

**Revision of the genera of Scolodontidae, part 3:
Entodina Ancey, 1887, *Keranella* gen. nov., *Martinella* Jousseaume, 1887,
 †*Patagocharopa* Miquel & P.E. Rodriguez, 2016, *Polygyratia* Gray, 1847,
Ridleyconcha Christensen, 2020, *Smenodonta* gen. nov.,
Systrophia L. Pfeiffer, 1855, and *Zilchistrophia* Weyrauch, 1960**

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Abstract. With this study, we continue the revision of the genera of Scolodontidae (Gastropoda: Stylommatophora), focusing on the taxa with tightly coiled, multiwhorled shells that often bear apertural and/or internal barriers. We analysed type material from all type species and studied some misclassified Charopidae and Streptaxidae. We provide redescrptions and better circumscription of the following Scolodontid taxa: *Entodina* Ancey, 1887, *Systrophia* L. Pfeiffer, 1855, and *Zilchistrophia* Weyrauch, 1960. *Martinella* Jousseaume, 1887 is transferred from Streptaxidae to Scolodontidae, and the extinct *Patagocharopa* Miquel & P.E. Rodriguez, 2016 is transferred from Charopidae; *Patagocharopa*, dating from the Miocene, represents the earliest fossil record of the family. *Keranella* gen. nov. and *Smenodonta* gen. nov. are erected. The genera *Polygyratia* J.E. Gray, 1847 and *Ridleyconcha* Christensen, 2020, despite recently revised, are also included here for comparison with the other taxa.

Key words. Land snails, Neotropics, Scolodontina, taxonomy, type specimens, *Keranella* gen. nov., *Smenodonta* gen. nov.

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INTRODUCTION

Scolodontidae (previously Systrophiiidae) is a family of stylommatophorans with a complicated taxonomic history, with some genera-level taxa having had more issues than others. This was especially the case with *Happia* Bourguignat, 1890 and related genera, which was the topic of our first in a series of papers on the genera of Scolodontidae (Roosen & Breure 2024a). In this third paper in the series, we continue the revision of scolodontid genera, addressing additional taxa.

Among the Scolodontidae (and Streptaxidae, which include some misplaced species from South America) there are several genera characterised by slowly enlarging

whorls, which results in a tightly coiled, multiwhorled shell when in apical view. The most well-known genera, with the largest known distribution of this group are *Systrophia* L. Pfeiffer, 1855 and *Zilchistrophia* Weyrauch, 1960 (e.g. Gray 1847; Pfeiffer 1855; Weyrauch 1960; Páll-Gergely & Asami 2014), but *Polygyratia* J.E. Gray, 1847 and *Ridleyconcha* Christensen, 2020 has recently received the most attention (Salvador 2019, 2021; Christensen 2020; Salvador & Cavallari 2020). *Polygyratia* and *Ridleyconcha* were only recently moved to the Scolodontidae based on a DNA analysis and conchological characteristics, and nomenclatural issues surrounding those two genera were resolved (Salvador 2019, 2021; Christensen 2020; Salvador & Cavallari 2020).

Systrophia and *Zilchistrophia* were also discussed in recent papers (Miquel 2020; Páll-Gergely & Asami 2015; Ramírez *et al.* 2012; Romero 2010), but a thorough revision has not been made. The absence of the type species *Systrophia systropha* (Albers, 1854) in those and most other studies is notable and can affect taxonomic conclusions on the genera. To stabilise *Systrophia* and accept *Entodina* Ancey, 1887 as a separate valid genus, as suggested by Simone (2006), Salvador (2021), and Roosen & Breure (2024b), the type species must be redescribed. The type species of *Zilchistrophia* is more well-known and was figured and described by Weyrauch (1960) and Páll-Gergely & Asami (2014).

To provide as complete an overview of the Scolodontidae as possible, we also examined morphologically similar genera and species from South America that are currently classified in other families. The first of those is *Martinella* Jousseaume, 1887, presently included in Streptaxidae though without clear arguments for being so (Thiele 1927; Richardson 1988; Simone 2006; Breure *et al.* 2022; Brown 2023). The genus was described to contain only *Martinella martinella* Jousseaume, 1887, a species that (at the time of description) was rather common in the Ecuadorian Andes, but which is currently possibly extinct (Jousseaume 1887; Breure *et al.* 2022). Only one other *Martinella* species has been described, *M. prisca* Thiele, 1927, but its generic identity is highly doubtful based on its type locality in southernmost Brazil and its shell's larger size, axial sculpture, and palatal plicae (Thiele 1927).

The second genus is *Patagocharopa* Miquel & P.E. Rodriguez, 2016, an extinct monotypic genus currently known only from the Miocene of Argentina. Its shell has apertural barriers and internal lamellae that are reminiscent of the internal structures known from *Entodina*, *Zilchistrophia*, *Ridleyconcha*, and *Polygyratia*.

In this study, we redescribe the type material of the type species of *Zilchistrophia*, *Entodina*, and *Systrophia* to facilitate further use of these genera. Some species are reclassified and presented here as new combinations. The conchological features and diagnoses of the genera are thoroughly discussed. *Ridleyconcha* and *Polygyratia* are also included here for completion, even though they have been recently revised, as they are potentially closely related to the former three genera. In addition, *Martinella* and *Patagocharopa* are redescribed and moved to the Scolodontidae. Lastly, we describe *Smenodonta* gen. nov. to allocate *Helix janeirensis* L. Pfeiffer, 1852 [= *Streptaxis crosseii* L. Pfeiffer, 1867], and *Keranella* gen. nov. to allocate *Helix cryptodon* S. Moricand, 1851 and *Martinella prisca* Thiele, 1927.

MATERIALS AND METHODS

We analysed the type material of all type species of the genera included here, as well as additional specimens when available. The specimens belong to the following natural history collections: MCZ—Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, USA; MHNbX—Muséum de sciences et nature, Bordeaux, France; MNHN—Musée National d'Histoire Naturelle, Paris, France; MHNG—Musée d'Histoire Naturelle, Geneva, Switzerland; MPM—Museo Regional Provincial “Padre Manuel Jesús Molina”, Río Gallegos, Santa Cruz Province, Argentina; NHMD—Natural History Museum, Copenhagen, Denmark; NHMUK—Natural History Museum, London, U.K.; NHMW—Naturhistorisches Museum, Wien, Austria; SMF—Senckenberg Naturmuseum, Frankfurt am Main, Germany; ZMB—Zoologisches Museum, Humboldt Universität, Berlin, Germany.

Shell height was measured parallel to columellar axis, and width is at the greatest dimension perpendicular to height.

SYSTEMATICS

Family Scolodontidae H.B. Baker, 1925

Genus *Entodina* Ancey, 1878

Type species. *Helix reyreii* Souverbie, 1858, by original designation.

Redescription. Shell small, strongly depressed conical-globular to discoid, with a depressed to slightly raised spire. Whorls increase slowly in size. Teleoconch sculpture consists of strong axial ribs, sometimes intersected by minute spiral striae. Final portion of the last whorl deflected, with a circular aperture with parietal fold. A palatal fold might also occur. At least some species have internal plicae at 1/6 whorl behind the aperture.

Species included. ?*Entodina alcidiana* (Ancey, 1892) **comb. nov.**, *E. cheilostrophia* (d'Orbigny, 1835), *E. derbyi* (Ihering, 1912), *E. gionensis* Lange de Morretes, 1940, *E. jekylli* F. Baker, 1914, *E. pollodonta* (d'Orbigny, 1835), and *E. reyreii* (Souverbie, 1858).

Comparisons. *Entodina* was often included as a subgenus of *Systrophia*. The latter is larger, has no barriers at 1/6 whorl behind the aperture, and has neither visible spiral sculpture nor axial ribbing. *Zilchistrophia* is also similar to *Entodina*, but *Zilchistrophia* only has plicae on the palatal wall, and there is no sculpture besides faint growth lines.

Geographic range. Ecuador, Brazil, Peru, Bolivia.

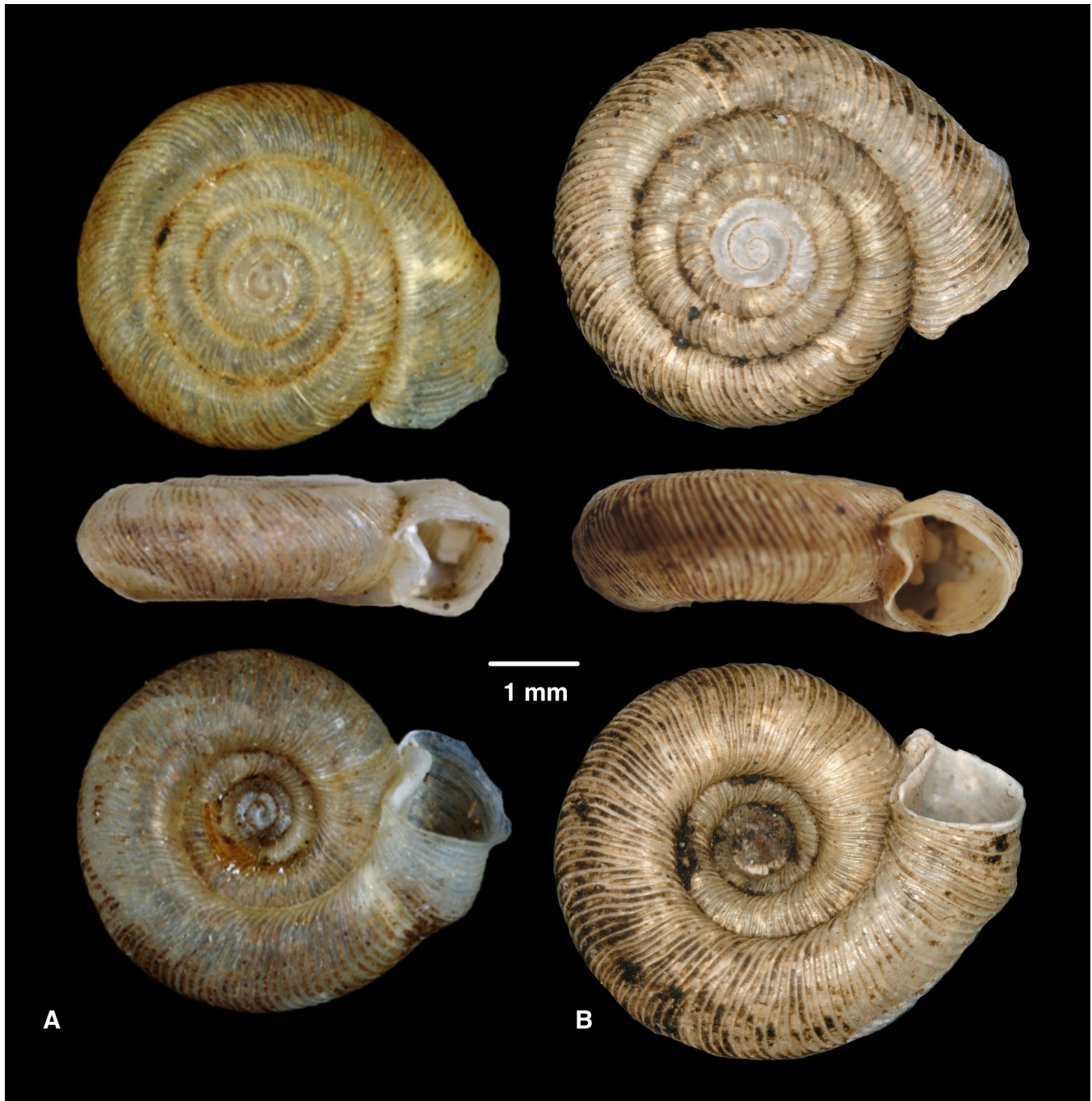


Figure 1. *Entodina reyrei* (Souverbie, 1858). **A**, MHNbX 2008.16975.3, syntype. **B**, MCZ 141466, syntype.

