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Revision of the genera of Scolodontidae, part 1: disentangling *Happia* Bourguignat, 1890 from *Austroselenites* Kobelt, 1905, *Drepanostomella* Bourguignat, 1890, *Hirtudiscus* Hylton Scott, 1973, *Luteostriatella* gen. nov., and *Systrophiella* H.B. Baker, 1925

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Abstract. Currently there are several problems with the genus-level taxa within the Scolodontidae. Multiple type-species designations have been proposed for some genera, type species are poorly described, and in some cases no clear decisions have been made in cases of homonymy or synonymy. This has resulted in wrongly identified species and genera within this group, which, among other problems, hinders the discovery and description of new species as well as the identification of known species. This paper is the first in a series in which all scolodontid genera will be redescribed based on type materials, starting with *Happia* Bourguignat, 1890 and its allies. Nomenclatural issues are resolved where possible. One new genus and a new species are described: *Luteostriatella* **gen. nov.** and *Austroselenites pichinchense* **sp. nov.** The following new combinations are made: *Happia andia* (Pilsbry, 1932) **comb. nov.**, *Systrophiella altivaga* (Crawford, 1939) **comb. nov.**, *Systrophiella cayennensis* (L. Pfeiffer, 1842) **comb. nov.**, *Systrophiella pygmea* (Spix *in* Spix & Wagner, 1827) **comb. nov.**, *Systrophiella snethlagei* (F. Baker, 1913) **comb. nov.**, *Systrophiella vitrina* (J.A. Wagner *in* Spix & Wagner, 1827) **comb. nov.**, and *Luteostriatella variegata* (F. Haas, 1949) **comb. nov.**

Key words. Neotropics, South America, Mollusca, Gastropoda, Eupulmonata, Scolodontina

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Introduction

Scolodontidae are a species-rich but understudied family of land snails (Ramírez 1993). Recent genetic studies suggest that the family forms its own suborder (Scolodontina) within the Stylommatophora (Bouchet *et al.* 2017; Saadi & Wade 2019). Scolodontids occur only in the Neotropical region and are mostly represented by small species (Ramírez 1993; Barbosa 2014). Many of these small species remain unknown to science, as shown by Wendebourg & Hausdorf (2019) and Ramirez Perez & Hausdorf (2022), who discovered many new species in the rainforests of the Peruvian Amazon and Ecuadorian Chocó, but most of these reported species could not be identified below the family level. A similar high diversity of unknown Scolodontidae is also recognised elsewhere in Ecuador (Roosen 2019).

Describing these taxa is currently hindered by two issues. Most taxa are only known from their shells, which show few characteristics for comparison, and the genera are poorly defined and their limits often seem confusing and overlapping. A good example of this is the recently published case of *Hirtudiscus excisa* (Reeve, 1854), which has been only figured by Reeve (1854) and Breure *et al.* (2022) and was used to define *Drepanostomella* Bourguignat, 1890 by Baker (1925a), Ramirez (1993), Hausdorf (2003), and Breure *et al.* (2022), even though it is much smaller and has a different sculpture than the type species of *Drepanostomella* (see Roosen 2023).

The most problematic genus is probably *Happia* Bourguignat, 1890, which is currently used for 42 species (MolluscaBase 2023a) of morphologically distinct scolodontids.

Happia was introduced by Bourguignat (1890) as a replacement name for *Ammonoceras* L. Pfeiffer, 1855 (*non* Lamarck, 1822). The type species of *Ammonoceras* is *Helix ammonoeras* Reeve, 1854, designated by absolute tautonymy in accordance with International Code of Zoological Nomenclature Article 68.4 (ICZN 2023). However, Bourguignat (1890) placed this species in *Drepanostomella*. Gude (1902) either overlooked this error or followed Pfeiffer & Clessin (1881) and designated *Helix vitrina* as the type species of *Happia*, an interpretation later adopted by many authors (e.g. Baker 1925a). To complicate matters, Baker (1925a) used *Helix ammonoceras* along with *Hirtudicus excisa* to establish the genus diagnosis of *Drepanostomella* (Roosen 2023) and *Helix euspira* Reeve, 1854, the type species of *Austroselenites* Kobelt, 1905, is currently included in *Happia* (e.g. Simone 2006; Agudo-Pádron 2023; MolluscaBase 2023b). *Austroselenites* has been placed in the family Haplotrematidae H.B. Baker, 1925 since the publication of Baker (1941).

