huacaipistana, river Tarma; FLMNH 110894 • same collection data as for preceding; FLMNH 203092.

Type locality. — Peru: Huacaipistana.

Other localities. — Peru: Dept. Junin, River Tarma, Huacaipistana (FLMNH 110894; 203092).

Illustration. — Pilshby (1944: pl. 11, fig. 18).

References. — Clench & Turner (1962).

Obeliscus moderatus Pilshby, 1933

* Obeliscus moderatus * Pilshby, 1933: 152. — Clench & Turner 1962: 99.

Museum deposits. — Dominican Republic • Barahora Province, Sierra de Bahoruco, 4 km North Polo; 12.IX.1983; Thompson F. leg.; FLMNH 045777 • Barahora Province, Sierra de Bahoruco, 4 km North Polo; 19.III.1974; Thompson F. leg.; FLMNH 045778 • Barahora Province, Sierra de Bahoruco, 5 km North Polo; 19.III.1974; Thompson F. leg.; FLMNH 210623 • Barahora Province, 7 km NNE of Polo; 19.III.1974; Thompson F. leg.; FLMNH 210626 • Estrelleta Province, 9 km North East of La Descubierta; 02.VI.1974; Thompson F. leg.; FLMNH 210628 • Barahora Province, 2 km NNE of Polo; 19.III.1974; Thompson F. leg.; FLMNH 210629 • Estrelleta Province, 6 km NW of Pozzer Rio; 02.VII.1974; Thompson F. leg.; FLMNH 210628 • Barahora Province, 14 km South of Cabral, 7 km NNE of Polo; 18.VI.1974; Thompson F. leg.; FLMNH 210629 • Estrelleta Province, 3 km North East of El Agucate; 30.VI.1974; Thompson F. leg.; FLMNH 210630.

Type locality. — Dominican Republic: Santo Domingo - Del Monte plantation, 5-6 min W of Barahora.

Other localities. — Dominican Republic: Barahora Province, Sierra de Bahoruco, 4 km North of Polo (FLMNH 045777; 045778); Barahora Province, 5 km North East of Polo (FLMNH 210623); Barahora Province, 7 km North East of Polo (FLMNH 210624); Estrelleta Province, 9 km North East of La Descubierta (FLMNH 210625); Barahora Province, 9 km North East of Polo (FLMNH 210626); Estrelleta Province, 6 km NW of Pozzer Rio (FLMNH 210627); Independencia Province, 4 km North East of El Agucate (FLMNH • 210628); Barahora Province, 14 km of Cabral, 7 km North East of Polo (FLMNH 210629); Estrelleta Province, 3 km North East of El Agucate (FLMNH 210630).

References. — Clench & Turner (1962).

Obeliscus obeliscus (Moricand, 1833)

* Helix (Cochlicella) obeliscus * Moricand, 1833: 540 (pl.1, fig.4).

* Helix obeliscus * – Moricand 1836: 424.

* Bulimus obeliscus * – Pfeiffer 1852: 107 (pl. 34, fig. 1).

* Obeliscus obeliscus * – Pilshby 1906: 245 (pl. 34, figs. 44-48, 51). — Salgado & Coelho 2003: 155. — Simone 2006: 187 (fig. 689).

Museum deposits. — Syntypes. Brazil • 3 shells; MCZ Malacology 27337.