Remarks. In most recent literature *Entodina* was either synonymized with or regarded as a subgenus of *Systrophia* L. Pfeiffer, 1855 (e.g. Salvador & Cavallari 2020; Breure *et al.* 2022). However, sculpture consists only of growth lines in *Systrophia*, the whorl size increases more slowly during growth, and all species are much larger than *E. reyrei*. Although anatomical and genetic data of the type species are lacking, we regard these conchological characteristics as suf-

ficient to separate the two genera. This is supported by the findings of Salvador (2021), whose molecular analysis recovered *E. jekylli* as sister to *Ridleyconcha*, instead of *Systrophia*.

Breure & Araujo (2017) included species belonging to *Entodina* in *Polygyratia*, but this was reassessed and rejected by Salvador & Cavallari (2020) based on the much larger shell and presence of multiple sets of internal lamellae of *Polygyratia polygyrata* (Born, 1778). Roosen & Breure

(2024b) went further and implied that *Entodina* should be a separate genus. Our present assessment agrees with Salvador & Cavallari (2020) and Roosen & Breure (2024b).

Entodina reyrei (Souverbie, 1858)

Figure 1

Helix reyrei Souverbie 1858: 65–66.

Entodina reyrei—Ancey 1878: 64; Roosen & Breure 2024b: fig. 6–10.

Systrophia (Entodina) reyrei—Ramírez 1993: 51–52; Salvador *et al.* 2020: 98.

Type material. MHNbX 2008.16975 (syntypes 12 shells, dry); MCZ 141466 (syntypes, 2 shells, dry).

Type locality. Guayaquil, Ecuador.

Redescription. Shell small, discoid. First ½ whorl smooth, after that, small wrinkles form next to the suture which develop into numerous strong axial ribs after one whorl. Minute spiral striae develop after 1.5 whorls. Sculpture present on the entire teleoconch. Final section of the last whorl enlarged; aperture deflected, subcircular, with a small parietal fold. Five plicae are visible at 1/6 of a whorl from the aperture: two parietal plicae, two palatal plicae, and one basal plica.

Measurements. Shell height: 1.90 mm; width: 5.40 mm; whorls: 5½.

Geographic range. Ecuador: Guayas: Guayaquil (type locality); Pedro Carbo, between Guayaquil and Manta (Breure *et al.* 2022).

Comparisons. Most Brazilian and Bolivian species are larger, and they either lack plicae at 1/6 of a whorl back from the aperture or that character is unknown. It is possible that these species belong to a different genus, but this cannot be proven at this time.

Remarks. The literature is ambiguous about the presence of internal plicae in this species, and it is unclear in most cases whether the plicae are absent or whether the authors did not look for these structures. This is probably one of the main reasons why *Entodina* was often confused or conflated with other genera. Another factor might have been the difficulty in accessing the syntypes of the type species in the NHMBx (Souverbie 1858 only published an image of the shell in umbilical view, which is not sufficient).

Genus *Keranella* gen. nov.

ZooBank identifier. urn:lsid:zoobank.org:act:1D9C7532-D88D-4B22-8A16-262BE4C8660F

Type species. *Helix (Streptaxis) cryptodon* S. Moricand, 1851.

Etymology. The genus name honours Kerana, the mother of the seven legendary monsters of Tupi-Guarani mythology. Grammatical gender: feminine.

Species included. *Keranella cryptodon* (S. Moricand, 1851) **comb. nov.**, *K. prisca* (Thiele, 1927) **comb. nov.**

Description. Shell small, width ≤10 mm, lenticular, with a step-like spire. Whorls *c.* 5, tightly coiled, with an angulation forming a shoulder. Suture well marked. Protoconch *c.* 2½ whorls, smooth. Teleoconch in some species sculptured by strong, regularly spaced, prosocline ribs which extend from near the whorl angulation to the suture; faint ribbing may also be present immediately around the umbilicus. Peristome slightly thickened. Aperture narrow, rectangular. Aperture with elongate basal/palatal barrier; parietal tooth may be present. Umbilicus relatively wide, *c.* 20% of shell width, deep.

Comparisons. *Keranella* gen. nov. can be easily distinguished from other Scolodontidae by its unique aperture, which is rectangular and with a single, elongate basal/palatal apertural barrier. *Martinella* is smaller, has a more elongated D-shaped aperture, and lacks apertural barriers. *Smenodonta* gen. nov. is similar but has a higher spire and much more complex apertural barriers.

Geographic range. Brazil, Bahia to Rio Grande do Sul.

Remarks. This new genus contains species formerly assigned to Streptaxidae.

Keranella prisca (Thiele, 1927) **comb. nov.**

Figure 2

Martinella prisca Thiele 1927: 318, pl. 26, fig. 10—Lange de Morretes 1949: 165; Richardson 1988: 230; Salgado & Coelho 2003: 169; Simone 2006: 194, fig. 725; Brown 2023: 327, text fig.; Salvador *et al.* 2024: 152.

Type specimen. ZMB.Moll 109742 (holotype, 1 shell, dry).

Type locality. “Taguara del Mundo Novo [sic] (Rio Grande do Sul)”. Brazil, Rio Grande do Sul, Taquara municipality.

Redescription. Shell small, width *c.* 5 mm, lenticular, with a step-like spire. Whorls 5, tightly coiled, with an angulation forming a shoulder. Suture well marked. Protoconch 2½ whorls, smooth, with abrupt transition to teleoconch. Teleoconch sculptured by strong, regularly spaced, prosocline ribs that extend from the whorl angulation to the suture; faint ribbing present immediately around umbilicus. Aperture narrow, rectangular, with single basal/palatal barrier.

Measurements. Shell height: *c.* 3 mm; width: *c.* 5 mm; whorls: 5.

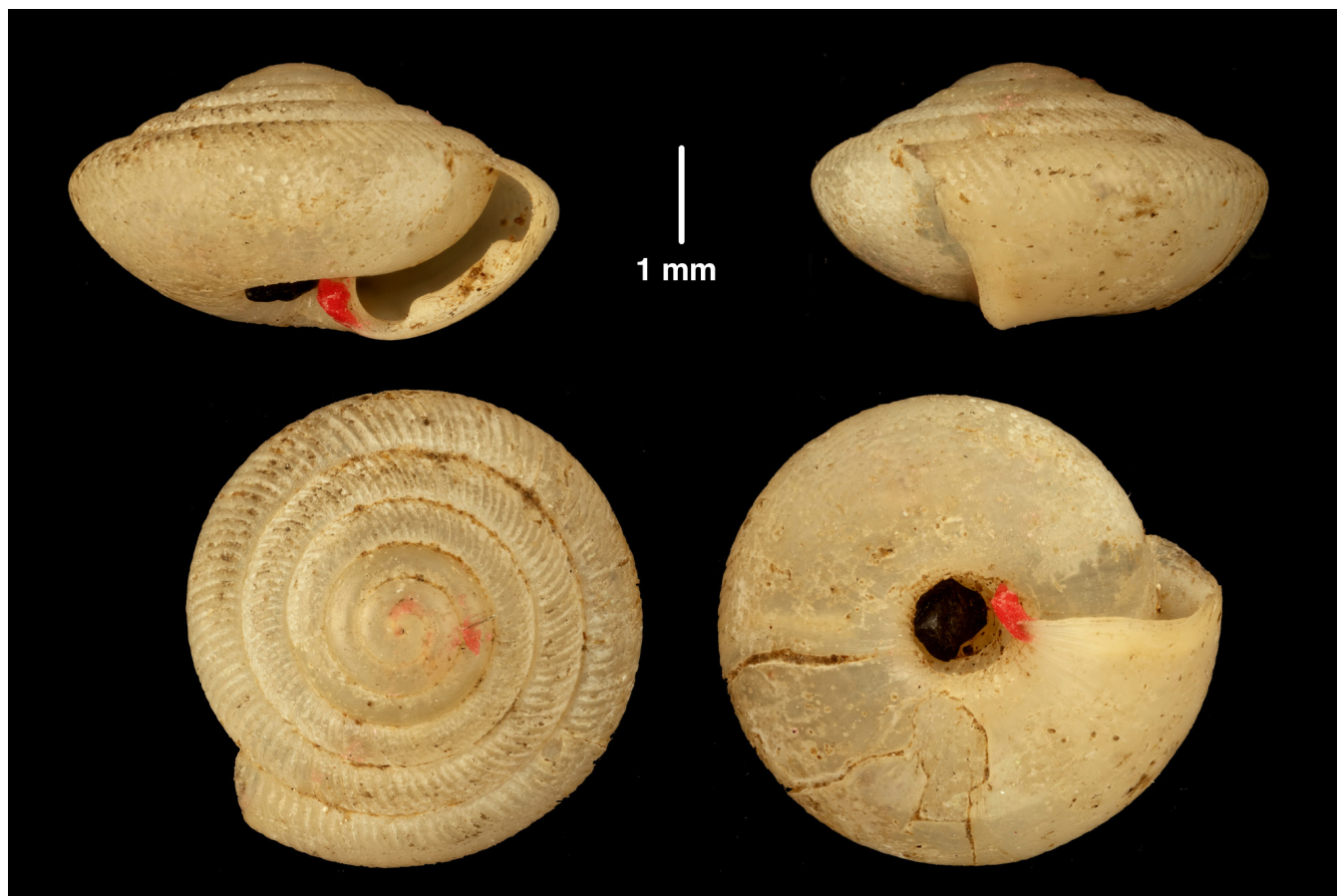


Figure 2. *Keranella prisca* (Thiele, 1927) comb. nov. ZMB.Moll 109742, holotype.

Comparisons. See *Keranella cryptodon*, the only similar species.

Geographic range. Brazil, restricted to Rio Grande do Sul state.

Remarks. It is uncertain whether the holotype and only known specimen represents an adult specimen or if it is immature, but it is likely an adult specimen based on the similarities to the type series of *K. cryptodon* comb. nov.

***Keranella cryptodon* (S. Moricand, 1851) comb. nov.**

Figure 3

Helix (*Streptaxis*) *cryptodon* S. Moricand 1851: 370, pl. 10, fig. 2a–d.

Streptaxis (*Discartemon*) *cryptodon*—Tryon 1885: 66, pl. 16 figs 87–89; Gude 1902: 226.

Streptartemon cryptodon—Richardson 1988: 246; Simone 2006: 196, fig. 731; Breure & Tardy 2016: 120, figs 80–82; Brown 2023: 340, text fig.; Salvador et al. 2024: 152.

Rectartemon cryptodon—Salgado & Coelho 2003: 170.

Type specimens. MHNG-INVE-68687 (syntypes, 5 shells, dry).

Type locality. “La province de Bahia”. Brazil, Bahia state.

Redescription. Shell small, width c. 5 mm, lenticular, with a step-like spire. Whorls 5–5¼, tightly coiled, with a rounded profile. Suture well marked. Protoconch 2–2½ whorls, smooth; transition to teleoconch without a well-marked change in sculpture. Teleoconch lacking sculpture; varix-like structures may be present on teleoconch at irregular intervals, indicating a temporary cessation of shell growth and thickening of peristome. Aperture narrow, rectangular, with two apertural barriers: one parietal tooth and one elongate basal/palatal barrier. Peristome slightly thickened.

Measurements. Shell height: c. 3 mm; width: c. 5 mm; whorls: 5¼.

Geographic range. Brazil, restricted to Bahia state.