These unresolved issues within scolodontid taxonomy hinder proper research of both known and unknown taxa. This family needs an urgent revision, especially at the genus level. Proper identification at the genus level is currently nearly impossible, and placement of some taxa within the Scolodontidae is doubtful at best. This is the first paper of a series we have in preparation that aims to properly diagnose scolodontid genera based on their type species and other relevant species. These papers are organized in a manner that facilitates disentangling the most prominent nomenclatural issues in this group and do not reflect currently accepted taxonomic order.

Materials and Methods

To revise the known scolodontid genera, we undertook a comprehensive study of all literature available to us containing information on these genera, the type specimens of the type species, and most species from Ecuador and Peru. The latter were already located in museum collections and imaged for unrelated projects and for that reason readily available for the current study (Breure *et al.* 2022). Shell characteristics useful for identification are highlighted and a new species relevant for the diagnosis of the genera is presented in this paper.

Specimens were imaged by scanning electron microscopy (SEM) and light microscopy under stereomicroscopes at the institutes where the specimens are deposited at or at the Royal Belgian Institute of Natural Sciences. Measurements were taken to the nearest 0.1 mm during the imaging process or with vernier callipers. The shell height (H) was measured from the apex to the lower lip of the aperture, width (W) at the widest section perpendicular to the coiling axis, height of the aperture (HA) from the lowest point of the peristome to the upper part of the whorl, and the umbilical width (UW) at the widest section starting at the columella. All measurements are in millimetres. Whorls were counted to the nearest ¼ whorl following Gittenberger *et al.* (2004). Other abbreviations used adapted from original descriptions are largest diameter (Diam. Maj.; D), smallest diameter (Diam. Min.; D3), height (alt., long.), and width (lat.).

For many genera only the shells of the type species are known. Therefore, we only use conchological characteristics of the type specimens to define the genera. DNA and anatomy should be studied, but this is beyond the scope of this paper. We have analysed type specimens or clear photographs of type specimens for all species treated in this paper. Taxa that we did not study should be treated as tentative members of the genera in which they are currently placed, with exception of *Happia*. The species of *Happia* not examined in this study are tentatively moved to *Systrophiella* unless indicated otherwise.

Specimens from the following museum collections were studied: Academy of Natural Sciences of Drexel University, Philadelphia, Pennsylvania, USA (ANSP); Field Museum of Natural History, Chicago, Illinois, USA (FMNH); Museo de La Plata, La Plata, Argentina (MLP); Muséum National d'Histoire Naturelle, Paris, France (MNHN), Natural History Museum, London, United Kingdom (NHM, NHMUK); Pontificia Universidad Católica del Ecuador, Quito, Ecuador (PUCE, QCAZI); Zoologische Staatssammlung München, Munich, Germany (ZSM, SNSB). Other institutes mentioned: Leibniz Institute for the Analysis of Biodiversity Change, Hamburg, Germany (LIB); Royal Belgian Institute of Natural Sciences, Brussels, Belgium (RBINS).

Systematics

Family Scolodontidae H.B. Baker, 1925

Scolodontidae Baker 1925b: 88.

In this paper we discuss six scolodontid genera with complex nomenclatural histories. To avoid further confusion, we list the most important conchological characteristics to distinguish the genera in Table 1.

Genus *Happia* Bourguignat, 1890

Ammonoceras L. Pfeiffer 1855: 122; junior homonym of *Ammonoceras* Lamarck, 1822.

Table 1. Key differences between the scolodontid genera discussed in this paper. The genera are ordered in accordance with their appearance in the main text of the paper.

Genus	Parietal incision	Maximum diameter (mm)	Sculpture
Happia Bourguignat, 1890	Yes	2.5–4.5	Spiral rows of papillae or striae
Drepanostomella Bourguignat, 1890	Yes	25–30	Absent or vestigial spiral sculpture
Hirtudiscus Hylton Scott, 1973	Yes	4–6	Protoconch with spiral lirae, teleoconch with periostracal hairs and wavy axial ribs
Systrophiella F. Baker, 1925	No	<18	Absent or vestigial spiral sculpture
Luteostriatella gen. nov.	No	<10	Absent, but periostracum with bands of colour
Austroselenites Kobelt, 1905	No	25–35	Fine axial ribbing

Happia Bourguignat 1890: 39. Type species: *Helix ammonoceras* Reeve, 1854 (typification of the replaced name).

