

# Taxonomy and distribution of enigmatic “helicoid” *Polygyratia* Gray, 1847 (Gastropoda, Stylommatophora)

Rodrigo Brincalepe Salvador<sup>1</sup>, Daniel Caracanhas Cavallari<sup>2</sup>

<sup>1</sup> Museum of New Zealand Te Papa Tongarewa, Wellington, New Zealand

<sup>2</sup> Faculdade de Filosofia, Ciências e Letras de Ribeirão Preto, Universidade de São Paulo. Ribeirão Preto, SP, Brazil

<http://zoobank.org/E87CE884-99A0-4900-96C1-C3F15E3B01A3>

Corresponding author: Rodrigo Brincalepe Salvador ([salvador.rodrigo.b@gmail.com](mailto:salvador.rodrigo.b@gmail.com))

Academic editor: Frank Köhler ♦ Received 12 February 2020 ♦ Accepted 1 March 2020 ♦ Published 13 March 2020

## Abstract

Herein, we present a taxonomic revision of the genus *Polygyratia* Gray, 1847, with a new systematic placement in Scolodontidae and containing only the species *Polygyratia polygyrata* (Born, 1778). We offer an updated morphological description and geographical distribution, based on museum specimens and occurrence data gathered from literature and online database iNaturalist. We synonymise *P. charybdis* Mörch, 1852 with *P. polygyrata*. The species is known only from Atlantic Forest areas in Bahia state, eastern Brazil. We exclude three other species from the genus *Polygyratia*, classifying them as: *Systrophia* (*Systrophia*) *heligmoida* (d’Orbigny, 1835) and *S. (Entodina) reyrei* (Souverbie, 1858), based on conchological features; and *S. (E.) pollodonta* (d’Orbigny, 1835), though tentatively, based on scant published data. Finally, we present the first report of *S. (S.) heligmoida* (d’Orbigny, 1835) from Brazil.

## Key Words

Atlantic Forest, Brazil, Eupulmonata, Helicoidea, iNaturalist, *Polygyratia polygyrata* (Born, 1778), Scolodontidae

## Introduction

*Polygyratia polygyrata* (Born, 1778) was one of the first terrestrial gastropods to be described from Brazil. After its original description, which did not provide a locality of origin, all subsequent major lists of terrestrial gastropods included the species, pinpointing its occurrence to the forests of Bahia (e.g. Beck 1837; Albers 1860). Despite being an instantly-recognisable species and a favourite item of shell collectors of old, the species remained scarcely studied after the 19<sup>th</sup> century, with a single additional species described (*P. charybdis* Mörch, 1852) and a brief revision presented by Pilsbry (1894).

Given that the knowledge about this species advanced very little since its description, we decided to reassess here all the information available regarding its taxonomy and geographical distribution, analysing museum specimens from worldwide collections, as well as online databases. We present here a formal re-description of the genus and its species, alongside venues for future research.

## Material and methods

The main museum collections worldwide that could harbour specimens of *Polygyratia* were visited or contacted. Specimens were analysed for conchological characters (see below for molecular analysis) and the available locality data was compiled for a distribution map. Collection dates are unknown for most of the historical specimens, but at least a minimum age can be given to those that belonged to private collections by using the owner’s date of death (Coan and Kabat 2018). The owners’ names were cross-checked with the report of Dance (1966), which lists where these former private collections are presently housed. Further photographic records of the species were extracted from the online database iNaturalist (<https://www.inaturalist.org>) and shell collector websites. Additional locality data was extracted from literature.

The only specimens with soft parts that could be sampled for molecular studies (MZSP 62060, 62061

and 98742) had small sections of their foot clipped for DNA extraction. The specimens, however, were in poor condition: largely decomposed, indicative of the ethanol having dried up at some point. Different types of DNA extraction kits (and protocols) were tried: DNeasy Blood & Tissue Kit (QIAGEN), NucleoSpin DNA RapidLyse (Macherey-Nagel) and E.Z.N.A. Mollusc DNA Kit (Omega Bio-tek). Unfortunately, none of the trials resulted in good quality DNA for amplification and sequencing.

Selected specimens were used for micro-computed tomography analysis (CT scan), scanned using a GE Phoenix v|tome|x s 240 industrial high-resolution CT & x-ray system at the Centro para Documentação da Biodiversidade (FFCLRP). This system is equipped with a DXR250RT 1,000 × 1,000 pixels detector; a diamond target was used with the following parameters: source operating at 60 kV, 100 µA, 1 × 1 binning, 333 ms exposure time, 1,200 projections, 1 frames skipped, 4 frames averaged, default offset and gain corrections. Image processing and 3D volume reconstruction were obtained using GE phoenix datos|x 2 and the subsequent volume analysis was carried out in VGSTUDIO 3.0 (Volume Graphics, Germany).

**Abbreviations: Institutions:** AMNH = American Museum of Natural History (New York, USA); ANSP = Academy of Natural Sciences of Drexel University (Philadelphia, USA); CMNH = Cleveland Museum of Natural History (Cleveland, USA); FMNH = Field Museum of Natural History (Chicago, USA); MNB = Muzeul Național Brukenthal, Muzeul de Istorie Naturală (Sibiu/Hermannstadt, Romania); MNCN = Museo Nacional de Ciencias Naturales (Madrid, Spain); MNZ = Museum of New Zealand Te Papa Tongarewa (Wellington, New Zealand); MZSP = Museu de Zoologia de Universidade de São Paulo (São Paulo, Brazil); NHMD = Statens Naturhistoriske Museum (Copenhagen, Denmark); NHMUK = Natural History Museum (London, UK); NHMW = Naturhistorisches Museum Wien (Vienna, Austria); NMR = Natuurhistorisch Museum Rotterdam (Rotterdam, The Netherlands); RMNH = Naturalis Biodiversity Center (former Rijksmuseum van Natuurlijke Historie; Leiden, The Netherlands); SMF = Senckenberg Naturmuseum (Frankfurt am Main, Germany); SNSD = Senckenberg Natural History Collections Dresden (Dresden, Germany); USNM = Smithsonian National Museum of Natural History (Washington, D.C., USA); ZMA = Naturalis Biodiversity Center (former Zoologisch Museum Amsterdam; Leiden, The Netherlands); ZMB = Museum für Naturkunde, Leibniz Institute for Evolution and Biodiversity Science (Berlin, Germany). **Specimens:** col = collector; colln = collection; D = greatest shell width (perpendicular to H); H = shell length (parallel to columellar axis); obs = observer; sh = shell(s); spm = specimen(s); W = number of whorls.

## Systematics

### Family Scolodontidae

#### Genus *Polygyratia* Gray, 1847

*Polygyratia* Gray, 1847: 173; Gude 1920: 59; Thiele 1931: 679; Morretes 1949: 163; Zilch 1960: 603; Richardson 1985: 262; Parkinson et al. 1987: 65; Salgado and Coelho 2003: 172; Schileyko 2006: 1844; Simone 2006: 247; Breure and Araujo 2017: 121; MolluscaBase 2018; Salvador 2019: 95.

*Ophiogyra* Albers, 1850: 91; Albers 1860: 94.

**Type species.** *Helix Polygyrata* Born, 1778, by monotypy.

**Included species.** *P. polygyrata* (Born, 1778).

**Diagnosis.** Shell planispiral, multi-whorled and large for family. Body whorls marked by three angulations: one dorsal, one median and one basal. Aperture large (for family), rounded, with reflected peristome. Presence of short internal (not visible from aperture) parietal and palatal lamellae on body whorl. Aperture without barriers.

**Description.** As *P. polygyrata* below.

**Remarks.** The name *Ophiogyra* was introduced by Albers (1850), who likely was not aware of the new name established by Gray just a few years prior. The only species included by Albers (1850) in the new genus was *Ophiogyra polygyrata*. Thus, *Ophiogyra* is an objective junior synonym of *Polygyratia*.