Comparisons. *Keranella cryptodon* comb. nov. has a similar shell and a very similar pattern of apertural barriers to *K. prisca* comb. nov. Compared to *K. prisca*, the whorls of *K. cryptodon* are more rounded and lack both the shoulder angulation and teleoconch sculpture. Even so, the rectangular aperture shape and the long basal/palatal barrier is strik-

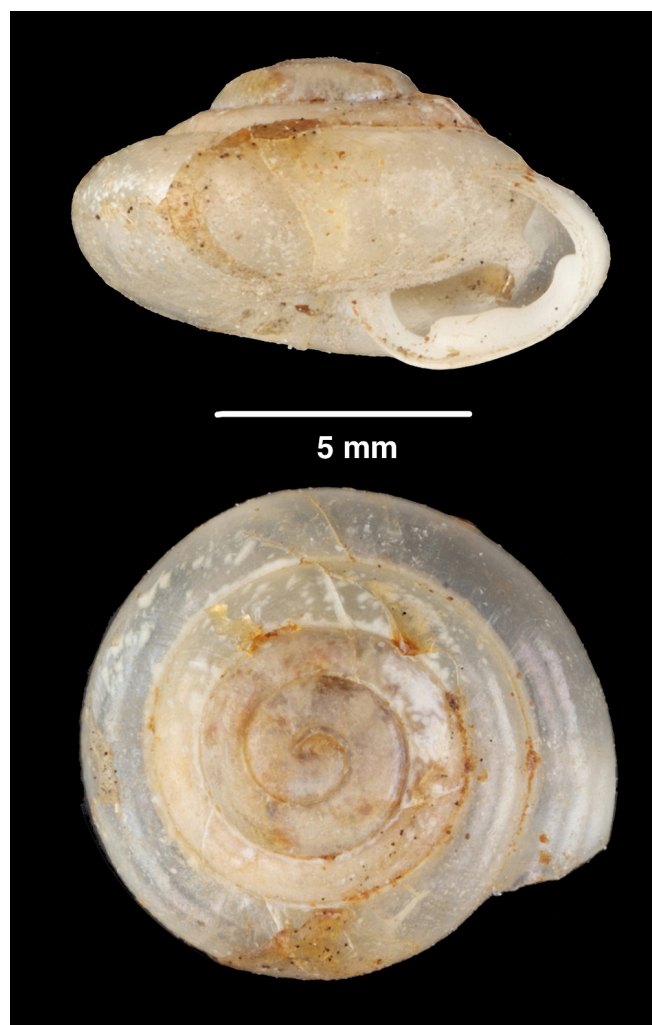


Figure 3. *Keranella cryptodon* (S. Moricand, 1851) comb. nov. MHNG-INVE-68687, syntype.

ingly similar. (*K. cryptodon* also has a parietal tooth that is absent in *K. prisca*.) Thus, while the overall shell morphology is rather distinct and the geographic occurrence reasonably distant, the striking similarity in apertural morphology led us to hypothesise a phylogenetic relationship between the two species and, consequently, we allocated both to the same genus.

Genus *Martinella* Jousseaume, 1887

Type species. *Martinella martinella* Jousseaume, 1887, by monotypy.

Redescription. Shell small, strongly depressed-conical-globular, whitish-transparent, with up to $7\frac{1}{4}$ whorls. Spire elevated. Whorls rather tightly coiled, slowly increasing in width. Protoconch undifferentiated. Teleoconch sculpture consists of indistinct growth lines. Aperture narrow, slightly

bent, slot-like. Peristome simple, neither thickened nor expanded. Umbilicus narrow, 23.3% of shell width.

Species included. *Martinella martinella* Jousseaume, 1887.

Comparisons. *Martinella* is similar to *Zilchistrophia* Weyrauch, 1960 in many aspects, but these genera can be easily separated by the absence of apertural barriers in *Martinella*. That said, we expect *Martinella* to be closely related to *Zilchistrophia* and possibly *Ridleyconcha* based on conchological similarities.

Geographic range. Ecuador.

Remarks. Breure *et al.* (2022) treated *Martinella* as a possible *nomen dubium*, as the type material could not be located at the time and no specimens had been collected since the genus was described. However, the type material of *M. martinella* was found in the MNHN in January 2023. Re-examination of this type material enables us to redescribe the genus and move it to the Scolodontidae based on conchological characteristics.

Interestingly, *Martinella* was also twice introduced as a new genus for insects after Jousseaume's description. Both these genera are junior homonyms of *Martinella* Jousseaume, 1887 and have been duly replaced by new generic names. *Martinella* Sicard, 1907 (Coleoptera: Coccinellidae) was replaced by *Trimallena* Pope, 1961 and *Martinella* Artigas & Papavero, 1995 (Diptera: Asilidae) was replaced by *Martintella* Artigas, 1996 (Artigas 1996; Fürsch 2002).

Martinella martinella Jousseaume, 1887

Figure 4

Martinella martinella Jousseaume 1887: 173, pl. 3 fig. 14—Kobelt 1906: 161, pl. 65 fig. 9; Richardson 1988: 230; Schileyko 2000: 772, fig. 1006; Breure *et al.* 2022: 102, fig. 126; Brown 2023: 327, text fig.

Type material. MNHN-IM-2000-38654 (syntypes, 31 shells, dry).

Type locality. Ecuador, Pichincha province, San Nicolas.

Redescription. Same as the genus, as only one species is currently known.

Measurements. Shell height: 1.9 mm; width: 3.4 mm; whorls: c. 7.

Comparisons. No other species of *Martinella* are known, because *Martinella prisca* is moved to *Keranella* gen. nov. However, *Zilchistrophia shiwiwarorum* Páll-Gergely & Asami, 2014, which is also known from Ecuador, is similar in having a small shell with slowly enlarging whorls. This species can be easily separated from *M. martinella* by its more angulate shoulder, lower spire, and presence of palatal plicae within the aperture.

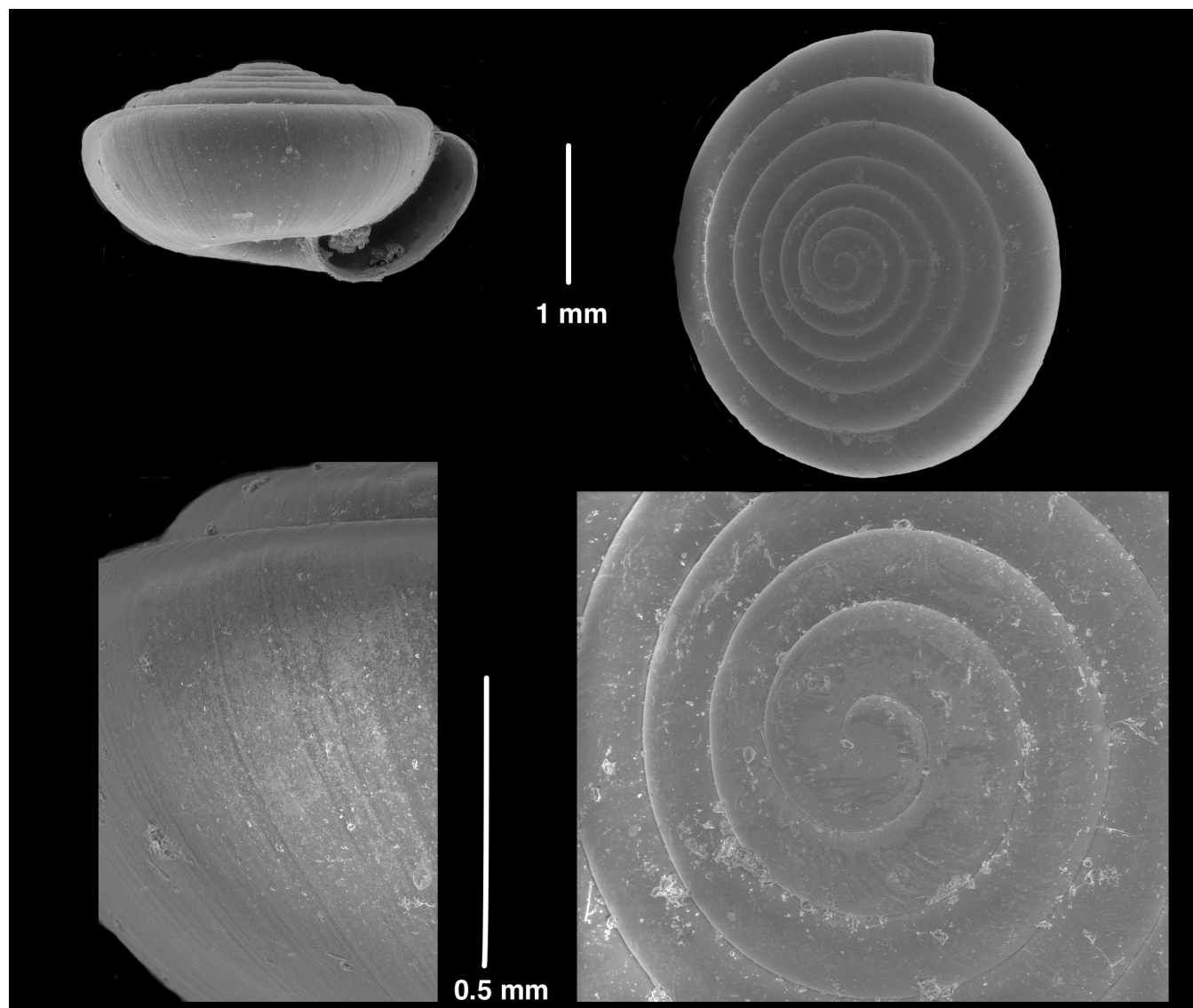


Figure 4. *Martinella martinella* Jousseume, 1887. MNHN-IM-2000-38654, syntype.

Geographic range. Ecuador: Pichincha province, San Nicolas.

Remarks. We recommend exploring parts of the Inter-Andean Valley in search of this species with the goal to find living specimens needed for anatomical study and genetic analysis.

Genus †*Patagocharopa* Miquel & P.E. Rodríguez, 2015

Type species. †*Patagocharopa enigmatica* Miquel & P.E. Rodríguez, 2015, by monotypy.

Redescription. Shell lenticular, minute, width 1.6 mm, height 0.7 mm). Protoconch and teleoconch smooth. Whorls uniformly increasing in size. Aperture narrow, D-shaped.

Apertural barriers tooth-like, rounded: three columellar, one parietal, six palatal, and one basal. The fossil is fragmentary, with part of the last whorl broken away, and with the columellar barriers seemingly repeating themselves at about $\frac{1}{4}$ whorl intervals.

Included species. †*Patagocharopa enigmatica* Miquel & Rodríguez, 2015.

Comparisons. The most similar shell, in overall size and the pattern of apertural barriers, is *Ridleyconcha*. In that genus, however, the barriers are lamellar and spiral within the shell. Internal barriers are also present in *Polygyratia*, which is more than 20 times larger and has a planispiral shell.

Geographic and stratigraphic range. Argentina, Miocene;

restricted to type locality and stratum of *P. enigmatica*.

Remarks. Miquel & Rodríguez (2015) tentatively placed this Miocene genus in Charopidae, and they commented that the shell morphology did not match any known Charopidae. However, this is to be expected, as the small, smooth, lenticular shell bearing numerous apertural barriers is instead characteristic of the Scolodontidae. Here, we transfer *Patagocharopa* to the Scolodontidae, as suggested by Salvador & Cavallari (2020).

As small scolodontids are poorly known and more species have been discovered recently (e.g. Roosen *et al.* 2023; Ravalo *et al.* 2023), it is possible that a living representative of the genus *Patagocharopa* will be found in the future as well.

†*Patagocharopa enigmatica* Miquel & Rodríguez, 2015
Figure 5

Patagocharopa enigmatica Miquel & Rodríguez 2015: 9, figs 7.1–7.3; Salvador *et al.* 2018: 258, fig. 2F–G.