* Brazil • 1 shell; donor Brown, A. D.; ANSP 3064 • 3 shells; donor Phillips, J. S.; ANSP 58374 • 16 shells; donor Philips, J. S. ANSP 58375 • 2 shells; provenance Swift Collection Moricand; ANSP 58376 • 2 shells; donor Webb, W. E.; ANSP 59329 • 1 shell; Bahia; provenance Naide, M. & B. Meyer; Naide Collection; ANSP 449608 • 1 shell; Espirito Santo, Aracruz, Serra do Golã; Oct. 1992; provenance I. Wistar Morris III, Hideo Katori Collection; ANSP 426505 • Pernambuco, Tapacura Dam; dry shell without animal; BMSM 96940 • Bahia, Canavieiras; under dead branches and leaves, dry shell without animal; BMSM 96909 • 1 shell; CMNH 62.14868 • Daurzenberg, P.; FLMNH 110900 • Espirito Santo, Foster M. leg.; FLMNH 118822 • 2 shells; FLMNH 36160 • 1 shell; FLMNH 36161 • 3 shells; FLMNH 100631 • 1 shell; RBINS 357518 • 1 shell; RBINS 538334 • 1 shell; RBINS 369515 • 1 shell; RBINS 566776 • 1 shell; RBINS 480428 • 1 shell; RBINS 575417 • 1 shell; RBINS 438330 • 7 shells; MCZ Malacology 27323 • 1 shell; near Campos, Serra do
Rio Preta [Serra do Rio Preto] • MCZ Malacology 27336 • 44 shells • Mollusca: 30581; 1 shell; Mollusca: 15038; 1 shell; Mollusca: 30580; 1 shell; Espírito Santo, Rio de Janeiro, Santa Maria Madalena; 16.II.2008; Salgado N. C. leg.; MNRJ: Mollusca: 20267; 1; 17.VIII.2015; Espírito Santo, Rio de Janeiro, Santa Maria Madalena, Rancho do Lelê; -20.004588 -41.934722; 428 elev.; 17.I.1975; Costa C. J. F. leg., specimens preserved in ethanol 70%; MNRJ: Mollusca: 13219; 4; Pernambuco; São Lourenço; 16.VI.2001; Salgado N. C. leg.; specimens preserved in ethanol 70%; MNRJ: Mollusca: 30399 • 8 shells; Ceará, Camocim; 10.VII.1996; Salgado N. C. leg.; MNRJ: Mollusca: 30399; 1; Cotantins, Barrolandia, Mata da SEPLAC; 20.II.1985; specimens in ethanol 70%; MNRJ: Mollusca: 32346; 1 shell; Bahia, Santa Cruz Cabrália (MNRJ: Mollusca: 32851; 13382); Rio de Janeiro, Macaé, Areia Branca; II.1977; MNRJ: Mollusca: 77558; 1; Bahia, Belmonte, Barrolandia; 20.II.1985; Costa C. J. F. leg.; specimens preserved in ethanol 70%; MNRJ: Mollusca: 18936; 5; Espírito Santo, Sul de Meaípe; I.X.1993; specimens preserved in ethanol 70%; MNRJ: Mollusca: 18937; 1 shell; Bahia, Cajaiba; IV.1987; MNRJ: Mollusca: 7755; 1; Bahia, Belmonte, Barrolandia; 20.II.1985; Costa C. J. F. leg.; specimens preserved in ethanol 70%; MNRJ: Mollusca: 31954 • 1 shell; Bahia, Porto Seguro; 28.II.2005; MNRJ: Mollusca: 31956; 1; Bahia, Campo Formoso; IX.2002; specimens preserved in ethanol 70%; MNRJ: Mollusca: 13219 • 4; Pernambuco; São Lourenço; 16.VI.2001; Salgado N. C. leg.; specimens preserved in ethanol 70%; MNRJ: Mollusca: 30399 • 8 shells; Ceará, Camocim; 10.VII.1996; Salgado N. C. leg.; MNRJ: Mollusca: 30399; 1; Cotantins, Barrolandia, Mata da SEPLAC; 20.II.1985; specimens in ethanol 70%; MNRJ: Mollusca: 32346; 1 shell; Bahia, Santa Cruz Cabrália (MNRJ: Mollusca: 32851; 13382); Rio de Janeiro, Macaé, Areia Branca; II.1977; MNRJ: Mollusca: 77558; 1; Bahia, Belmonte, Barrolandia; 20.II.1985; Costa C. J. F. leg.; specimens preserved in ethanol 70%; MNRJ: Mollusca: 18936; 5; Espírito Santo, Sul de Meaípe; I.X.1993; specimens preserved in ethanol 70%; MNRJ: Mollusca: 18937; 1 shell; Bahia, Cajaiba; IV.1987; MNRJ: Mollusca: 7755; 1; Bahia, Belmonte, Barrolandia; 20.II.1985; Costa C. J. F. leg.; specimens preserved in ethanol 70%; MNRJ: Mollusca: 31954 • 1 shell; Bahia, Porto Seguro; 28.II.2005; MNRJ: Mollusca: 31956; 1; Bahia, Campo Formoso; IX.2002; specimens preserved in ethanol 70%; MNRJ: Mollusca: 13219 • 4; Pernambuco; São Lourenço; 16.VI.2001; Salgado N. C. leg.; specimens preserved in ethanol 70%; MNRJ: Mollusca: 30399 • 8 shells; Ceará, Camocim; 10.VII.1996; Salgado N. C. leg.; MNRJ: Mollusca: 30399; 1; Cotantins, Barrolandia, Mata da SEPLAC; 20.II.1985; specimens in ethanol 70%; MNRJ: Mollusca: 32346; 1 shell; Bahia, Matas do Novo Mundo; I.1970; MNRJ: Mollusca: 41354; 1 shell; Bahia, Santa Cruz Cabrália (MNRJ: Mollusca: 32851; 13382); Rio de Janeiro, Macaé, Areia Branca (MNRJ: Mollusca: 41611; near Campos, Serra do Rio Preto (Malacology 27336); Rio Grande do Sul, Taguaçu (Pilsbury 1906); Rio Grande do Sul, Albufeira (Malacology 119454). Venezuela (Malacology 27324). Colombia (USNM 251168). Ecuador (USNM 426531). Mexico (USNM 316229).