#### *Polygyratia polygyrata* (Born, 1778)

Figs 1, 2

*Helix Polygyrata* Born, 1778: 382; Wilhelm 1802: 356.

*Helix polygyrata*: Born, 1780: 373, pl. 14, figs 19–20; Schröter 1784: 266; Chemnitz 1786: 98, pl. 127, figs 1124–1125; Dillwyn 1817: 908; Férussac 1819: 4, pl. 69A, figs 7–9, pl. 69B, fig. 5; Férussac 1821: 40; Deshayes in Lamarck 1838: 98; Moricand 1846: 151, pl. 5, figs 1–3; Pfeiffer 1848: 405; Mörch 1852: 7; Reeve 1854: species 541, pl. 98; Hupé 1857: 12; Hidalgo 1870: 32; Hidalgo 1893: 80.

*Helix polygyra* [sic] Gmelin, 1788: 3624.

*Helix Elongata* Röding, 1798: 107.

*Helix (Helicella) polygyrata*: Moricand, 1836: 422.

*Polygyra?* *Polygyrata*: Beck 1837: 23.

*Polygyratia polygyrata*: Gray 1847: 173; d'Orbigny 1849: pl. 19, figs 14–16; Mörch 1852: 7; Thiele 1931: 679; Zilch 1960: 603, fig. 2119; Richardson 1985: 262; Parkinson et al. 1987: pl. 13, fig. 6; Abbott 1989: 142, textfig.; Salgado and Coelho 2003: 172; Schileyko 2006: 1844, fig. 2359; Simone 2006: 247, fig. 946; Schileyko 2016: fig. 4; Breure and Araujo 2017: 121, figs 47D–F; Sei et al. 2017: table 9, fig. 5n; MolluscaBase 2019a; Salvador 2019: 95.

*Ophiogyra polygyrata*: Albers 1850: 91; Albers 1860: 94.

*Polygyratia charybdis* Mörch, 1852: 7.  
*Polygyratia* (detrita.): Mörch 1852: 7.  
*Helix charybdis*: Mörch 1852: 170.  
*Helix Charybdis*: Hupé 1857: 12.  
*Helix* (*Anchistoma*) *polygyrata*: Brauer 1878: 181.  
*Polygyra* (*Polygyratia*) *polygyrata*: Tryon 1887: 111, 124, pl. 25, figs 72–74.  
*Polygyra* (*Polygyratia*) *polygyrata* var. *charybdis*: Tryon 1887: 124.  
*Anchistoma polygyrata*: Tryon 1887: pl. 25, figs 72–74.  
*Polygyratia* (*Polygyratia*) *polygyrata*: Pilsbry 1894: 81, pl. 20, figs 37–38.  
*Polygyratia* (*Polygyratia*) *charybdis*: Pilsbry 1894: 81.  
*Polygyratia polygyratia* [sic] Gude 1920: 59.  
*Polygyratia polygyrata polygyrata*: Morretes 1949: 163.  
*Polygyratia polygyrata charybdis*: Morretes 1949: 163.  
*Polygyratia charybdis*: Simone 2006: 247, fig. 945.

**Type locality.** Unknown (Born, 1778); “Brazil” according to Schileyko (2006); restricted to Bahia state herein.

**Type material.** NHMW-MO-14371, holotype (Fig. 1A; see also Brauer 1878).

**Common name.** Reported (and maybe given) by Born (1778), in German: “die Schnirkelscheibe”. “Schnirkelschnecken” is a general term often applied to any member of family Helicidae, so the German name can be roughly translated to English as “discoid helix”; or, allowing for a broader interpretation, it could be translated as “ornate disc”. However, using those names could bring unwanted confusion, because it would make the classification of *P. polygyrata* unclear by conflating it with Helicidae and disc snails (family Discidae).

Férussac (1819), Deshayes (*in* Lamarck 1838) and Reeve (1854), as usual in their works, proposed vernacular names that were direct translations of the Latin name (then *Helix polygyrata*): respectively, “hélice polygyre” and “many-whorled Helix”. While this name is somewhat descriptive, it is not distinct enough for a vernacular name. Abbott (1989) suggested a more appropriate name, although a rather clumsy one: “Brazilian gyrating snail”. Therefore, we propose here to adopt a simpler, yet descriptive, common name, “gyre snail”, returning to Born’s (1778) interpretation of a planispiral ornate spire and streamlining Abbott’s (1989) proposal.

**Distribution.** Eastern Bahia state, Brazil (Fig. 3).

**Specific occurrences. Museum specimens:** Pará state (likely mistaken, see below). Bahia state: Baía de Todos-os-Santos (Todos-os-Santos Bay), Cachoeira (road to Una), Canavieiras, Ilhéus, Itabuna, Itacaré, Itaparica, Olivença, Pimenteira, Salvador, Serra Grande, Uruçuca, Una, Una Biological Reserve. **Literature data:** Cachoeira (Férussac, 1819, as “Caxoeira”). **iNaturalist:** Bahia state: São Sebastião do Passé. **Internet:** Bahia state: Ilhéus, Valença.

**Habitat.** Atlantic Forest.

**Diagnosis.** As for genus above.

**Description.** Shell (Fig. 1) planispiral, multiwhorled. Spire typically slightly depressed, but often flat. Whorl profile markedly convex, with soft angulation marking borders of apical and umbilical regions; a central angulation on the body whorl can be seen in some specimens. Whorls closely packed together, regularly increasing in size. Body whorl bent abapically near the aperture. Presence of internal parietal (typically one) and palatal (typically two) lamellae on body whorl (Fig. 2; see also Suppl. material 1); lamellae short, disposed in two or three sets, positioned circa  $\frac{1}{3}$  and  $\frac{2}{3}$  of a whorl away from aperture. A different number of lamellae may be present in some specimens, which may have additional smaller lamellae or even lack one of the main three lamellae. Aperture rounded to D-shaped; callus may be present. Peristome lightly reflexed. Umbilicus very wide and deep. **Sculpture:** Protoconch of  $2\frac{1}{4}$ – $2\frac{1}{2}$  whorls, apparently smooth (typically eroded). Teleoconch sculpture by coarse growth lines that become coarser and more irregular towards aperture; often, growth lines acquire a papillose aspect. **Colour:** Shell predominantly chestnut brown, but often ochre. Some regions typically ochre: spiral band on adapical angulation of whorl (not always present); spire top (protoconch and first whorls); abapical region (excluding a chestnut coloured subsutural spiral band). Rarely, abapical (umbilical) portion of shell can be chestnut brown. Peristome white. **Measurements:**  $n = 26$ .  $H = 12.3 \pm 0.9$  mm (max 14.1, min 10.7);  $D = 43.5 \pm 3.7$  mm (max 56.7, min 38.2);  $W = 8\frac{3}{4} \pm \frac{1}{3}$  (max  $9\frac{1}{2}$ , min 8).