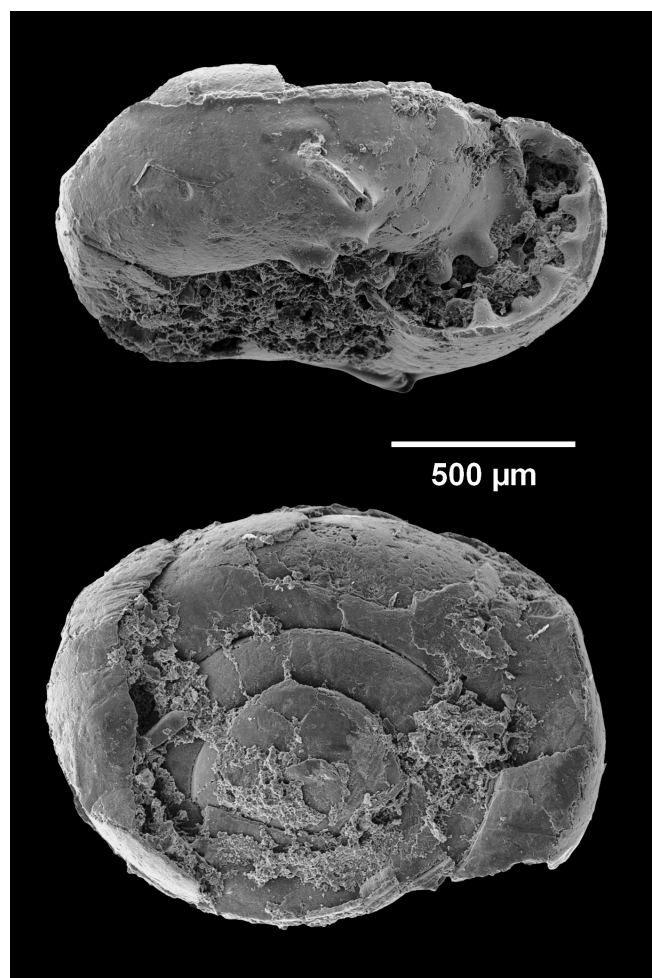


Figure 5. †*Patagocharopa enigmatica* Miquel & Rodríguez, 2015. MPM PI 3316, holotype.

Type material. MPM PI 3316 (fossil, holotype).

Type locality. Argentina, Santa Cruz Province, Puesto de la Estancia La Costa (=Corriguen Aike), between the Coyle and Gallegos Inlets, 51° 12' 08.2" S 069° 03' 35.6" W.

Type stratum. Santa Cruz Formation, Estancia La Costa Member, Fossiliferous Level 6 *sensu* Tauber (1997). Age: Miocene, late Burdigalian (c. 17.5 Ma; Fleagle *et al.* 2012).

Redescription. Same as genus.

Measurements. Shell height: 0.7 mm; width: 1.6 mm; whorls: 3 (holotype juvenile/fragmentary).

Geographic and stratigraphic range. Argentina, restricted to type locality and stratum.

Comparisons. No similar species are known.

Remarks. *Patagocharopa enigmatica* represents the earliest record of the family, dating back to the Early/Middle Miocene. The species is only known from its holotype, a juvenile or fragmentary specimen in poor condition. Hence, new intact adult specimens would be valuable in better understanding this species and its familial placement.

Genus *Polygyratia* J.E. Gray, 1847

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

Synonym. *Ophiogyra* Albers, 1850.

Vernacular name. Brazilian gyre snails.

Redescription. Shell planispiral, large, width 40–47 mm, height 11–13 mm, multiwhorled; whorls 8½–9. Spire typically slightly depressed, but often flat. Whorl profile markedly convex, with gentle angulation marking borders of apical and umbilical regions; a central angulation on the body whorl can be seen in some specimens. Whorls tightly coiled, slowly and regularly enlarging. Protoconch of 2¼–2½ whorls, apparently smooth. Teleoconch with scale-like, reticulated sculpture often superimposed by coarse growth lines; growth lines tend to become coarser and more irregular towards aperture. Body whorl bent abapically near the aperture. Presence of internal parietal (typically one) and palatal (typically two) lamellae in body whorl; lamellae short, disposed in two or three sets, positioned c. ⅓ and ⅔ of a whorl behind aperture. The number of lamellae may differ in some specimens, which may have additional smaller lamellae or even lack one of the three main lamellae. Aperture rounded to D-shaped; parietal callus may be present. Peristome slightly reflexed. Umbilicus very wide and deep.

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

Comparisons. There is no other species within Scolodontidae that can be confused with *P. polygyrata*. Its shell is very



Figure 6. *Polygyratia polygyrata* (Born, 1778). NHMW-MO-14371, syntype.

large for the family, planispiral, and multiwhorled. Furthermore, there are two sets of internal lamellae on the body whorl.

The scale-like teleoconch sculpture is similar to the spiral sculpture and axial ribs in *Entodina*, a genus which also has complex sets of plicae/lamellae. However, *Entodina* never exceeds 10 mm, and the placement of the plicae is substantially different.

Geographic range. Brazil, Bahia state (Salvador & Cavallari 2020).

Remarks. The genus and species were revised by Salvador & Cavallari (2020), who placed them in Scolodontidae based on shell morphology. Their DNA extraction failed.

Polygyratia polygyrata (Born, 1778)

Figure 6

Helix polygyrata Born 1778: 382—Wilhelm 1802: 356; 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, text fig.; Salgado & Coelho 2003: 172; Schileyko 2006: 1844, fig. 2359; Simone 2006: 247, fig. 946; Schileyko 2016: fig. 4; Breure & Araujo 2017: 121, figs 47D–F; Sei *et al.* 2017: table 9, fig. 5n; Salvador 2019: 95; Salvador & Cavallari 2020: 92, figs 1, 2; Salvador *et al.* 2024: 153, 169.

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

Polygyratia charybdis Mörch 1852: 7.

Polygyratia (detrita.) Mörch 1852: 7.

Helix charybdis—Mörch 1852: 170; Hupé 1857: 12.

Helix (Anchistoma) polygyrata—Brauer 1878: 181.

Polygyra (Polygyratia) polygyrata—Tryon 1887: 111, 124, pl. 25 figs 72–74; Pilsbry 1894: 81, pl. 20 figs 37–38.

Polygyra (Polygyratia) polygyrata var. *charybdis*—Tryon 1887: 124.

Anchistoma polygyrata—Tryon 1887: pl. 25, figs 72–74.

Polygyratia (Polygyratia) charybdis—Pilsbry 1894: 81.

Polygyratia polygyratia [sic]—Gude 1920: 59.

Polygyratia polygyrata polygyrata—Lange de Morretes 1949: 163.

Polygyratia polygyrata charybdis—Lange de Morretes 1949: 163.

Polygyratia charybdis—Simone 2006: 247, fig. 945.

Type specimens. NHMW-MO-14371 (2 shells, dry). NHMD 615842 (possible holotype of *Helix charybdis*).

Type locality. Unknown (“patria ignota”; Born, 1780). Restricted to “Brazil, Bahia state” by Salvador & Cavallari (2020).

Redescription. Same as the genus, as it is the only species.

Measurements. Shell height: 11–13 mm; width: 40–47 mm; whorls: 8½–9.

Geographic range. Brazil, eastern Bahia state: Atlantic Forest along the coast (Salvador & Cavallari 2020).

Comparisons. No similar species are known. One other species, *Polygyratia charybdis* Mörch, 1852, was previously recently recognised, but this is currently considered to be a synonym of *P. polygyrata* (Salvador & Cavallari 2020).

Remarks. Shell colour can be rather variable within the species. Coloration is predominantly chestnut brown, but often ochre. Some regions of the shell are typically ochre, such as the spiral band (not always present) on the adapical angulation of the whorl, the protoconch and first whorls of the spire, and the abapical region but excluding a chestnut-brown subsutural spiral band. Rarely, the abapical (umbilical) portion of shell is chestnut-brown. The peristome is white. Almost nothing is known of the biology of *P. polygyratia*, but one aspect of great interest is its diet. If this species is a carnivore (or omnivore), like many other scolodontids, it would be one of the largest predatory snails in South America. However, Barker & Efford (2004), based on the morphology of the buccal mass and radula of some species, suggested that some scolodontids might be facultative carnivores or even completely herbivores or detritivores. The latter would be more likely for *P. polygyrata*.

This is one of the most unique species in Brazil and has a very restricted geographic distribution, within an area with large anthropic impacts (Salvador & Cavallari 2020). We currently lack the data to assess how populations are faring in the wild, but all things considered this species could be a primary target for land-snail conservation in Brazil.

Genus *Ridleyconcha* Christensen, 2020

Type species. *Helix* (*Ophiogyr*) *quinquelirata* E.A. Smith, 1890, by typification of the replaced name.

Synonyms. *Ridleya* Ancey, 1901 (non Delage & Hérouard, 1899); *Rydleya* Ancey, 1901 (unavailable incorrect subsequent spelling of *Ridleya* Ancey, 1901).

Redescription. Shell discoid to lenticular, small, width 5.5–5.8 mm, height 3.1–3.2 mm, with 6–6¼ tightly coiled whorls. Suture well marked. Body whorl with two slight angulations, one positioned at shoulder and another medial on the whorl; a slighter angulation (variable in strength among specimens) present around the umbilicus. Protoconch smooth. Teleoconch sculptured by fine, sinuous ribs. Aperture narrow, D-shaped. Four lamellae present: two parietal lamellae extend from the aperture to the first whorls; two short basal/palatal lamellae starting further away from the aperture and extending into the shell. Peristome reflected, more prominently so in basal region of the aperture. Umbilicus wide, deep.

Species included in the genus. *Ridleyconcha quinquelirata* (E.A. Smith, 1890).

Comparisons. In shape the shell is most similar to *Martiniella*, *Zilchistrophia*, and *Smenodonta* gen. nov., but none of those genera have parietal lamellae and the sculpture differs. Within the Scolodontidae, parietal lamellae are only known in *Xenodiscula* Pilsbry, 1919, which is much smaller, discoidal, with sculpture consisting of axial grooves, and with one more prominent parietal lamella positioned in the middle of the parietal wall (Roosen et al. 2023; Roosen & Breure 2024b). Internal lamellae have also been observed in *Polygyratia* (Salvador & Cavallari 2020), but in that genus they are short tooth-like barriers and not elongate as in *Ridleyconcha*.

Geographic range. Brazil, endemic to the Fernando de Noronha Archipelago.

Remarks. A preliminary DNA analysis by Salvador (2021) indicated a close relationship to *Entodina jekylli*, but the sampling of scolodontid genera in that study was limited.

Ridleyconcha quinquelirata (E.A. Smith, 1890)

Figure 7

Helix (*Ophiogyr*?) *quinquelirata* Smith 1890: 500, pl. 30 fig. 7.

Patula quinquelirata—Ancey 1901: 17 (used in discussion).

Ridleya quinquelirata—Ancey 1901: 17; Lopez & Alvarenga 1957: 181; Miquel & Cádiz Lorca 2008: 334, fig. 14; Freitas et al. 2019: 67, fig. 2B; Salvador 2019: 93–94, fig. 2J–L.

Polygyratia (*Ridleya*) *quinquelirata*—Gude 1920: 59.

Rydleya quinquelirata—Salgado & Coelho 2003: 154 (incorrect subsequent spelling of the genus); Serafini et al. 2010: 290.

Ridleyconcha quinquelirata—Christensen 2020: 66; Salvador 2021: 65, fig. 2; Salvador et al. 2024: 153.