ILLUSTRATION. — Moricand (1833: pl. 1; fig. 4); Pfeiffer (1852: pl. 34, fig. 1); Pilsbury (1906: pl. 34, figs 44-48, 51).

REFERENCES. — Moricand (1836); Pfeiffer (1852); Pilsbury (1906); Salgado & Coelho (2003).

Obeliscus pattalus Pilsbury, 1906

Obeliscus pattalus Pilsbury. Pilsbury 1906: 249, pl. 36, fig. 70. — Clench & Turner 1962: 115. — Salgado & Coelho 2003: 155. — Simone 2006: 188 (fig. 690).

MUSEUM DEPOSITS. — Lectotype. Brazil • 1; 4.VI.1908; ANSP 59335. Paralecotype. Brazil • 1; 21.VIII.2015; ANSP 465076.

TYPE LOCALITY. — Brazil, no specific locality.

OTHER LOCALITIES. — Species known only from the type locality.

ILLUSTRATION. — Pilsbury (1906: pl. 36, fig. 70).

REFERENCES. — Clench & Turner (1962); Salgado & Coelho (2003).

Obeliscus peregrinus (Pfeiffer, 1855)

Obeliscus peregrinus Pfeiffer. 1855: 9. Obeliscus peregrinus — Pilsbury 1906: 258.

TYPE LOCALITY. — Unknown.

OTHER LOCALITIES. — Unknown.

ILLUSTRATION. — Not figured.

REFERENCES. — Pilsbury (1906).

Obeliscus planospirus (Pfeiffer, 1852)

Obeliscus planospirus Pfeiffer, 1852: 108. pl. 34, fig. 3.

Obeliscus planospirus — Pilsbury 1906: 247, pl. 34, fig. 44. — Salgado & Coelho 2003: 155. — Simone 2006: 187.

MUSEUM DEPOSITS. — Brazil • Espírito Santo, Rio Doce; ANSP A9714 • 2 shells; Espírito Santo, Rio Doce; 24.V.1910; ANSP 100535 • 1 shell; CM: Mollusks 62.13330.
Rediscovery of *Obeliscus agassizi*

Type locality. — Unknown.

Other localities. — Brazil: head waters of the Mucury river in eastern Minas Gerais (Pilsbry, 1906).

Brazil: Espírito Santo, Rio Doce (ANSP100535).

Illustration. — Pfieffer (1852: pl. 34, fig. 3); Pilsbry (1906 pl. 34; fig. 44).

References. — Pfieffer (1852); Pilsbry (1906); Salgado & Coelho (2003).

*Obeliscus subuliformis* (Moricand, 1836)

*Helix subuliformis* Moricand, 1836: 427, pl. 2, fig. 3.