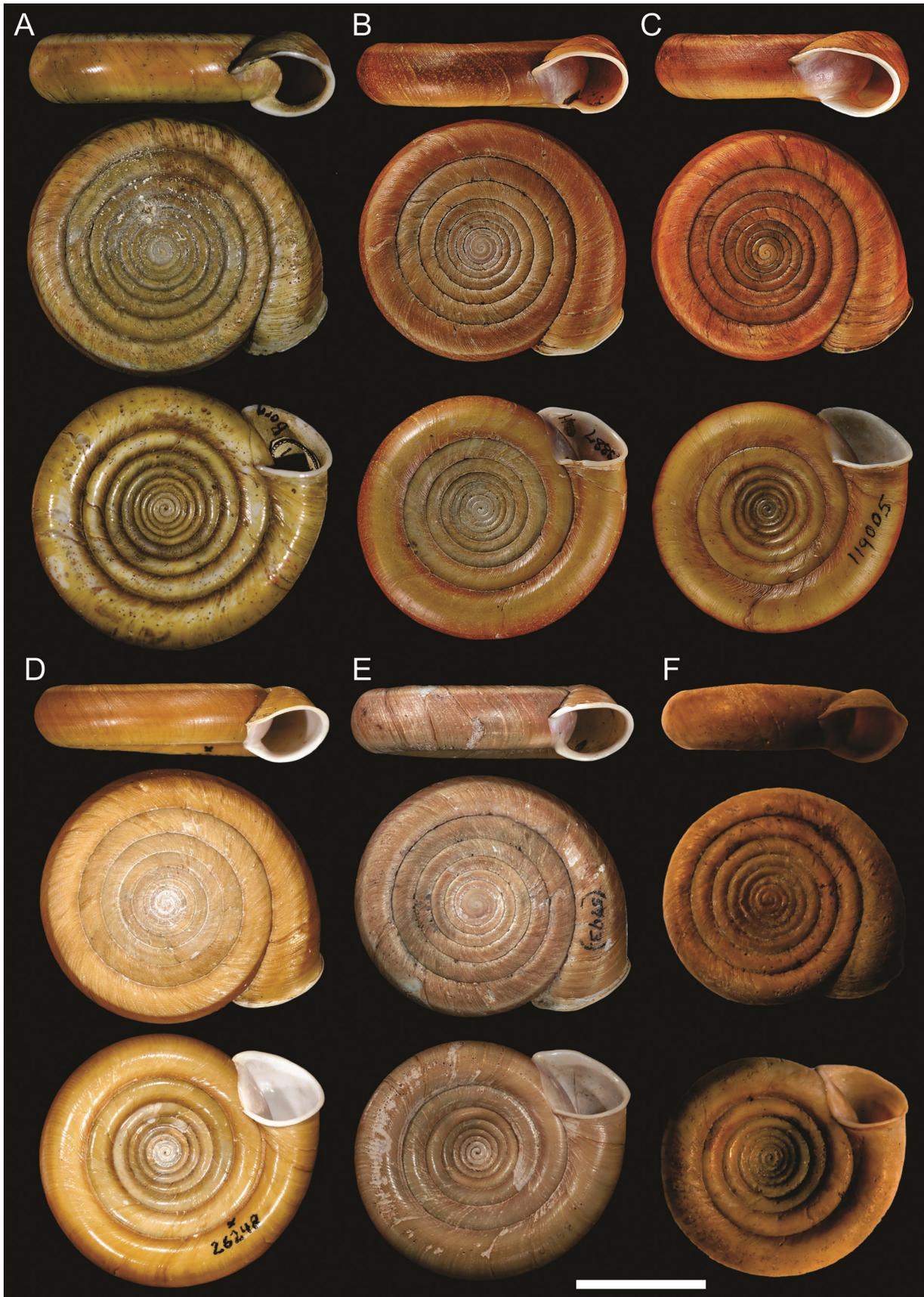
**Material analysed.** BRAZIL. **Uncertain locality:** AMNH 43888 (3 sh, pre-1911, ex J.J. Crooke colln.); AMNH 43889 (2 sh, ex Steward colln.); AMNH 43890 (2 sh, pre-1891, ex J.C. Jay colln.); AMNH 53755 (1 sh, pre-1905, ex J.A. Constable colln.); AMNH 294063 (1 sh, pre-2001, col. Krassner, ex N.A. Katsaras colln.); ANSP 1450 (1 sh, pre-1886, ex A.D. Brown colln.); ANSP 23777 (1 sh, ex Swift colln.); ANSP 33049 (1 sh, pre-1865, ex T.B. Wilson colln.); ANSP 217111 (1 sh, ex Higgins colln.); ANSP 361998 (1 sh, ex Alfred University colln.); FMNH 165 (4 sh, pre-1893, ex Ward’s Natural Science Establishment colln.); FMNH 40632 (3 sh, pre-1924, ex W.F. Webb colln., ex G.K. Gude colln., ex Smith colln.); FMNH 57464 (2 sh, pre-1954, ex O. Park colln.); FMNH 62570 (1 sh, pre-1956, ex E.E. Hand colln., ex W.F. Webb colln.); FMNH 75810 (1 sh, pre-1951, ex J. Zetek colln., ex W.F. Clapp colln.); FMNH 100081 (1 sh, pre-1877, ex F. Button colln., ex J.G. Anthony colln.); FMNH 365269 (1 sh, ex CMNH coll., ex Ward’s Natural Science Establishment colln.); MNB unnumbered (3 sh, ex Linnaea colln., ex ZMB colln.); MNB unnumbered (1 sh); MNB unnumbered (1 sh); MNCN 15.05/39937 (4 sh, col. J.G.

Hidalgo); MNZ M.233517 (1 sh, pre-1918, ex H.A. Suter colln. 5793); NHMD 615840 (1 sh, ex Lind colln., possibly ex A.M.D'A.G. Yoldi colln.); NHMD 615841 (1 sh); NHMD 615842 (possible holotype of *Polygyratia charybdis*, ex Lind colln., possibly ex A.M.D'A.G. Yoldi colln.); NHMD 615855 (1 sh, pre-1945, ex C.M. Steenberg colln.); NHMD 615856 (2 sh); NHMD 615857 (2 sh); NHMUK unnumbered (1 sh, pre-1952, ex J.E. Cooper colln. 2150); NHMUK unnumbered (2 sh, pre-1940, ex V.W. MacAndrew colln. 1563); NHMUK unnumbered (3 sh, pre-1941, ex B.R. Lucas colln. 2351); NHMUK unnumbered (2 sh, pre-1910, ex C.T. Trechmann colln. 2176); NHMUK unnumbered (1 sh, pre-1905, ex Blanford colln.); NHMUK unnumbered (3 sh, pre-1948, ex A.S. Kennard colln. 1824); NHMUK unnumbered (1 sh, pre-1991, ex "Mrs." De Burgh colln. 1822); NHMUK unnumbered (1 sh, ex Connolly colln.); NHMW-MO-14371 (holotype; ex I.v. Born colln.); NHMW-MO-9215 (1 sh); NHMW-MO-72546 (2 sh); NHMW-MO-unnumbered (1 sh, pre-1930, ex A. Oberwimmer colln.); NHMW-MO-unnumbered (2 sh, v/1881); NHMW-MO-unnumbered (2 sh, ex G. Brandt colln.); MNCN 15.05/14101 (1 sh, col. Paz); RMNH.MOL.289966 (2 sh, pre-1942, ex H.C. Fulton colln.); RMNH.MOL.289967 (2 sh, pre-1895, ex Geological Museum of Wageningen University colln., ex ZMB colln., ex F.W. Zürcher colln., ex Linnaea colln.); SMF 26245 (1 sh, ex Lömel colln.); SMF 26246 (2 sh, ex K. Haskagen colln.); SMF 26247 (1 sh); SMF 26248 (1 sh, pre-1903, ex O.v.F. Moellendorf colln.); SMF 26249 (1 sh, pre-1876, ex O. Reinhardt colln., ex H.C. Küster colln.); SMF 26250 (1 sh, pre-1894, ex O. Boettger colln., ex Linnaea colln.); SMF 82611 (1 sh, pre-1928, ex Jetschin colln.); SMF 82612 (1 sh, pre-1893, ex K.L. Pfeiffer colln., ex Linnaea colln.); SMF 62613 (2 sh, pre-1905, ex C.R. Boettger colln.); SMF 216143 (1 sh, pre-1970, ex S.H.F. Jaeckel colln., ex Feldmann colln.); SMF 297043 (1 sh, pre 1937, ex H.F.P. Ehrmann colln., ex W. Schlüter colln.); SMF (297044 (1 sh, G. Maegle colln.); SMF 297045 (2 sh, pre-1929, ex W. Schlüter colln., ex F.H. Rolle colln.); SMF 297046 (2 sh, pre-1929, ex F.H. Rolle colln.); SMF 297047 (2 sh, pre-1937, ex H.R.G. Kaltenbach colln.); SMF 297048 (1 sh, pre-1963, ex H.R.G. Kaltenbach colln.); SNSD 10578 (1 sh, pre-1895, ex Piper colln.); SNSD 32859 (4 sh, col. Bomeier 1939, ex Regius colln.); SNSD 56391 (1 sh, ex Theodor & Paul Reibisch colln.); USNM 21057 (1 sh); USNM 57280 (3 sh, ex Stearns colln.); USNM 106423 (1 sh, ex Lea colln.); USNM 217252 (3 sh, ex Henderson colln.); USNM 307601 (1 spm, ex Henderson colln.); USNM 307626 (1 sh, ex Henderson colln.); USNM 316168 (1 sh, ex Evezard colln.); ZMA.MOLL.397226 (1 sh, ex R.J. van Lennep colln.); ZMA.MOLL.397227 (1 sh). **Pará(?) state:** AMNH 119005 (1 sh, pre-1964, ex Julius Wisoff colln.). **Bahia state:** AMNH 43887 (2 sh, pre-1868, ex W.A. Haines colln.); ANSP 400548 (1 sh, col. "farm worker" iii/1983, Salvador municipality, on ground in forest, ex D. Naide & J. Naide colln.); ANSP 426504 (1 sh, viii/1993, N Itabuna municipality [Guadu], under dead