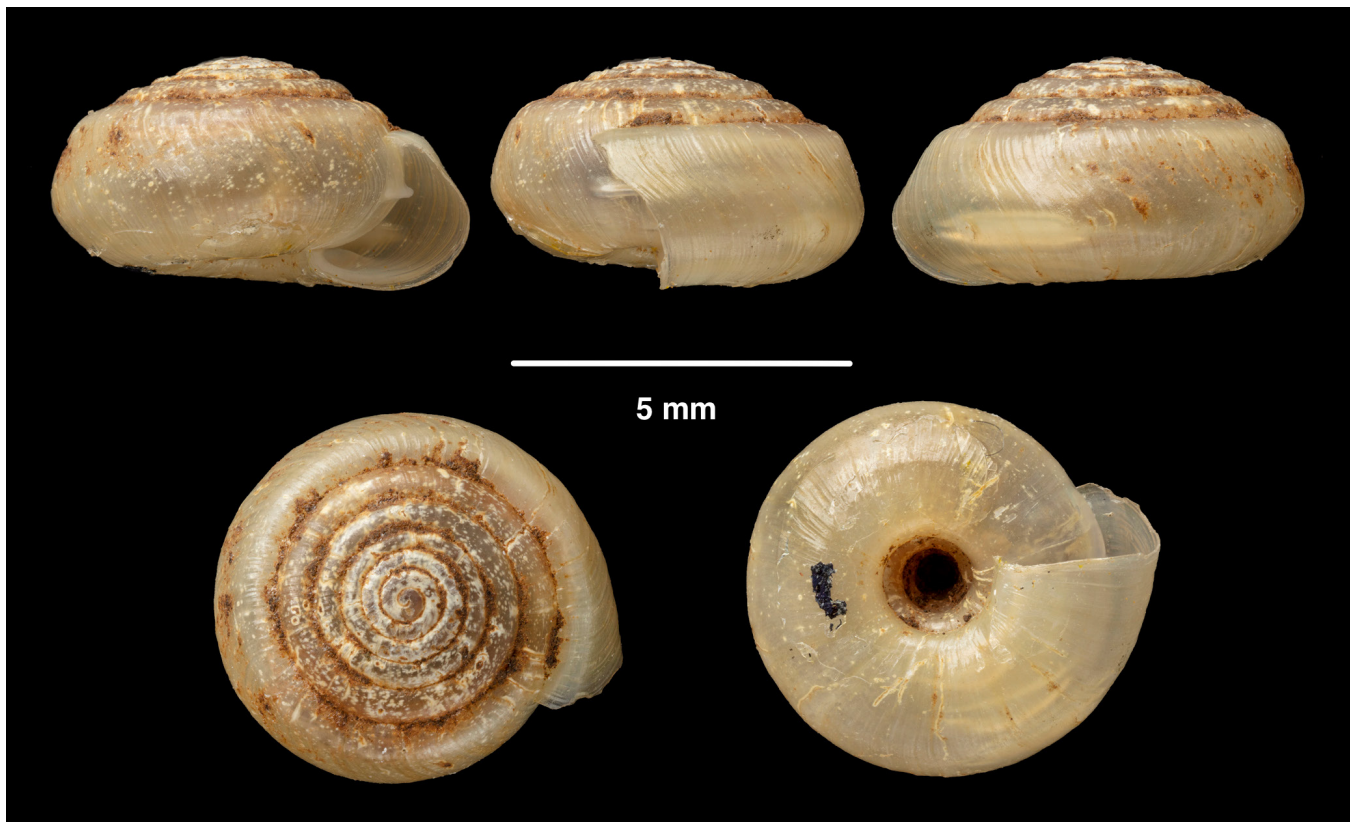


Figure 7. *Ridleyconcha quinquelirata* (E.A. Smith, 1890). NHMUK 1988.6.27.135–140, syntype.

Rydleya quinquelinata—Arias 2021: 80 (incorrect subsequent spelling of the species).

Type material. NHMUK 1988.6.27.135–140 (syntypes, 6 shells, dry).

Type locality. Brazil, Fernando de Noronha Archipelago, Fernando de Noronha Island, north end of island.

Genetic data. ITS2+28S: GenBank acc. nr. MZ130665 and MZ130666.

Redescription. Same as genus.

Measurements. Shell height: 3.1–3.2 mm; width: 5.5–5.8 mm; whorls: 6–6¼.

Geographic range. Brazil, Fernando de Noronha Archipelago (Fernando de Noronha Island and Rata Island) (Salvador 2021).

Comparisons. So far, only a single species is known in this genus.

Remarks. Miquel & Cádiz Lorca (2008) mentioned five spiral sculptural elements on the protoconch as characteristic for the species. Salvador (2019) examined the material studied by those authors, along with over 20 other specimen lots of *R. quinquelirata*, including the type series, and noted that the protoconch is smooth, although often eroded.

Genus *Smenodonta* gen. nov.

ZooBank identifier. urn:lsid:zoobank.org:act:4BDC148D-35D1-4F34-83F1-CC38F1A6E711

Type species. *Helix janeirensis* L. Pfeiffer, 1852.

Etymology. From Ancient Greek “smēnos” (σμήνος), meaning beehive, which is an allusion to the shape of these snails’ shells like an old-fashioned beehive. It is combined with “odonto” (toothed, from Ancient Greek through Latin), meaning tooth, in allusion to the shell’s apertural barriers. Grammatical gender: feminine.

Vernacular name. The suggested vernacular name for species of this genus is “toothed beehive snails”.

Species included in the genus. *Smenodonta janeirensis* (L. Pfeiffer, 1852) **comb. nov.** [= *Streptaxis crosseii* L. Pfeiffer, 1867], *S. sp.* (undescribed species of Barbosa 2014, as *Entodina sp.*).

Description. Shell small, width ≤ 10 mm, lenticular to conical, with a stepped spire. Whorls > 5 , tightly coiled, with an angulation forming a shoulder. Suture well marked. Protoconch $c. 2\frac{1}{2}$ whorls, smooth; transition to teleoconch distinct. Teleoconch sculptured by strong, regularly spaced, prosocline ribs that runs extending from the angulation to

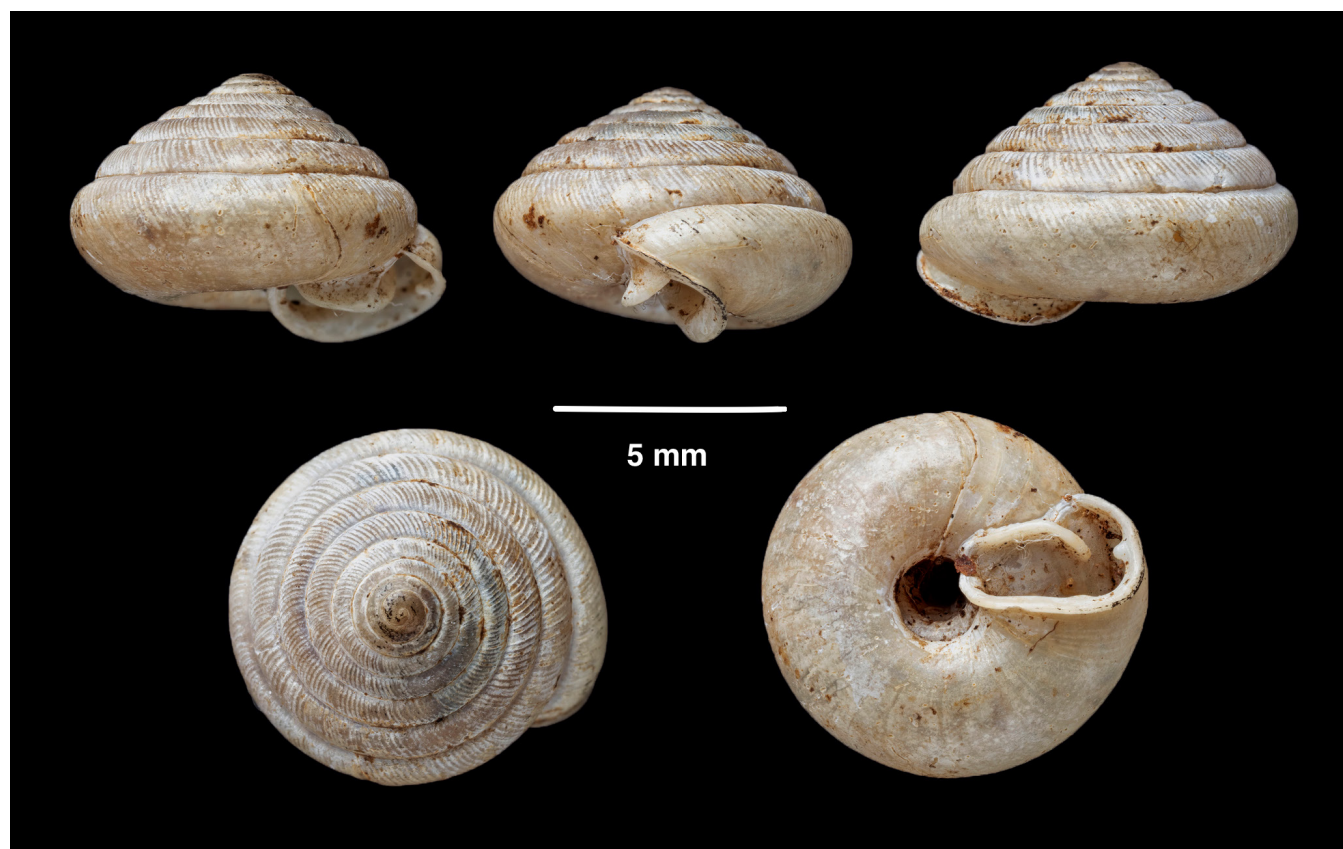


Figure 8. *Smenodonta janeirensis* (L. Pfeiffer, 1852) comb. nov. NHMUK 1859.5.2.1, syntype.

the suture; faint ribbing pattern may also be present immediately around the umbilicus. Body whorl bent abapically immediately before the aperture in adults. Peristome slightly thickened and reflected. Aperture narrow, prosocline, D-shaped to rectangular. Aperture with barriers, including 1 basal and 1 or more palatal teeth, and a long parietal barrier that bears its own transverse plicae. Umbilicus relatively wide, c. 20% of shell width, deep.

Comparisons. *Smenodonta* gen. nov. can be easily distinguished from other scolodontids by the lenticular to conical shell with a raised spire. *Martinella* is similar in overall shell shape, but it is much smaller and has no discernible sculpture or apertural barriers. *Keranella* gen. nov. is somewhat similar in shell shape but lacks the parietal barrier in the aperture and presents, instead, a fused basal-palatal barrier. Despite superficial similarities in sculpture and apertural barriers, the shell of *Entodina* is usually flat, has axial sculpture on the entire teleoconch, a subcircular aperture, and its apertural barriers are limited to folds in parietal wall. *Entodina jekylli* is the species most similar to *Smenodonta* gen. nov., due to its slightly more raised spire and weaker ribbing on the abapical portion of the whorls. Finally, the shell of *Zilchistrophia* is

also somewhat similar, but the palatal plicae are differently shaped, the aperture is always lunulate or subcircular, and there is no prominent teleoconch sculpture.

Geographic range. Brazil, southeast and south regions.

Remarks. The new genus brings together species that were formerly allocated in both Scolodontidae and Streptaxidae, showcasing the complexity surrounding some members of this family.

***Smenodonta janeirensis* (L. Pfeiffer, 1852) comb. nov.**

Figure 8

Helix janeirensis L. Pfeiffer 1852: 128—Pfeiffer 1853: 265.

Streptaxis crosseii L. Pfeiffer, 1867: 43, pl. 1 fig. 1—Martens 1868: 209; Hidalgo 1870: 39; Hidalgo 1872: 43, pl. 3 figs 1, 2; Hidalgo 1893a: 87; Hidalgo 1893b: 139; Tryon 1885: 67, pl. 16 figs 3, 4.

Streptaxis (*Streptartemon*) *crosseii*—Kobelt 1906: 35.

?*Systrophia* (*Entodina*) *janeirensis*—Kobelt 1906: 89.

Artemon crosseii—Lange de Morretes 1949: 167.

Streptartemon crosseii—Richardson, 1988: 245; Salgado & Coelho 2003: 171.

Systropia (*Entodina*) *janeirensis*—Ramírez 1993: 50.

Entodina janeirensis—Simone 2006: 224, fig. 850.

Streptaxis crossei—Simone 2006: 190, fig. 705; Breure & Araujo 2017: 97, fig. 36D–E; Brown 2023: 314, text figs; Salvador et al. 2024: 152.

Systrophia janeirensis—Salvador et al. 2024: 153.

Type specimen. NHMUK 1859.5.2.1 (syntype, dry shell). MNHN-IM-2000-30920 (syntype of *Streptaxis crossei* L. Pfeiffer, 1867, dry shell).

Type locality. Brazil, Rio de Janeiro. It is uncertain whether this refers to the city of Rio de Janeiro or to the homonymous province/state, but it likely refers to the former.

Redescription. Shell small, width *c.* 10 mm, conical, with a stepped spire. Whorls 7–8, tightly coiled, with an angulation forming a shoulder. Suture well marked. Protoconch $2\frac{1}{2}$ whorls, smooth; transition to teleoconch distinct. Teleoconch sculptured by strong, regularly-spaced, prosocline ribs that extend from the whorl angulation to the suture; faint ribbing may also be present immediately around umbilicus. Body whorl bend abapically immediately before the aperture in adults. Peristome slightly thickened and reflected. Aperture narrow, prosocline, D-shaped. Apertural barriers: basal/palatal barrier very weak; palatal tooth; parietal barrier long, bearing its own transversal plicae. Umbilicus *c.* 20% of shell width, deep.