*Obeliscus subuliformis* – Pilsbry 1906: 251, pl. 36, fig. 75. — Salgado & Coelho 2003: 155. — Simone 2006: 188, fig. 692.

Museum deposits. — *Paratypes*. Brazil • 1 shell; Bahia: Malacology 177339 (MCZ) • 1; USNM 316229 • 1; USNM 117490 • shell; RMNH.MOL.271464 (NBCN).

Type locality. — Brazil: Bahia, São Gonçalves forest. Brazil: Bahia (Moricand 1836).

Other localities. — Brazil: head waters of the Mucury river in eastern Minas Gerais, Brazil. (Pilsbry 1906).

Type locality and, later, French Guiana: Cayenne (FMNH 36173).

Other localities. — Species known only from the type locality.

Illustration. — Da Costa (1898: pl. 6, fig. 10); Pilsbry (1906: pl. 36, fig. 81).

References. — Pilsbry (1906).

DISCUSSION

Habitat of species of *Obeliscus*

Fragmentary information obtained from taxonomic literature allows concluding that the species of the genus *Obeliscus* rather dwell in leaf litter (Moricand 1836; Cousin 1887; Vanatta 1918). With reference to the habitat of *Obeliscus sylvaticus*, for example, Moricand (1836: 10) said that this species is very common in forests, under the trees, under dead and humid leaves. According to Vanatta (1918: 238) *Obeliscus abotti* was found in debris. Some other species, as *Obeliscus bacterionides*, have been found “under stones” (Pilsbry 1906). Other obeliscine genera probably are leaf-litter-dwelling as well. According to Cousin (1887: 239), *Protobeliscus jousseaumei* (Cousin, 1887) was found buried in the humus or hide under dead leaves. According to Hylton-Scott (1946: 366), *Rectobelus birabeni* was collected in the leaf-litter.

Distribution of *Obeliscus* in Brazil

Information on the distribution of *Obeliscus* species from Brazil is very scant. For some species as *Obeliscus carphodes*, *Obeliscus pattalus*, *Obeliscus agassizi* and *Obeliscus columnella*, the type locality was given simply as Brazil (Pfiesser 1852; Pilsbry 1906). The information available in the literature on the distribution of the other species is also very limited. *Obeliscus obeliscus* was recorded for Bahia and Rio Grande do Sul states and *Obeliscus sylvaticus* for Piauí, Bahia and Rio de Janeiro states. *Obeliscus subuliformis* and *Obeliscus boitata* are known only for their type localities at Bahia and Minas Gerais states, respectively (Spix & Wagner 1827; Moricand 1833; 1836; Pfieffer 1852; Simone & Salvador 2016). *Obeliscus planospirus* was described without reference to the type locality and, later, Pilsbry (1906) added “head waters of the Mucury river in eastern Minas Gerais, Brazil”.

In the present study, the research in collection databases allowed to expand the recognized distribution of the species *O. planospirus*, which is now recorded in Espírito Santo state, *O. obeliscus* now recorded in Tocantins, Ceará, Pernambuco, Alagoas, Sergipe, Espírito Santo and Rio de Janeiro states, as well as *O. sylvaticus* now recorded in French Guiana, besides Brazil.

Life history traits of *Obeliscus*

Although there is no study on the life history of species of *Obeliscus*, fragmentary data on reproduction can be found in the taxonomic literature. Some information given by Moricand (1836: 11, pl. 2, fig. 28) and reaffirmed by Pilsbry (1906: 246) on *O. obeliscus* indicate that this species is ovoviviparous,
releasing non-calcified eggs formed by a thin and transparent membrane containing shelled embryos. About *Obeliscus sufitianus* (Pfeiffer, 1852), Pilsbry (1906) affirmed: “…none of the specimens seen contains eggs, such as are commonly seen in *Opeas*. It is probably viviparous, like all Obelisci.”

Since this author mentioned only oviparity and viviparity, discriminating viviparous species as those containing shelled embryos in the spermovoiduct, we believe that this species is in fact ovoviviparous. Ovoviviparity and egg retention seem to be widespread reproductive modes in subulinids (Pilsbry 1906; Baker 1927; Batts 1957; Araújo & Keller 1993; Schileyko 1999; Carvalho et al. 2009; Pilate 2013) and may be common to obeliscine snails (Moricand 1836; Pilsbry & Vanatta 1899; Pilsbry 1899, 1906).