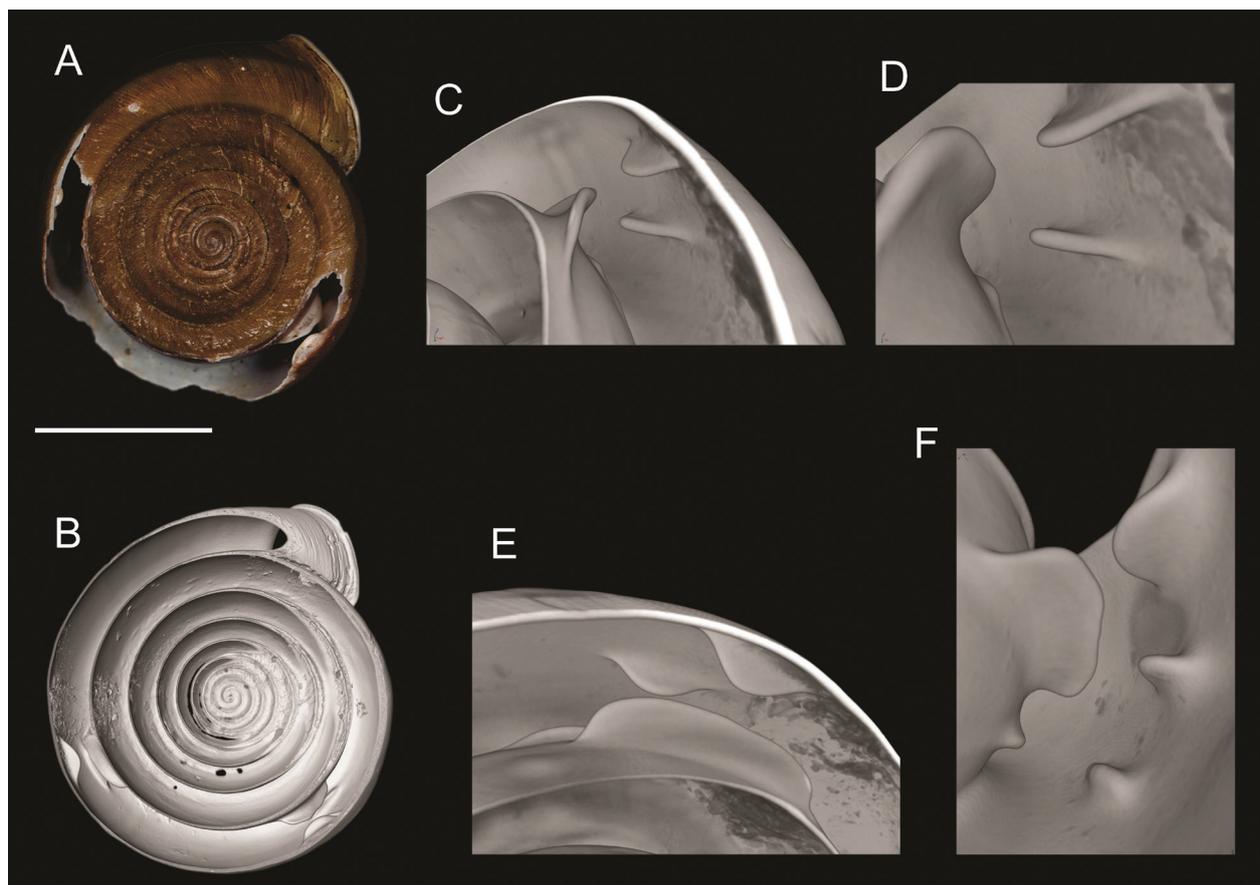
leaves in tropical forest, ex I. Wistar Morris III colln.); ANSP 448465 (1 sh, iv/1993, NNE Ilhéus municipality, under dead leaves, ex I. Wistar Morris III colln.); FMNH 193212 (1 sh, Una forest [likely Una Biological Reserve], col. R. Harley & B. Verdcourt 29/i/1977); NHMUK unnumbered (2 sh, col. G.P. Lewis & B. Verdcourt 2/xii/1981, Una municipality, 30–35 km S of Olivença, Ilhéus-Una road, restinga forest by roadside, ca. 40 m a.s.l. [likely Una Biological Reserve]); MNCN 15.05/39938 (3 sh, col. Azpeitia); MZSP 1640 (3 sh); MZSP 34823 (2 spm, Pimenteira municipality); MZSP 38809 (1sh, Ilhéus municipality, col. B. Jahyny); MZSP 47683 (2 sh, eastern Bahia, ex M. Roxo colln.); MZSP 47695 (4 sh, eastern Bahia, ex M. Roxo colln.); MZSP 62060 (1 spm, Serra Grande municipality, Praia do Pé da Serra, col. M.C. Guerrazzi 29/x/2004); MZSP 62061 (1 spm, Uruçuca municipality, Estância Fonte das Águas, col. M.C. Guerrazzi 10/xi/2004); MZSP 66950 (2 sh, Ilhéus municipality, col. A. Bodart x/2001); MZSP 72058 (1 sh, Itacaré municipality, col. P. Gonçalves x/2005); MZSP 73581 (1 sh, Ilhéus municipality, col. A. Bodart x/2001); MZSP 81075 (1 sh, col. L.R.L. Simone 1972); MZSP 96518 (1 sh, Ilhéus municipality, col. J.H.C. Delabie); MZSP 98742 (1 spm, Canavieiras municipality, 15°20'34"S, 39°01'00"W, col. J.R.M. Santos 13/v/2010); MZSP 116519 (1 sh, Itaparica municipality, col. A. Wallerstein xi/1973, ex J. Vaz colln.); MZSP 129318 (9 sh, Pimenteira municipality, col. A. Bianchi vi/2012); NHMD 615854 (2 sh, 1863, ex Andrea colln.); NHMW-MO-unnumbered (8 sh, Cachoeira [Cachoeirinha] - Una, F. Adolpho col.); NHMW-MO-unnumbered (2 sh, pre-1960, Cachoeira [Cachoeirinha] - Una, ex Edlauer colln.); NHMW-MO-unnumbered (6 sh, pre-1980, Cachoeira [Cachoeirinha] - Una, ex Klemm colln.); NMR 12118 (1 sh); SMF 216144 (1 sh, "Santos" [likely Todos-os-Santos Bay], pre-1970, ex S.H.F. Jaeckel colln.); SMF 316773 (1 sh, pre-1896, ex Z.I. Heidelberg colln. 1897Moll.1443); USNM 307595 (3 sh, ex Henderson colln., ex Redfield colln.); USNM 1202125 (3 sh, NE Ilhéus, under dead leaves, col. A. Bianchi x/2001).