Measurements. Shell height: *c.* 6 mm; width: *c.* 10 mm; whorls: 7–8.

Geographic range. Brazil, restricted to Rio de Janeiro state.

Comparisons. *Streptaxis crossei* was described from the Corcovado, a locality within the city of Rio de Janeiro. So far, it has been maintained as a distinct species in Streptaxidae (e.g. Simone 2016; Breure & Araujo 2017), while *Smenodonta janeirensis* has been traditionally placed in *Systrophia* or *Entodina* in Scolodontidae. Besides the overlap of type localities of these two species, their shells are similar in size. The syntype *Streptaxis crossei* has an extra half whorl in comparison to that of *Smenodonta janeirensis*, and there are negligible differences in the position and strength of the apertural barriers. Therefore, here we consider *Streptaxis crossei* as a junior synonym of *Smenodonta janeirensis*.

Remarks. Photographic records in iNaturalist (<https://www.inaturalist.org/>) show what very likely is a juvenile *Smenodonta janeirensis* preying on juvenile orthalicoid snails. These observations (<https://www.inaturalist.org/observations/95894827>, accessed 2025-II-3 and <https://www.inaturalist.org/observations/103817465>, accessed 2025-II-3) were previously reported by Rosa et al. (2022) in their overview of Brazilian terrestrial gastropods on iNaturalist and offer a small and serendipitous glimpse into the natural history of this species.

Smenodonta sp.

Entodina sp.—Barbosa 2014: 99, figs 20, 21.

Remarks. Barbosa (2014) surveyed the fauna of Ilha Grande, a continental island on the southern coast of Rio de Janeiro state, and reported specimens of an undescribed species of *Smenodonta* that he allocated to *Entodina* sp. Judging by available photographs (Barbosa, 2014: figs 20, 21), it is smaller than *S. janeirensis*, but similar in size, number of whorls, and overall shell shape to *Keranella prisca*. Its apertural barriers are also slightly different from *S. janeirensis*: it has one basal tooth (absent in *S. janeirensis*), one basal/palatal tooth, and one palatal teeth, all strong; the basal/palatal and palatal teeth are in a similar position to those of *S. janeirensis* (only the apical tooth is strong in the latter species); the parietal barrier is very similar to that of *S. janeirensis*, albeit bearing a second, smaller transversal plica on top of it.

Genus *Systrophia* L. Pfeiffer, 1855

Type species. *Helix systrophia* Albers, 1854, by subsequent designation (Baker 1925).

Redescription. Shell relatively large, discoid to subdiscoid, with a whitish-transparent or corneous. Protoconch smooth, slightly larger than the first teleoconch whorl, giving it a node like appearance. Typical species have 8–14 tightly coiled whorls, giving the shell a maze-like appearance from the apical view. Aperture deflected, impressed from the palatal side, sometimes creating a small palatal fold. Peristome simple. Umbilicus wide, usually 40–50% or more of shell width.

Species included. *Systrophia affinis* (Pilsbry, 1900), *S. argentina* (Strobel, 1874), *S. eatoni* F. Baker, 1914, *S. haasi* Weyrauch, 1960, *S. helicycloides* (d'Orbigny, 1835), *S. heligmoida* (d'Orbigny, 1835), *S. impressa* F. Haas, 1951, *S. ortonii* (Crosse, 1871), *S. pilsbryi* Weyrauch, 1958, *S. platygyra* (Albers, 1857), *S. platysma* F. Haas, 1951, *S. sargenti* (Pilsbry, 1900), *S. siolii* F. Haas, 1955, *S. stenogyra* (L. Pfeiffer, 1854), *S. stenostrepta* (L. Pfeiffer, 1857), *S. stenostrepta declinata* (Pilsbry, 1900), *S. systrophia* (Albers, 1854), *S. tortilis* (Morelet, 1863) **comb. nov.**

Species removed from the genus. ?*Entodina alcidiana* (Ancey, 1892) **comb. nov.**, “*Helix circumplexa* (Férussac in Férussac & Deshayes, 1839), *Entodina cheilostrophia* (d'Orbigny, 1835), *Systrophella cuzcana* (Philippi, 1869) **comb. nov.**, *Entodina derbyi* (Ihering, 1912), *Zilchistrophia entodonta* (L. Pfeiffer, 1859), *Systrophella footei* (Dall, 1912) **comb. nov.**, *Entodina gionensis* Lange de Morretes, 1940, *Systrophella gyrella* (Morelet, 1863) **comb. nov.**, *Systrophella gyrellina* (F. Haas, 1951) **comb. nov.**, *Happiella insignis* (d'Orbigny, 1835) **comb. nov.**, *Entodina jekylli* F.

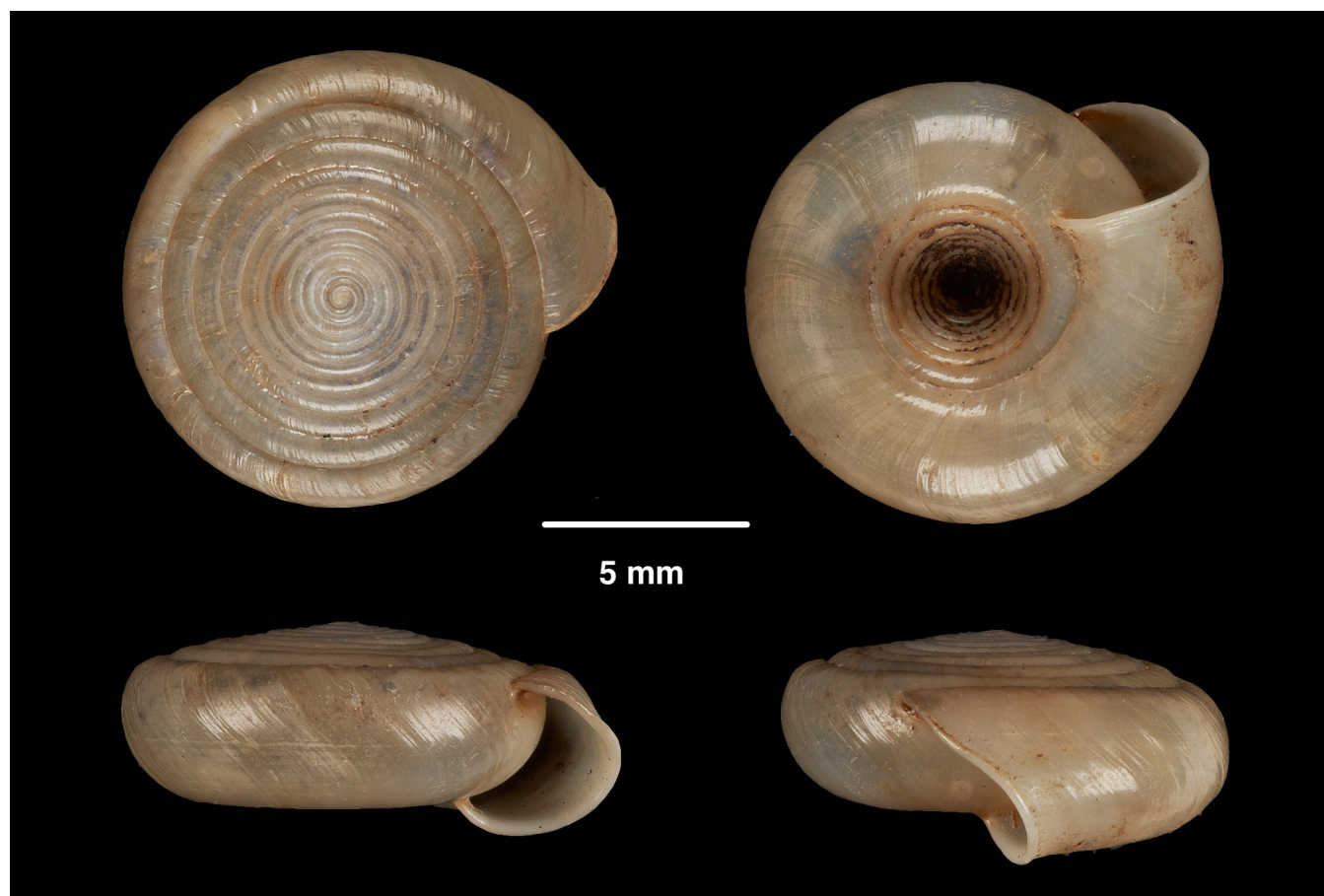


Figure 9. *Systrophia systropha* (Albers, 1854). ZMB.Moll 5466a, syntype.

Baker, 1914, *Entodina pollodonta* (d'Orbigny, 1835), *Systrophiiella polycycla* (Morelet, 1860) **comb. nov.**, *Systrophiiella planior* (F. Haas, 1951) **comb. nov.**, *Systrophiiella pseudoplanorbis* (Lubomirski, 1880) **comb. nov.**, *Entodina reyreii* (Souverbie, 1858), *Scolodonta starkei* H.B. Baker, 1925, *Systrophiiella zeteki* (Pilsbry, 1930) **comb. nov.**

Unassessed species. *Systrophia altorum* Weyrauch, 1967, *Systrophia decagyra* (Philippi, 1869), *Systrophia moellendorffii* Rolle, 1904, *Systrophia planispira* Weyrauch, 1967.

Comparisons. *Systrophia* is often confused with *Zilchistrophia*, *Entodina*, and *Polygyratia*. All these genera have some form of internal plicae. In *Systrophia* these are absent. *Entodina* and *Polygyratia* also have a more complex teleoconch sculpture. *Systrophiiella* is often regarded as a subgenus of *Systrophia*, but the former often has less whorls at a similar shell size, has more convex whorls and never has a deflected aperture.

Geographic range. Colombia, Ecuador, Brazil, Peru, Bolivia, and Argentina. Based on its currently known distribution, we expect the genus to be present in all countries with

Amazon or Chocó rainforest.

Remarks. It is likely that *Systrophia*, as presently understood, is not monophyletic. The morphological differences between the type species, *S. systropha*, and some other members of the genus (e.g. *S. ortonii*) are significant. Genetic data will be needed to assess the monophyly of the group.

***Systrophia systropha* (Albers, 1854)**

Figure 9

Helix systropha Albers 1854: 215.

Helix (Systrophia) systropha—Pfeiffer 1855–1856: 136.

Polygyra (Polygyratia) systropha—Tryon 1887: 127, pl. 26 figs 22–24.

Anchistoma systropha—Tryon 1887: 289.

Systrophia systropha—Baker 1925: 14.

Systrophia (Systrophia) systropha—Ramírez 1993: 63, 145.

Type material. ZMB.Moll 5466a (syntypes, 14 shells, dry).

Type locality. “Columbia ad fluvium Maranhon” (= Rio Marañón, Peru), leg. Warszewicz (Albers 1854).

Redescription. Shell of medium size, subdiscoidal, with

a slightly raised spire. First whorls smooth, earlier whorls with minute growth striae. No clear distinction between protoconch and teleoconch whorls. Vestigial spiral grooves visible on the ultimate whorl. Final portion of the last whorl slightly enlarged, widened. Aperture lunulate, with a slight depression on the apical side. Peristome thickened and slightly deflected. Umbilicus narrow for the genus, 43% of shell width.

Measurements. Shell height: 5.0 mm; width: 12.9 mm; whorls: 12.

Geographic range. Peru, along the Rio Marañón.

Comparisons. Most species currently included in *Systrophia* are easily distinguished by their discoid shell shape and the presence of a stronger depression near the aperture. In *S. helicycloides* (d'Orbigny, 1835) this depression is absent, but the spire is slightly sunken, and the teleoconch has stronger growth striae.

Remarks. Even though *S. systropha* is the type species of *Systrophia*, it is barely mentioned in the literature and type material has not been previously photographed. This likely contributed to the confusion around the identity of *Systrophia* and allied genera.

