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

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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 19th 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.Mo- lusc 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 Zoölogisch 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; Gade 1920: 59; Thiele 1931: 679; Morrison 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

Helis Polygyrata Born, 1778: 382; Wilhelm 1802: 356.

Helis 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 1830: 48; Moricand 1846: 151, pl. 5, figs 1–3; Pfeiffer 1848: 405; Mörch 1852: 6; Thiele 1931: 679; Albers 1850: 91; Albers 1860: 94.

Ophiogyra 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.
Polygyratia charybdis Möch, 1852: 7.
Polygyratia (detrita.): Möch 1852: 7.
Helix charybdis: Möch 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 polygyrata [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, 1780); “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 (1899) 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 Abbot’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, Urucuca, 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 ⅓ and ⅔ 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 2½–2½ whors, 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); spine top (protoconch and first whors); 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 ± 0.9 mm (max 14.1, min 10.7); D = 43.5 ± 3.7 mm (max 56.7, min 38.2); W = 8¾ ± ⅓ (max 9½, 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.); FMNH 57464 (2 sh, pre-1954, ex O. Park colln.); FMNH 62570 (1 sh, pre-1956, ex E.E. Hand colln.); FMNH 75810 (1 sh, pre-1951, ex N. Zetek colln.); FMNH 100081 (1 sh, pre-1877, ex F. Button colln.); FMNH 537462 (1 sh, ex CMNH colln., 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.
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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 (“Brasilia”)
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).
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 18th 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) Ancey, 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. polygarata*. 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-
sistantly 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 helicoid 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 helicoids *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.

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**Figure 3.** Map of Bahia state showing the known distribution of *Polygyratia polygyrata*. Squares: museum specimens. Circles: online records. Triangle: literature data.
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 Ancy, 1887, which is often considered a synonym or subgenus of Systrophia (Ramirez et al. 2012) and Patagocharopa Miquel & Rodriguez, 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 Ancy, 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, Pilbsry (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. Pilbsry (1894) also tentatively included Coxia Ancy, 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 “helioid” 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 radius of some species, it is thought that many scolodontids 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 naturalist occurrences point towards a typical terrestrial habit.

Excluded taxa

Pilsbry (1894) listed two additional species in Polygyratia, namely Ridleya quinquivelirata (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. reyniei (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) reyniei (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.
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tion des principales espèces qui s’y rapportent: précédée d’une intro-
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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).

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