**Online records. iNaturalist:** BRAZIL. **Bahia state:** id 13527047 (São Sebastião do Passé municipality, lat -12.44740646 long -38.41546864, obs. Ben Phalan "deboas" 17/vi/2018 13:25:06 UTC); id 14349827 and id 14349831 (São Sebastião do Passé municipality, lat -12.45972252 long -38.40000153, obs. "sidnei-sampaio" 14/vii/2018 13:56:40 UTC). **Other websites:** BRAZIL. **Bahia state:** Allspira (Valença municipality, under dead leaves, 2006; <http://allspira.com>); Conchology (Ilhéus municipality, under dead leaves in tropical rain forest; <https://www.conchology.be>); Forum Francophone des Coquillages Actuels (Pimenteira municipality, under dead leaves in tropical forest, vi/2012; <http://www.forumcoquillages.com/>)

**Remarks.** Even though Born (1778, 1780) noted the provenance of his specimen (Fig. 1A) as unknown ("patria ignota"), it was almost certainly collected in Brazil. Schileyko (2006), in fact, gave Brazil ("Brasília")



**Figure 1.** Shells of *Polygyratia polygyrata*, showing the variation in conchological characters such as size, number of whorls and aperture shape, as well as colouration. Scale bar = 2 cm. **A.** Holotype, NHMW-MO-14371 (NHMW). **B.** AMNH 43887 (AMNH). **C.** AMNH 119005 (AMNH). **D.** SMF 26248 (SMF). **E.** Example of a weathered specimen, which acquires a washed-off ochre/brown colouration, MNZ M.233517 (MNZ). **F.** Possible holotype of *Polygyratia charybdis*, NHMD 615842 (NHMD).



**Figure 2.** Internal lamellae in the shell of *Polygyratia polygyrata*. **A.** Broken specimen showing the second set of internal lamellae, FMNH 40632 (FMNH). **B–F.** CT scan image showing the internal structures of an intact shell (MZSP 129318). **B.** Whole shell showing the two sets of internal lamellae. **C, D.** First set of internal lamellae. **E, F.** Second set of internal lamellae. Scale bar: 2 cm (**A, B**).

as the locality for Born's holotype. Given that the only confirmed locality in Brazil is Bahia state (which was a usual stop for shell collectors in the late 18<sup>th</sup> century), Born's specimen, in all likelihood, stems from there.

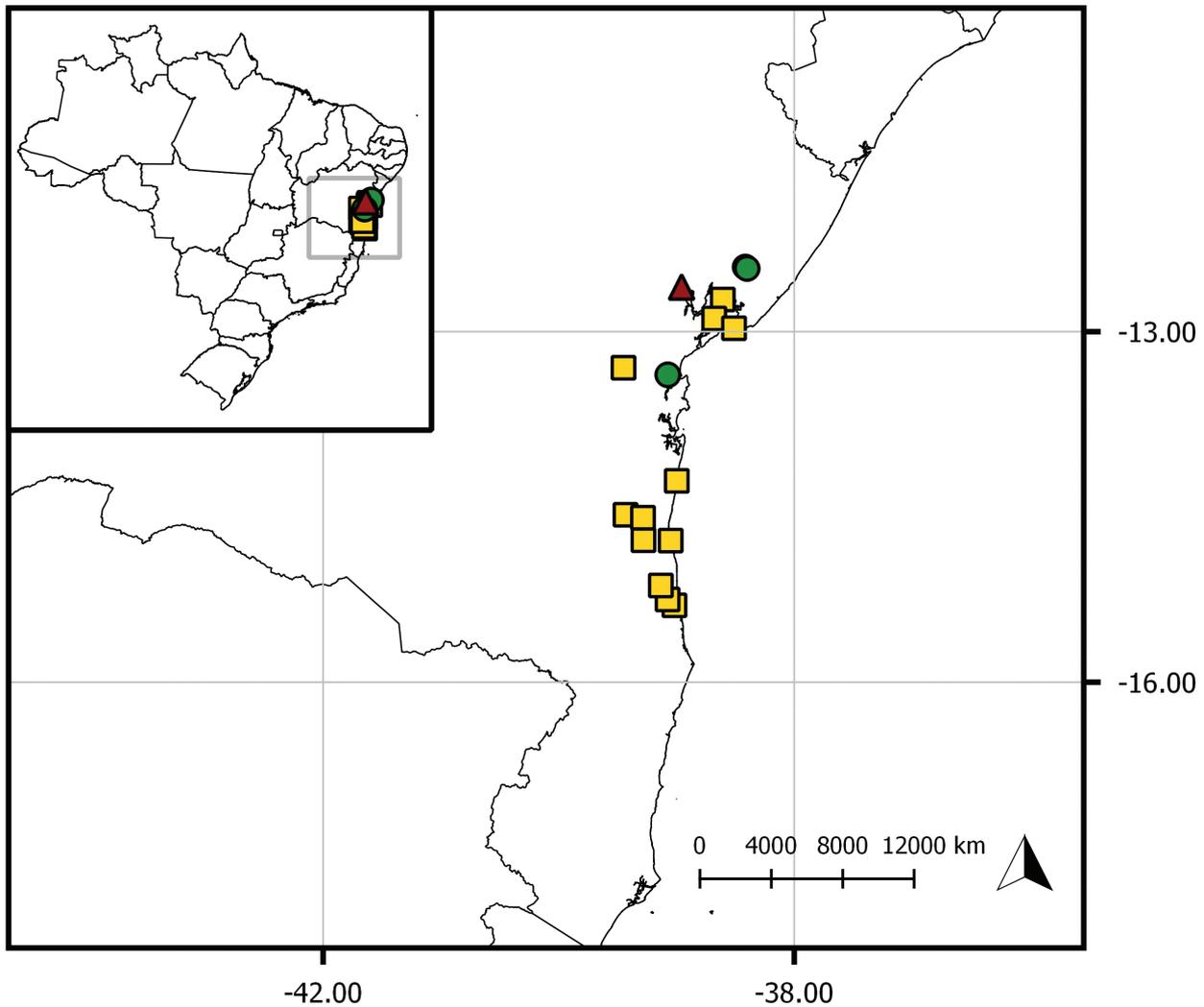
One of the localities of occurrence indicated by Simone (2006), the municipality of Central, is mistaken. It was based on the work of Lima and Oliveira (1992), who reported *P. polygyrata* from an archaeological setting in that municipality. Their identification is erroneous and their specimen (Lima and Oliveira 1992: fig. 4) actually belongs to *Systrophia (Entodina)* Ancy, 1887, given the shell size and parietal fold in the aperture.

The only locality indicated by a specimen outside Bahia state is Pará state, in northern Brazil (predominantly an Amazon Forest region), found on a specimen from a private shell collector (AMNH 119005; Fig. 1C). This specimen, despite having a slightly smaller size than average and a wider aperture, is overall indistinguishable from specimens from Bahia. Thus, this locality must be considered likely erroneous, as no other specimen from a trustworthy source is known from there.

*Polygyratia charybdis* was described by Mörch (1852) and has alternatively been considered in literature as a full species, a subspecies or a synonym of *P.*

*polygyrata*. Mörch's types are partially housed in the NHMUK and the NHMD (Dance 1966) and we could trace a possible holotype in the collection of the latter (NHMD 615842, Fig. 1F). The work of Mörch (1852) served as a catalogue of the collection of the Count of Yoldi for an auction. The possible holotype bears the typical label of Yoldi's collection (Tom Schiøtte, pers. comm.), including the species number in the catalogue (145). Furthermore, Mörch (1852) reported that his specimen measured 38 mm, which is perfectly in line with the specimen. As such, there is a good likelihood that this specimen is the holotype; however, it is not in pristine condition (Fig. 1F).