Genus *Zilchistrophia* Weyrauch, 1960

Type species. *Zilchistrophia tridentata* Weyrauch, 1960, by original designation.

Redescription. Shell small, with a flat or slightly raised spire. Protoconch and teleoconch nearly smooth, with only growth lines. Whorls tightly coiled; last quarter of the last whorl enlarged in some species. Aperture lunulate to subcircular; peristome thin, only slightly deflected. Two or three axially oriented palatal plicae are visible at irregular intervals throughout the shell in all species.

Species included. *Zilchistrophia angigyra* (F. Haas, 1949), *Z. entodonta* (L. Pfeiffer, 1859), *Z. hilaryae* Páll-Gergely, 2014, *Z. obvoluta* (F. Haas, 1949), *Z. shiwarorum* Páll-Gergely, 2014, *Z. tridentata* Weyrauch, 1960.

Comparisons. The genus differs from most other genera discussed in this paper by the presence of palatal plicae. *Ridleyconcha* also has palatal lamellae or plicae, but there are also lamellae on the parietal wall.

Geographic range. Peru and Ecuador.

Remarks. Gude (1920) recognized *Zilchistrophia* as a separate group during his study on apertural barriers in gastropods, in which he included *Z. entodonta*, but never officially introduced a name for it.

Zilchistrophia tridentata Weyrauch, 1960

Figure 10

Zilchistrophia tridentata Weyrauch 1960: 27–28, pl 3, fig. 6. *Zilchistrophia tridentata*—Ramírez 1993: 89; Schilevko 2000: 755; Ramírez *et al.* 2003: 277; Breure 2012: 13; Páll-Gergely & Asami 2014: 3.

Type material. SMF 162006 (one shell, dry), holotype.

Type locality. “Mittel-Peru am Osthang der östlichen Anden: Bergwerk Pichita Caluga (2200 m), in Zuflußtal des Río Chanchamayo, im Ucayali-Becken, unter Stein in Steinhäufen, in dichtem, schattigem, immergrünem, subtropischem Nebelwald” (= In cloud forest around the Río Chanchamayo tributary (2200 m a.s.l.), East of the Andes, central Peru).

Measurements. Shell height: 3.2 mm; width: 5.7 mm; whorls: 7½.

Redescription. Shell whitish-transparent, with a strongly depressed spire. Early whorls smooth, later whorls sculptured with minute growth lines. No clear distinction between protoconch and teleoconch whorls. Whorl shouldered, with a weak angulation near the suture and another near the umbilicus. Aperture subcircular, with a simple peristome. Sets of three internal plicae are present, in the holotype only one set ½ whorl behind aperture. Umbilicus narrow, *c.* 34% of shell width.

Comparisons. The shell is larger than that of *Z. shiwarorum* and *Z. hilaryae*. The overall shell shape and number of plicae also differ. *Zilchistrophia obvoluta* is larger and has a lower spire than *Z. tridentata*, whereas *Z. angigyra* is similar in size to *Z. tridentata* and differs by its stronger sculpture and higher spire. The plicae in *Z. angigyra* and *Z. obvoluta* could not be studied, but according to Weyrauch both species have two elongate plicae-like structures (Weyrauch 1960). *Zilchistrophia entodonta* has plicae that are similar to *Z. tridentata*, but the spire is flat.

Geographic range. Ecuador and Peru.

Remarks. Although two species were thoroughly studied by Páll-Gergely and Asami (2014), the type species of *Zilchistrophia* is still relatively poorly known.

DISCUSSION AND CONCLUSIONS

There are many more scolodontid genera with slowly enlarging whorls and internal barriers than previously recognised. *Entodina* is recognised as a full genus, and *Smenodonta* gen. nov. is separated from it. *Martinella* and *Keranella* gen. nov. are moved from the Streptaxidae to the Scolodontidae.



Figure 10. *Zilchistrophia tridentata* Weyrauch, 1960. SMF 162006, holotype.

Similarly, *Patagocharopa* is moved from the Charopidae to Scolodontidae and, thus, represents the earliest fossil record of the family from the Early/Middle Miocene. Table 1 pro-

vides a summary of the main characters of each genus.

With this revision, we hope to reduce the confusion among genera of Scolodontidae, although we recognize that our revision, based on conchological characters, is just a first step. Like with other scolodontids (Roosen & Breure 2024a, 2024b, 2024c), anatomical features should be studied in further detail and genetic data acquired to build reliable phylogenetic frameworks. The latter will allow us to better assess the relationships among scolodontid genera and understand the evolution of shell morphology within the family. We expect *Systrophia* and *Entodina* to be polyphyletic in a genetic analysis.

Of all taxa studied here, we call attention to the Ecuadorian species *Martinella martinella*, as it is odd that the species was never found again after its description. Breure *et al.* (2022) suggested that this species may be going or has already gone extinct due to habitat loss. Wider field surveys are lacking, but if *Martinella* is still extant, we need more data so that actions can be taken to preserve this remarkable snail.

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REFERENCES

- ALBERS JC. 1850. *Die Heliceen nach natürlicher Verwandtschaft systematisch geordnet*. Enslin, Berlin, 262 pp. doi: 10.5962/bhl.title.11507
- ALBERS JC. 1854. Novorum Heliceorum diagnoses. *Malakozoologische Blätter* 1: 213–221. <https://www.biodiversitylibrary.org/page/15864676>
- ANCEY CF. 1878. Description of new genera and subgenera of Helicidae. *The Conchologists' Exchange* 1: 64. <https://www.biodiversitylibrary.org/page/28528930>
- ANCEY MCF. 1901. Conciderations sur les faunes Malacologiques

Table 1. Summary of the main shell features and geographic distribution of the studied genera.

Genus	Average shell width (mm)	Apertural barriers	Internal lamellae/plicae	Teleoconch sculpture	Geographic distribution
<i>Entodina</i> (Fig. 1)	5.5	Parietal fold. Palatal fold may also be present	One set at c. 1/6 whorl from aperture	Axial ribs and minute spiral striae	Ecuador, Brazil, Peru, Bolivia
<i>Keranella</i> gen. nov. (Figs 2, 3)	5.0	Fused basal/palatal barrier	None	Axial ribs on shoulder and around umbilicus. Absent in <i>K. cryptodon</i> .	Eastern and southern Brazil
<i>Martinella</i> (Fig. 4)	3.5	No	None	None	Ecuador
† <i>Patagocharopa</i> (Fig. 5)	1.5 (juvenile)	Unknown	At least two sets of parietal and palatal plicae, c. 1/4 whorl from each other	None	Argentina [Miocene]
<i>Polygyratia</i> (Fig. 6)	45	No	2 or 3 sets of parietal and palatal lamellae, c. 1/3 whorl from each other	Scale-like reticulated background often superimposed by coarse growth lines	Brazil (Bahia state)
<i>Ridleyconcha</i> (Fig. 7)	5.5	Parietal and basal/palatal lamellae	Parietal lamellae run continuously from first whorls to aperture	Fine sinuous axial ribs	Brazil (Fernando de Noronha Archipelago)
<i>Smenodonta</i> gen. nov. (Fig. 8)	10.0	Parietal barrier with plicae. Basal tooth. One or more palatal teeth.	None	Axial ribs on shoulder and around umbilicus.	Southeastern and southern Brazil
<i>Systrophia</i> (Fig. 9)	>10.0	Parietal and/or palatal folds may be present	None	Growth striae or fine axial ribbing	Colombia, Ecuador, Brazil, Peru, Bolivia, Argentina
<i>Zilchistrophia</i> (Fig. 10)	5.5	None	2 or 3 sets of palatal plicae	None	Ecuador, Peru

des parties Australes du globe. *Journal de Conchyliologie* 49: 12–33. <https://www.biodiversitylibrary.org/page/15860169>

ARIAS VE. 2021. *Eolianitos Quaternários do Nordeste do Brasil*. Unpublished doctoral thesis, Universidade de São Paulo, São Paulo, 259 pp. doi: 10.11606/t.44.2021.tde-15032021-104433

ARTIGAS JN. 1996. *Martintella* a new name for *Martinella* Artigas y Papavero, 1995 (Diptera, Asilidae). *Boletín de la Sociedad de Biología de Concepción* 67: 75. <https://www.biodiversitylibrary.org/page/31650353#page/77/>

BARBOSA AB. 2014. *Morfologia, taxonomia e sistemática das espécies de Scolodontidae (Baker, 1925) (Gastropoda, Heterobranchia, Pulmonata, Stylommatophora) do estado do Rio de Janeiro*. Unpublished doctoral thesis, Universidade do Estado do Rio

de Janeiro, Rio de Janeiro, 147 pp. <http://www.bdt.d.uerj.br/handle/1/16201>

BAKER HB. 1925. The Mollusca collected by the University of Michigan–Williamson expedition in Venezuela, Part 3. Pupillidae to Oleacinidae. *Occasional Papers of the Museum of Zoology, University of Michigan* 156: 1–58. <https://hdl.handle.net/2027.42/56595>

BARKER GM, EFFORD MG. 2004. Predatory gastropods as natural enemies of terrestrial gastropods and other invertebrates. Pp. 279–403 in: Barker GM (Ed.) *Natural Enemies of Terrestrial Molluscs*. CABI, Wallingford.

BORN IV. 1778. *Index rerum naturalium Musei Caesarei Vindobonensis. Pars 1, Testacea. Verzeichniss der Natürlichen Seltenheiten*