**Taxonomic Remarks**

Schileyko (1999) estimated about 10 species of *Obeliscus*. In the present work, we listed 16 species of *Obeliscus*, nine of them recorded in Brazil. Among the species occurring in Brazil, six are endemic to this country.

The species of *Obeliscus* have been traditionally distinguished by shell characters, mainly the general shell shape, number of whorls proportionally to the shell size, shell ornamentation, the shape of the protoconch, and aperture size and shape. The distinction between species is often subtle. Considering that shell features may be not sufficient as single taxonomic characters, other evidences of species boundary, especially anatomical characters, is needed.

*Obeliscus agassizi* and *O. sylaticus* were found by Pilsbry (1906) cohabiting in the same collecting site. This fact, along with the close resemblance in their shells, indicates the need to provide a differential diagnosis for these species, through a more exhaustive anatomical characterization. Currently, the two species can be differentiated mainly by the shape of the shell aperture. *Obeliscus sylaticus* has a more slender shell with a smaller aperture, which is also quadrangular in shape, while the shell aperture of *O. agassizi* is somewhat oblique and ovate in shape. The strength of shell traits to delimit species of *Obeliscus* should be evaluated in the future, with the accumulation of information on the anatomy of the soft parts and with the use of molecular markers.

Presently it is not possible to evaluate the taxonomic significance of the various morphological traits of the soft parts for the Obeliscinae genera as there is information only on four species from four genera. The data on the anatomy of the genital system of *O. agassizi* (present study), *Neobeliscus calcareus* provided by Pilsbry (1899, 1906), *Stenogyra tersbrater* provided by Schileyko (1999) and *Rectobelus birabeni* provided by Hyton-Scott (1946), did not allow a comprehensive comparative analysis, but some anatomical differences among the representatives of these four genera are worth of mentioning. *Obeliscus agassizi* differs from *N. calcareus* in the site of insertion of the vas deferens into the penial complex, the site of insertion of the bursa copulatrix duct relative to the size of the free oviduct, the site of insertion of the penial retractor muscle and the size of the bursa copulatrix duct relative to the size of the free oviduct. *Obeliscus agassizi* differs from *R. birabeni* in the site of insertion of the vas deferens into the penial complex, the site of insertion of the penial retractor muscle and the size of the bursa copulatrix duct relative to the size of the free oviduct and in the site of insertion of the vas deferens into the penial complex.

Considering the anatomical characteristics common to the genera *Obeliscus, Neobeliscus, Stenogyra*, some traits are possible diagnostic characters for this subfamily. This concerns characters of the genital system, i.e., atrium and vagina short; long, club-shaped penial complex and terminal penial retractor muscle; of the circulatory and excretory systems, i.e., venation faint; of the respiratory system, i.e., pulmonary vein unbranched; and of the excretory system, i.e., kidney more than double the length of the pericardium, and kidney length contained about 3½ times in that of the mantle. The genus *Rectobelus* Baker, 1927, share with the genera *Obeliscus, Neobeliscus, Stenogyra* the presence of short atrium and vagina, and long, club-shaped penial complex. This genus must to be reexamined since there is no description of the circulatory and excretory systems. The penial complex of *R. birabeni* is not long and club-shaped as observed for the other three genera.

This preliminary analysis gives an idea of potential diagnostic characters, but it is still necessary to evaluate if they are consistent in examining a great number of species from these and the other Obeliscinae genera, along with the intra generic variability on these traits.

**Author’s contributions**

SD conceived and designed the study, performed anatomical and taxonomic analysis, original illustrations and wrote this manuscript. LRLS edited the plates and co-wrote this manuscript. LFCO performed shell SEM analysis and revised this manuscript. CL collected the studied specimens and revised this manuscript. PM collected the studied specimens and co-wrote this manuscript.

**Competing interests**

The authors declare that there is no conflict of interests regarding the publication of this paper.

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