The original description (Mörch 1852), as well as later works that repeated it, listed very unspecific diagnostic characters: a more flat and concave shell, broader whorls, a narrower and deeper umbilicus and a smaller diameter (38 mm). The type locality is simply "Brazil" and there is no indication of other places (Mörch 1852). Albers (1860) indicated Bolivia as a second locality of occurrence; whether this was a misunderstanding on his part or an error based on specimens he misidentified, remains unknown. In any event, the erroneous locality "Bolivia" has been con-



**Figure 3.** Map of Bahia state showing the known distribution of *Polygyratia polygyrata*. Squares: museum specimens. Circles: online records. Triangle: literature data.

sistently reproduced in literature ever since (e.g. Simone 2006). Even so, there are no known specimens from that country and this locality must be considered erroneously listed.

The possible holotype (Fig. 1F) and a few other specimens (e.g. AMNH 119005, Fig. 1C) are indeed smaller and present features that could be interpreted as diagnostic of *P. charybdis*, such as a deeper umbilicus. Nevertheless, when all the specimens are taken together (Fig. 1), it is clear that these “diagnostic” features are just artefacts of morphological constraints due to the specimens being slightly smaller than the species’ mean diameter. That is, by reaching adulthood with a smaller size (and consequently fewer whorls), some specimens inevitably end up displaying a narrower and deeper umbilicus. Here, we consider this is simple morphological variability of the species and treat *P. charybdis* as a synonym of *P. polygyrata*.

## Discussion

*Polygyratia* has always been classified in Helicoidea, albeit in diverse families, which mostly reflected the changing classification schemes of the Latin American helicooid lineages. Historically, it was classified in: Pleurodontidae (Thiele 1931; Morretes 1949; Schileyko 2006; Breure and Araujo 2017), Camaenidae (Zilch 1960; Nordsieck 1986; Salgado and Coelho 2003; Schileyko 2016) and Solaropsidae (Parkinson et al. 1987; Simone 2006; Sei et al. 2017; MolluscaBase 2018; Salvador 2019).

The most recent works place the genus in Solaropsidae which, for a long time, was deemed a part of Helicoidea. It is now, however, considered to belong in Sagdoidea (Bouchet et al. 2017), but the affinities of the Latin-American helicooids *lato sensu* are generally poorly resolved. Nordsieck (1986) included *Polygyratia* in his new subfamily Solaropsinae, but remarked that it could be more closely related to other groups, due to its distinctive shell characters.

Despite our best efforts, we could not acquire specimens of *Polygyratia* suitable for molecular analysis. However, the unique shell morphology and conchological features are enough to sustain a revision of the historical classification and present a new family allocation for *Polygyratia*: the Scolodontidae.

*Polygyratia*, by conchological features alone (typically planispiral and multi-whorled shell; Fig. 1), seems to be closely related to *Systrophia* L. Pfeiffer, 1855. It should remain a distinct genus, though, given its much larger size (at least twice the size of typical *Systrophia* spp.), body whorl profile with three angulations, presence of internal lamellae and disjunct distribution. Presently, *Systrophia* spp. can be found in the Amazonian region in Brazil and neighbouring countries (Simone 2006).

Most Scolodontidae do not have teeth or lamellae, except for *Entodina* Ancey, 1887, which is often considered a synonym or subgenus of *Systrophia* (Ramírez et al. 2012) and *Patagocharopa* Miquel & Rodríguez, 2015, a possible scolodontid from the Miocene of Argentina (presently classified in Charopidae; Salvador et al. 2018). However, these cases consist solely in apertural barriers, not internal lamellae. Nevertheless, shells of the monotypic genus *Ridleya* Ancey, 1901, recently transferred to Scolodontidae (Salvador 2019), have two continuous parietal lamellae that run from the first whorls until the aperture and two short basal/palatal lamellae that might or not be visible from the aperture. This latter form of lamella is very reminiscent of those observed in *Polygyratia* (Fig. 2).

There is scarce information in literature regarding internal lamellae in other scolodontids (e.g. Zilch 1960; Schileyko 2000; Hausdorf 2006), but it is unclear if other species do not have them or have never been searched for it. For instance, Pilsbry (1894) reported that *Systrophia* lack internal lamella, but Gude (1920) mentioned at least one *Entodina* species where they are present. Even for *Polygyratia polygyrata*, very few authors recognised the existence of the internal lamellae (Moricand 1846; Pilsbry 1894; Gude 1920).

Curiously, Pilsbry (1894) had already placed *Polygyratia* closely related to scolodontids; in fact, he listed both *Systrophia* and *Entodina* as sections of the subgenus *Polygyratia* (*Polygyratia*). Why his work has been summarily ignored by later authors (exceptions are Gude 1920 and Richardson 1985) remains a mystery, but the fact that, back then, the family was simply “Helicidae” might have played a role in this (he indicated the subfamily as Polygyrinae, though). In any event, as outlined above, *Polygyratia* should be classified as a separate genus. Pilsbry (1894) also tentatively included *Coxia* Ancey, 1887 as a subgenus of *Polygyratia*, but the similarities are only superficial; presently *Coxia* is classified in Trochomorphidae (MolluscaBase 2019b).

More certainty in the present classification of *Polygyratia* in Scolodontidae can only be achieved once fresh specimens are collected for molecular studies. Unfortunately, there is no information to be gleaned from the fossil record, as there are no known scolodontid fossils or “helicoïd” forms similar to *Polygyratia* (Salvador et al. 2018).

One meaningful implication of the proposed new classification is that scolodontids are generally supposed to be carnivores (but their biology remains largely unknown; Barker and Efford 2004). *Polygyratia polygyrata* would thus be one of the country’s largest predatory snails. However, due to morphological features of buccal mass and radula of some species, it is thought that many scolodontids species might be only facultative carnivores or even completely herbivores or detritivores (Barker and Efford 2004).

There is an interesting piece of information in literature (Hupé 1857) about the habits of *Polygyratia polygyrata*, stating that the species can be usually found partially immersed in water. However, this has never been supported by later observations. In fact, the collection localities of some specimens (e.g. leaf litter) and iNaturalist occurrences point towards a typical terrestrial habit.

## Excluded taxa

Pilsbry (1894) listed two additional species in *Polygyratia*, namely *Ridleya quinquelirata* (Smith, 1890) and *Helix pollodonta* d’Orbigny, 1835. The former is a Scolodontidae from the Fernando de Noronha archipelago in NE Brazil (Salvador 2019). It has long been considered a separate genus, a position we maintain here based on its minute size, raised spire and presence of two continuous parietal lamellae, as well as two short basal/palatal lamellae. The latter, from Bolivia, has scarce entries in literature ever since that time. By d’Orbigny’s description and illustrations (d’Orbigny 1835, 1847), it appears to belong to *Entodina*, due to its small size, apertural fold and teleoconch sculpture (axial ribs). As such, herein we tentatively classify it as *Systrophia* (*Entodina*) *pollodonta* (d’Orbigny, 1835).

Breure and Araujo (2017) recently listed two other species in *Polygyratia*, namely *P. heligmoida* (d’Orbigny, 1835) and *P. reyrei* (Souverbie, 1858), both from Ecuador and originally classified in *Helix* Linnaeus, 1758. The former species (Breure and Araujo 2017: figs 47G–I) is indeed reminiscent of *Polygyratia*, as some *Systrophia* spp. are (see above), due to the flattened shell profile and large number of whorls. However, the shape of the body whorl (with a larger abapical region), the small shell size and the presence of a parietal fold and palatal tooth are more in line with *Systrophia*. The same is valid for the latter species (Breure and Araujo 2017: figs 47J–L), which in addition, has fewer whorls and a strong axil ribbing pattern, reminiscent of *Systrophia* (*Entodina*) spp. Therefore, we propose here that these two species should be excluded from *Polygyratia* and classified as *Systrophia* (*Systrophia*) *heligmoida* (d’Orbigny, 1835) and *Systrophia* (*Entodina*) *reyrei* (Souverbie, 1858). We also take the opportunity to report here the first occurrence in Brazil of *S. (S.) heligmoida*, based on a single museum specimen (NHMUK unnumbered, ex J.E. Cooper colln. 2150). It was collected prior to 1950 and does not have a precise locality other than “Brazil”. In any event, it is the first specimen of this species referred to the country.