- des K.K. *Naturalien Kabinets zu Wien*. Erster Theil, Schalthiere. Officina Krausiana, Vienna. doi: 10.5962/bhl.title.11581
- BREURE ASH. 2012. Weyrauch's type localities: a clarification; with illustrations of types of Orthalicoidea (Mollusca, Gastropoda, Stylommatophora) in the Tucumán museum. *Folia Conchyliologica* **17**: 4–24.
- BREURE ASH, ARAUJO R. 2017. The Neotropical land snails (Mollusca, Gastropoda) collected by the “Comisión Científica del Pacífico”. *PeerJ* **5**: e3065. doi: 10.7717/peerj.3065
- BREURE ASH, TARDY E. 2016. From the shadows of the past: Moricand senior and junior, two 19th century naturalists from Geneva, with their newly described taxa and molluscan types. *Revue Suisse de Zoologie* **123**: 113–138. doi: 10.5281/zenodo.46292
- BREURE ASH, ROOSEN MT, ABLETT JD. 2022. Land and freshwater molluscs of mainland Ecuador: an illustrated checklist. *Iberus* **40**: 1–290.
- BROWN K. 2023. *A guide to the hunter shells. Vol. 2. The Streptaxoidea. The Enneinae, Orthogibbinae, Marconiinae, Odontartemoninae, Streptaxinae and the Diapheridae*. ConchBooks, Germany, 648 pp.
- CHRISTENSEN CC. 2020. *Ridleyconcha* Christensen, gen. nov., a replacement name for the land snail genus *Ridleya* Ancey, 1901 (Mollusca: Scolodontidae), a junior homonym of *Ridleya* Delage & Hérouard, 1899 (Porifera: Polymastiidae). *American Malacological Bulletin* **38**: 66–67. doi: 10.4003/006.038.0107
- FLEAGLE JG, PERKINS ME, MATTHEW T, HEIZLER MT, NASH B, BOWN TM, TAUBER AA, DOZO MT, TEJEDOR MF. 2012. Absolute and relative ages of fossil localities in the Santa Cruz and Pinturas Formations. Pp. 41–58 in: Vizcaíno SF, Kay RF, Bargo MS (Eds) *Early Miocene Paleobiology in Patagonia: High-latitude Paleocommunities of the Santa Cruz Formation*. Cambridge University Press, New York.
- FREITAS AVL, MIRANDA MS, PASSOS FD. 2019. Land snails of the Fernando de Noronha archipelago, Brazil. *American Malacological Bulletin* **37**: 66–69. doi: 10.4003/006.037.0204
- FÜRSCH H. 2002. Die Gattung *Trimallena* Pope (Coleoptera: Coccinellidae, Sticholotidinae). *Mitteilungen der Münchner Entomologischen Gesellschaft* **92**: 109–116. <https://www.biodiversitylibrary.org/page/29007476>
- 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*. GE Beer, Leipzig, 889 pp.
- 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. <https://www.biodiversitylibrary.org/page/12862913>
- GUDE GK. 1920. Presidential Address. The armature of land Mollusca. *Proceedings of the Malacological Society of London* **14**: 52–73. <https://www.biodiversitylibrary.org/page/30346763>
- HAAS F. 1951. Remarks on and descriptions of South American non-marine shells. *Fieldiana: Zoology* **31**: 503–545. <https://www.biodiversitylibrary.org/page/2784155>
- HIDALGO JG. 1870. Catalogue des coquilles terrestres recueillies par les naturalists de la commission scientifique espagnole sur divers points de l'Amérique méridionale. *Journal de Conchyliologie* **18**: 27–70. <https://www.biodiversitylibrary.org/page/15160446>
- HIDALGO JG. 1872 [“1869”]. Moluscos del Viaje al Pacífico verificado de 1862 a 1865 por una comisión de naturalistas enviada por el Gobierno Español. Parte Primera, Univalvos Terrestres. Bailly-Ballière, Madrid, 152 pp. doi: 10.5962/bhl.title.10265
- HIDALGO JG. 1893a. 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.) *1893–1900 Obras Malacológicas. Parte III, Descripción de los moluscos recogidos por la Comisión Científica enviada por el Gobierno Español a la América Meridional*. Aguado, Madrid, 75–134.
- HIDALGO JG. 1893b. Descripción de los moluscos terrestres recogidos durante el viaje al Pacífico, verificado de 1862 a 1865 por una Comisión de naturalistas enviada por el Gobierno español. In: Hidalgo JG (ed.) *1893–1900 Obras Malacológicas. Parte III, Descripción de los moluscos recogidos por la Comisión Científica enviada por el Gobierno Español a la América Meridional*. Aguado, Madrid, 134–331.
- KOBELT W. 1906. Die raublungenschncken (Agnata) zweite abtheilung: Streptaxidae und Daudebardiidae. *Systematisches Conchylien Cabinet* **1** (12): 1–211. doi: 10.5962/bhl.title.123970
- LANGE DE MORRETES F. 1949. Ensaio de catálogo dos moluscos do Brasil. *Arquivos do Museu Paranaense* **7**: 1–216.
- LOPEZ HS, ALVARENGA M. 1957. Contribuição ao conhecimento dos moluscos da Ilha de Fernando de Noronha – Brasil. *Boletim do Instituto Oceanográfico* **6**: 157–190. doi: 10.1590/s0373-55241955000100005
- MARTENS E VON. 1868. Ueber südbrasilianische land- und süßwassermollusken. *Malakozoologische Blätter* **15**: 169–217. <https://www.biodiversitylibrary.org/page/16224128>
- MILLER K. 1878. Die Binnenmollusken von Ecuador. *Malakozoologische Blätter* **25**: 153–199. <https://www.biodiversitylibrary.org/page/15855524>
- MIQUEL SE, CADÍZ LORCA FJ. 2008. *Araucocharopa gallardoi* gen. et sp. n. de Charopidae (Mollusca: Gastropoda: Stylommatophora) del sur de Chile. *Revista del Museo Argentino de Ciencias Naturales, nueva serie* **10** (2): 329–340. doi: 10.22179/revmacn.10.287
- MIQUEL SE, RODRÍGUEZ PE. 2015. A novel late Early Miocene assemblage of terrestrial gastropods from Santa Cruz (Patagonia, Argentina). *Journal of Paleontology* **89** (5): 748–761. doi: 10.1017/jpa.2015.66

- 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, 170 pp. doi: 10.5962/bhl.title.11189
- MORICAND S. 1851. Description de deux espèces d'hélices (S.G. *Streptaxis*). *Journal de Conchyliologie* **2**: 369–371. <https://www.biodiversitylibrary.org/page/15855244>
- PILSBRY HA. 1894. *Manual of Conchology, Structural and Systematic, with Illustrations of the Species, Second Series: Pulmonata, Vol. 9: Helicidae Vol. 7*. Academy of Natural Sciences of Philadelphia, Philadelphia, 126 pp. doi: 10.5962/bhl.title.6534
- PFEIFFER L. 1852. Neue Heliceen. *Zeitschrift für Malakozoologie* **8** (8): 127–128. <https://www.biodiversitylibrary.org/page/16300627>
- PFEIFFER L. 1853. *Monographia Heliceorum Viventium. Volumen Tertium*. F.A. Brockhaus, Lipsiae, 711 pp. doi: 10.5962/bhl.title.10791
- PFEIFFER L. 1855–1856. Versuch einer Anordnung der Heliceen nach natürlichen Gruppen. *Malakozoologische Blätter* **2**: 112–185. <https://www.biodiversitylibrary.org/page/15864853>
- PFEIFFER L. 1859a. Description of twenty-seven new species of land-shells, from the collection of H. Cuming. *Proceedings of the Zoological Society of London* **27**: 23–29. <https://www.biodiversitylibrary.org/page/44707276>
- PFEIFFER L. 1859b. Einige Nachträge zum zweiten Supplemente meiner Monographia Heliceorum (Fortsetzung). *Malakozoologische Blätter* **6**: 1–53. <https://www.biodiversitylibrary.org/page/16014099>
- PFEIFFER L. 1867. Descriptions de deux nouvelles espèces de *Streptaxis*. *Journal de Conchyliologie* **15**: 43–44. <https://www.biodiversitylibrary.org/page/15381956>
- RAMÍREZ R. 1993. A generic analysis of the family Systrophiiidae (Mollusca: Gastropoda): taxonomy, phylogeny and biogeography. Unpublished master's dissertation, University of Kansas, Kansas City, 218 pp. <https://hdl.handle.net/1808/25695>
- RAMÍREZ R, PAREDES C, ARENAS J. 2003. Moluscos del Perú. *Revista de Biología Tropical* **51** (suppl. 3): 225–284. <https://revistas.ucr.ac.cr/index.php/rbt/article/view/26386>
- RICHARDSON CL. 1989. Streptaxacea: catalog of species, part 2. *Tryonia* **18**: 1–152.
- RIDLEY HN. 1890. Notes on the zoology of Fernando Noronha. *Zoological Journal of the Linnean Society* **20**: 473–570. doi: 10.1111/j.1096-3642.1886.tb02243.x
- 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, 199 pp. doi: 10.5962/bhl.title.10588
- RAVALO LGO, GARGOMINY O, SALVADOR RB. 2023. New species of Miradiscops (Gastropoda: Scolodontidae) from Martinique. *Folia Malacologica* **31**: 129–135. doi: 10.12657/folmal.031.018
- ROOSEN MT, BREURE ASH. 2024a. Revision of the genera of Scolodontidae part 1: *Happia* Bourguignat, 1890 from *Austroselenites* Kobelt, 1905, *Drepanostomella* Bourguignat, 1890, *Hirtudiscus* Hylton Scott, 1973, *Luteostriatella* gen. nov., and *Systrophiiella* H.B. Baker, 1925. *Journal of Conchology* **45**: 91–110. doi: 10.61733/jconch/4511
- ROOSEN MT, BREURE ASH. 2024b. *Helix entodonta* L. Pfeiffer, 1859, a terrestrial snail from Ecuador, is a species of *Zilchistrophia* Weyrauch, 1960 (Gastropoda: Scolodontidae): Implications for the diagnosis and interpretation of *Systrophia* Pfeiffer, 1855 and *Entodina* Ancey, 1887. *Folia Malacologica* **32**: 186–190. doi: 10.12657/folmal.032.016
- ROOSEN MT, BREURE ASH. 2024c. Revision of the genera of Scolodontidae, part 2: *Guestieria* Crosse, 1872, *Xenodiscula* Pilsbry, 1919, and a misidentified planorbid. *Journal of Conchology* **45**: 245–250. doi: 10.61733/jconch/4524
- ROOSEN MT, WEIJSSENFELD J, DORADO C. 2023. Notes on the genus *Xenodiscula* Pilsbry, 1919 (Gastropoda, Scolodontidae), with the description of a new species from NW Ecuador. *Folia Malacologica* **31**: 100–106. doi: 10.12657/folmal.031.014
- ROSA RM, CAVALLARI DC, SALVADOR RB. 2022. iNaturalist as a tool in the study of tropical molluscs. *PLOS ONE* **17**: e0268048. doi: 10.1371/journal.pone.0268048
- SALGADO N, COELHO AC. 2003. Moluscos terrestres do Brasil (Gastropodes operculados ou não, exclusive Veronicellidae, Milacidae e Limacidae). *Revista de Biología Tropical* **51** (Supplement 3): 149–189. <https://revistas.ucr.ac.cr/index.php/rbt/article/view/26367>
- SALVADOR RB. 2018. Notes on a new collection of Streptaxidae (Gastropoda: Stylommatophora) from Brazil, with descriptions of two new species of *Streptaxis*. *Integrative Systematics (Stuttgart Contributions to Natural History)* **1**: 25–33. doi: 10.18476/insy.v01.a4
- 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. 2021. Phylogenetic position of the genus *Ridleyconcha* (Gastropoda, Stylommatophora). *American Malacological Bulletin* **38**: 63–71. doi: 10.4003/006.038.0212
- SALVADOR RB, CAVALLARI DC. 2020. Taxonomy and distribution of the enigmatic “helicoid” *Polygyratia* Gray, 1847 (Gastropoda, Stylommatophora). *Zoosystematics and Evolution* **96**: 91–101. doi: 10.3897/zse.96.51047
- 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**: 249–280. doi: 10.1127/njgpa/2018/0760
- SALVADOR RB, CAVALLARI DC, CHRISTENSEN CC, FREITAS AVL, MIRANDA MS, PASSOS FD. 2022. The endemic land snails of the Fernando de Noronha Archipelago, Brasil. *Tentacle* **30**: 6–8.
- SALVADOR RB, MIRANDA MS, SILVA FS, OLIVEIRA CDC, ARRUDA JO, CAVALLARI DC, GOMES SR, LA PASTA A, PENA MS, OVANDO XMC, ROSA RM, SALLES ACA, SANTOS SB, SIMONE LRL, MACHADO FM. 2024. Checklist of the terrestrial gastropods of Brazil. *Journal of Conchology* **45**: 141–185. doi: 10.61733/jconch/4516
- SERAFINI T'Z, FRANÇA GB, ANDRIGUETTO-FILHO JM. 2010. Ilhas oceânicas brasileiras: biodiversidade conhecida e sua relação com o histórico de uso e ocupação humana. *Revista da Gestão Costeira Integrada* **10**: 281–301. doi: 10.5894/rgci178
- SOUVERBIE SM. 1858. Description d'espèces nouvelles. *Journal de Conchyliologie* **7**: 63–66. <https://www.biodiversitylibrary.org/page/15863036>
- SIMONE LRL. 2006. *Land and freshwater molluscs of Brazil*. EGB/FAPESP, São Paulo, 390 pp.
- TAUBER AA. 1997. Bioestratigrafia de la Formación Santa Cruz (Mioceno Inferior) en el extremo sudeste de la Patagonia. *Ameghiniana* **34**: 413–426.
- THIELE J. 1927. Über einige brasilianische Landschnecken. *Abhandlungen der Senckenbergischen Naturforschenden Gesellschaft* **40**: 308–329.
- TRYON GW. 1885. *Manual of Conchology, Structural and Systematic, with Illustrations of the Species, Second Series: Pulmonata, Vol. 1: Testacellidae, Oleacinidae, Streptaxidae, Helicoidea, Vitrinidae, Limacidae, Arionidae*. G.W. Tryon, Philadelphia, 363 pp. doi: 10.5962/bhl.title.6534
- 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. doi: 10.5962/bhl.title.6534
- WEYRAUCH WK. 1960. Zwanzig neue Landschnecken aus Peru. *Archiv für Molluskenkunde* **89**: 23–48.

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