## Acknowledgements

We are very thankful to the following people for sending information and photographs about the specimens or for granting access to the collections under their care: Lily Berniker (AMNH); Paul Callomon (ANSP); Jochen Gerber (FMNH); Ana-Maria Păpureanu (MNB); Rafael Araujo (MNCN); Luiz R.L. Simone (MZSP); Tom Schiøtte (NHMD); Jon Ablett (NHMUK); Anita Eschner (NHMW); Sigrid Hof (SMF); André Reimann and Katrin Schniebs (SNSD); Ellen Strong (USNM). We are also grateful to Barbara M. Tomotani (MNZ) for the help with molecular work; to Julia Kasper (MNZ) for the discussion regarding the species' German name; to Steve Thurston (AMNH), Jean-Claude Stahl (MNZ), P.G. Albano (NHMW), T. Schiøtte, J. Gerber and S. Hof for photos of the specimens from their institutions and permission to use them here; to Bram Breure and Robert Forsyth for the helpful revision of our manuscript; to iNaturalist for providing and maintaining a fine global natural history platform; and to Biodiversity Heritage Library (BHL) for making original literature freely available online. RBS received support from the SYNTHESYS Project (project grant GB-TAF-6613, European Community Research Infrastructure Action, FP7 Integrating Activities Programme), the Malacological Society of London (Early Career Research Grant) and the Bruce Fraser Hazelwood Fund (MNZ). DCC acknowledges the support of Centro para Documentação da Biodiversidade (FFCLRP).

## References

- Abbot RT (1989) Compendium of Landshells. A Color Guide to More than 2,000 of the World's Terrestrial Shells. American Malacologists, Melbourne.
- Albers JC (1850) Die Heliceen nach natürlicher Verwandtschaft systematisch geordnet. Enslin, Berlin. <https://doi.org/10.5962/bhl.title.11507>
- Albers JC (1860) Die Heliceen. Wilhelm Engelmann, Leipzig.
- Barker GM, Efford MG (2004) Predatory gastropods as natural enemies of terrestrial gastropods and other invertebrates. In: Barker GM (Ed.) Natural Enemies of Terrestrial Molluscs. CABI, Wallingford: 279–403. <https://doi.org/10.1079/9780851993195.0279>
- Beck HH (1837) Index Molluscorum praesentis aevi Musei Principis Augustissimi Christiani Frederici. Fasciculus primus et secundus. Mollusca Gastracopoda Pulmonata. H. Beck, Copenhagen. <https://doi.org/10.5962/bhl.title.77331>
- Born Iv (1778) Index rerum naturalium Musei Caesarei Vindobonensis. Pars I, Testacea. Verzeichniss der Natürlichen Seltenheiten des K.K. Naturalien Kabinets zu Wien. Erster Theil, Schalthiere. Officina Krausiana, Vienna. <https://doi.org/10.5962/bhl.title.11581>
- Born Iv (1780) Testacea Musei Caesarei Vindobonensis. Sumptibus Joannis Pauli Kraus, Vienna. <https://doi.org/10.5962/bhl.title.152209>
- Bouchet P, Rocroi J-P, Hausdorf B, Kaim A, Kano Y, Nützel A, Parkhaev P, Schrödl M, Strong EE (2017) Revised classification, nomenclator and typification of gastropod and monoplacophoran families. Malacologia 61: 1–526. <https://doi.org/10.4002/040.061.0201>
- Brauer F (1878) Bemerkungen über die im kaiserlich zoologischen Museum aufgefundenen Original-Exemplare zu Ign. v. Born's Testaceis Musei Caesarei Vindobonensis. Sitzungsberichte der Kaiserlichen Akademie der Wissenschaften, Mathematisch-Naturwissenschaftliche Classe 77: 117–192.
- Breure ASH, Araujo R (2017) The Neotropical land snails (Mollusca, Gastropoda) collected by the 'Comisión Científica del Pacífico'. PeerJ 5: e3065. <https://doi.org/10.7717/peerj.3065>
- Chemnitz JH (1786) Neues systematisches Conchylien-Cabinet. Neuntzen Banbes erste Abtheilung. G.N. Raspe, Nuremberg. <https://doi.org/10.5962/bhl.title.123898>
- Coan EV, Kabat AR (2018) 2,400 Years of Malacology, 15<sup>th</sup> ed. American Malacological Society, USA.
- Dance SP (1966) Shell Collecting: An Illustrated History. University of California Press, Berkeley.
- Dillwyn LW (1817) A Descriptive Catalogue of Recent Shells. Volume 2. J. & A. Arch, London.
- Férussac AEJPFd'A (1819) Histoire Naturelle Générale et Particulière des Mollusques Terrestres et Fluviales tant des Espèces que l'on Trouve Aujourd'hui Vivantes, que des Dépouilles Fossiles ce Celles qui N'existent Plus; Classés d'après les Caractères Essentiels que Présentent ces Animaux et Leurs Coquilles. Tome Premier. Chez J.-B. Beillière, Paris. <https://doi.org/10.5962/bhl.title.132272>
- Férussac AEJPFd'A (1821) Tableaux Systematiques des Animaux Mollusques Classés en Familles Naturelles, dans Lesquels on a Établi la Concordance de Tous les Systèmes; Suivis d'un Prodrome Général po Tous les Mollusques Terrestres ou Fluviales, Vivants ou Fossiles. Arthur Bertrand, Paris.
- Gmelin JF (1788) Systema naturae per regna tria naturae: secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Editio decima tertia, acuta, reformata. Tom. 1. Pars 6. G.E. Beer, Leipzig.
- Gray JE (1847) A list of the genera of recent Mollusca, their synonymy and types. Proceedings of the Zoological Society of London 15: 129–219.
- Gude GK (1920) The armature of land Mollusca. Proceeding of the Malacological Society of London 14: 52–73.
- Hausdorf B (2006) The systematic position of *Scolodonta* Döring, 1875 and Scolodontidae H. B. Baker, 1925 (Gastropoda: Pulmonata). Zoologischer Anzeiger 245: 161–165. <https://doi.org/10.1016/j.jcz.2006.05.007>
- Hidalgo JG (1870) Catalogue des coquilles terrestres recueillies par les naturalistes de la commission scientifique espagnole sur divers points de l'Amérique méridionale. Journal de Conchyliologie 18: 27–70.
- Hidalgo JG (1893) Catálogo de las conchas terrestres recogidas por los naturalistas de la comisión científica española en diversos puntos de la América meridional. In: Hidalgo JG (Ed.) Obras Malacológicas. Parte III, Descripción de los moluscos recogidos por la comisión científica enviada por el Gobierno Español á la América Meridional. Aguado, Madrid: 75–134.
- Hupé MH (1857) Mollusques. In: Castelnau F (Ed.) Animaux nouveaux ou rares recueillis pedant l'expédition dans les parties centrales de l'Amérique du Sud, de Rio de Janeiro a Lima, et de Lima au Para. P. Bertrand, Paris: 1–96. <https://doi.org/10.5962/bhl.title.10268>
- Lamarck JBPA (1838) Histoire naturelle des animaux sans vertèbres: présentant les caractères généraux et particuliers de ces animaux, leur distribution, leurs classes, leurs familles, leurs genres, et la cita-

- tion des principales espèces qui s'y rapportent: précédée d'une introduction offrant la détermination des caractères essentiels de l'animal, sa distinction du végétal et des autres corps naturels, enfin, l'exposition des principes fondamentaux de la zoologie. Tome huitième. J.B. Baillière, Paris. <https://doi.org/10.5962/bhl.title.46287>
- Lima LC, Oliveira MP (1992) Pleistocene gastropods from Toca da Esperança, Municipality of Central, State of Bahia, Brazil. *Memórias do Instituto Oswaldo Cruz* 87(3): 423–427. <https://doi.org/10.1590/S0074-02761992000300013>
- MolluscaBase (2018) *Polygyratia* Gray, 1847. <http://molluscabase.org/aphia.php?p=taxdetails&id=996655> on 2019-05-08
- MolluscaBase (2019a) *Polygyratia polygyrata* (Born, 1778). <http://www.molluscabase.org/aphia.php?p=taxdetails&id=1320928> [Accessed on 2019-05-08]
- MolluscaBase (2019b) MolluscaBase. *Coxia* Ancey, 1887. <http://www.molluscabase.org/aphia.php?p=taxdetails&id=995238> [Accessed on 2019-05-28]
- Mörch OAL (1852) *Catalogus Conchyliorum quae Reliquit D. Alphonso d'Aguirra & Gadea, Comes de Yoldi, Regisdaniae Cubiculariorum Princeps, Ordinis Dannebrogici in Prima Classe & Ordinis Caroli Terth Eques. L. Kleini, Copenhagen.* <https://doi.org/10.5962/bhl.title.11189>
- Moricand S (1836) Mémoire sur les coquilles terrestres et fluviatiles, envoyées de Bahia par M. J. Blanchet. *Memoires de la Société de physique et d'histoire naturelle de Genève* 7(2): 415–446. <https://doi.org/10.5962/bhl.title.49510>
- Moricand S (1846) Troisième supplément au mémoire sur les coquilles terrestres et fluviatiles de la province de Bahia, envoyées par M. Blanchet. *Memoires de la Société de physique et d'histoire naturelle de Genève* 11: 147–160.
- Morretes FL (1949) Ensaio de Catálogo dos Moluscos do Brasil. *Arquivos do Museu Paranaense* 7: 5–216.
- Nordsieck H (1986) The system of the Stylommatophora (Gastropoda), with special regard to the systematic position of the Clausiliidae, II. Importance of the shell and distribution. *Archiv für Molluskenkunde* 117: 93–116.
- d'Orbigny A (1835) Synopsis terrestrium et fluviatilium molluscorum, in suo per American Meridionalem itinerere. *Magasin de Zoologie* 5(6): 1–44.
- d'Orbigny A (1847) Voyage dans l'Amérique Méridionale (Le Bresil, la République Orientale de l'Uruguay, la République Argentine, la Patagonie, la République du Chili, la République de Bolivie, la République du Pérou), Exécuté Pendant les Années 1826, 1827, 1828, 1829, 1830, 1831, 1832 et 1833. P. Bertrand, Paris.
- d'Orbigny CD (1849) Dictionnaire Universel d'Histoire Naturelle. Atlas. Tome 3. M.M. Renard, Paris. <https://doi.org/10.5962/bhl.title.100771>
- Parkinson B, Hemmen J, Groh K (1987) Tropical Land Shells of the World. Christa Hemmen, Wiesbaden.
- Pfeiffer L (1848) *Monographia Heliceorum Viventium. Volumen primum.* F.A. Brockhaus. Leipzig.
- Pilsbry HA (1894) *Manual of Conchology. Second Series: Pulmonata. Volume 9: Helicidae, Vol. 7.* Academy of Natural Sciences of Philadelphia, Philadelphia.
- Ramírez R, Borda V, Romero P, Ramirez J, Congrains C, Chirinos J, Ramírez P, Velásquez LE, Mejía K (2012) Biodiversidad y endemismo de los caracoles terrestres *Megalobulimus* y *Systrophia* en la Amazonia occidental. *Revista Peruana de Biología* 19: 59–74. <https://doi.org/10.15381/rpb.v19i1.798>
- Reeve LA (1854) Monograph of the genus *Helix*. *Conchologia Iconica* 7: 1–210.
- Röding PF (1798) *Museum Boltenianum sive Catalogus cimeliorum e tribus regnis naturae quae olim collegerat Joa. Fried. Bolten M. D. p. d. Pars Secunda continens Conchylia sive Testacea univalvia, bivalvia et multivalvia.* Johan Christi Trappii, Hamburg.
- Richardson L (1985) Camaenidae: Catalogue of Species. *Tryonia* 12: 1–479.
- Salgado NC, Coelho ACS (2003) Moluscos terrestres do Brasil (gastropodes operculados ou não, exclusive Veronicellidae, Miladidae e Limacidae). *Revista de Biología Tropical* 51(suppl. 3): 149–189.
- Salvador RB (2019) Brazilian, Uruguayan and Argentinian terrestrial gastropods in the collection of the Museum of New Zealand Te Papa Tongarewa. *Tuhinga* 30: 82–98.
- Salvador RB, Cabrera F, Martínez S, Miquel SE, Simone LRL, Cunha CM (2018) Annotated catalogue of the fossil Hygrophila and Eupulmonata (Mollusca: Gastropoda) from South America (Cretaceous – Neogene). *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* 289(3): 249–280. <https://doi.org/10.1127/njgpa/2018/0760>
- Sei M, Robinson DG, Geneva AJ, Rosenberg G (2017) Doubled helix: Sagdoidea is the overlooked sister group of Helicoidea (Mollusca: Gastropoda: Pulmonata). *Biological Journal of the Linnean Society* 122(4): 697–728. <https://doi.org/10.1093/biolinnean/blx082>
- Schileyko AA (2000) *Treatise on recent terrestrial pulmonate molluscs. Part 6. Rhytididae, Chlamydephoridae, Systrophiiidae, Haplotrematidae, Streptaxidae, Spiraxidae, Oleacinidae, Testacellidae.* *Ruthenica, Supplement 2*: 731–880.
- Schileyko AA (2006) *Treatise on recent terrestrial pulmonate molluscs. Part 13. Helicidae, Pleurodontidae, Polygyridae, Ammonitellidae, Oreohelicidae, Thysanophoridae.* *Ruthenica, Supplement 2*: 1765–1906.
- Schileyko AA (2016) Functional interrelations between conchological and anatomical characters in Stylommatophora (Mollusca, Gastropoda). *Archives of Zoological Museum of Lomonosov Moscow State University* 54: 269–297.
- Schröter JS (1784) *Einleitung in die Conchylienkenntniss nach Linné. Zweiter Band.* B.J. Gebauer, Halle.
- Simone LRL (2006) *Land and Freshwater Mollusks of Brazil.* EGB/FAPESP, São Paulo.
- Thiele J (1931) *Handbuch der systematischen Weichtierkunde. Erster Band, Teil 2.* Gustav Fisher Verlag, Jena.
- Tryon GW (1887) *Manual of Conchology; Structural and Systematic, with illustrations of the species. Second series: Pulmonata. Vol. 3. Helicidae: Vol. 1.* G.W. Tryon, Philadelphia.
- Wilhelm GT (1802) *Unterhaltungen aus der Naturgeschichte. Der Würmer, zweyter Theil.* Augsburg: Engelbrechtischen Kunsthandlung. <https://doi.org/10.5962/bhl.title.79363>
- Zilch A (1959–1960) Euthyneura. In: Wenz W (Ed.) *Handbuch der Paläozoologie* 6(2). Gebrüder Borntraeger, Berlin: 1–835.

---

## Supplementary material 1

### **Internal shell structures of *Polygyratia polygyrata* (Born, 1778)**

Authors: Rodrigo Brincalepe Salvador, Daniel Caracanhas Cavallari

Data type: image

Explanation note: CT scan animation showing the internal lamellae in the shell of *P. polygyrata* (Born, 1778).

Copyright notice: This dataset is made available under the Open Database License (<http://opendatacommons.org/licenses/odbl/1.0/>). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Link: <https://doi.org/10.3897/zse.96.51047.suppl1>

---