Diagnosis. Shell small, discoid to subdiscoid, transparent-whitish. First whorl without sculpture. Second, third, and fourth whorls with weak growth striae and spiral rows of papillae or microscopic spiral grooves. Umbilicus wide. Aperture broadly lunulate. Peristome simple, with an acute incision in parietal angle.

Species included in the genus. *Happia ammonoceras* (Reeve, 1854), *Happia andia* (Pilsbry, 1932) comb. nov.

Species tentatively included in the genus. *?Happia lyzarzaburui* (Jousseaume, 1887).

Geographic range. Colombia and Peru. Questionably Ecuador.

Comparisons. In size and general shape true *Happia* is most similar to *Hirtudiscus* Hylton Scott, 1973 and *Xenodiscula* Pilsbry, 1919. However, they do not have a punctate or striate microsculpture, which is typical of *Happia*. Moreover, *Xenodiscula* does not have an acute incision in the parietal angle. *Drepanostomella* Bourguignat, 1890 is also a group of discoid scolodontids with an incision in the parietal angle of the aperture, but this genus has no punctate or striate microsculpture and the adult shells are much larger. For more information on *Xenodiscula*, we refer to Pilsbry (1919) and Roosen *et al.* (2023).

In this study, only species for which the spiral rows of papillae (Fig. 1A–E) or microscopic spiral grooves are confirmed by detailed SEM photomicrographs are included in *Happia*, as we consider this type of spirally oriented microsculpture typical for the genus. Within the Scolodontidae only *Miradiscops* H.B. Baker, 1925 and its subgenera have similar pitted or striate microsculpture, which was especially well documented by Ravalo *et al.* (2023). However, *Happia* differs from *Miradiscops* by its sunken spire, less convex whorls, and acute incision in parietal angle of the peristome. The group of *Miradiscops* will be discussed in a subsequent paper.

Remarks. The confusion about the identity of the type species of *Happia* pre-dates the replacement of *Ammonoceras* L. Pfeiffer, 1855 (*non* Lamarck, 1822) by *Happia* in Bourguignat (1890). No clear type designation was given in any of Pfeiffer's papers, but according to ICZN Article 68.4, *Helix ammonoceras* Reeve, 1854 should be regarded as the type species by absolute tautonymy. As several authors (e.g. Baker 1925a; Breure *et al.* 2022) have acknowledged this species as the type of *Ammonoceras* (and by extension *Happia*) and it is the oldest known type designation, it cannot be replaced by a later designation, as stated in ICZN Article 70.2. As there is confusion around the identity of *Happia* (see below), the decision to go back to the original type species is needed to stabilise *Happia*.

So where did the original definition of *Happia* get lost? As early as 1863, Thomas Bland considered *Helix euspira* L. Pfeifer, 1854—the type species of *Austroselenites* Kobelt, 1905—to be the type species of *Ammonoceras* (= *Happia*) (Bland 1863). In a paper published after Pfeiffer's death (Clessin & Pfeiffer 1881), *Helix vitrina* J.A. Wagner *in* Spix & Wagner, 1827 is the proposed type species of *Ammonoceras*. After this, Tryon (1885) further complicated matters by regarding *Helix ammoniformis* d'Orbigny, 1835—the type species of *Drepanostomella* Bourguignat, 1890—as the type species of *Ammonoceras*. Bourguignat (1890) later replaced *Ammonoceras* with *Happia*, but moved its type species, *Helix ammonoceras*, to *Scolodonta* Doering, 1874, and Gude (1902) designated *Helix vitrina* J.A. Wagner *in* Spix & Wagner, 1827 as the type species of *Happia*. Baker (1925a) recognised the problems with Gude's type designation, but he followed it regardless and defined *Drepanostomella* using *H. ammonoceras* along with *Helix excisa* Reeve, 1854, which is a species of *Hirtudiscus* Hylton Scott, 1973 according to Roosen (2023). Baker's views were later

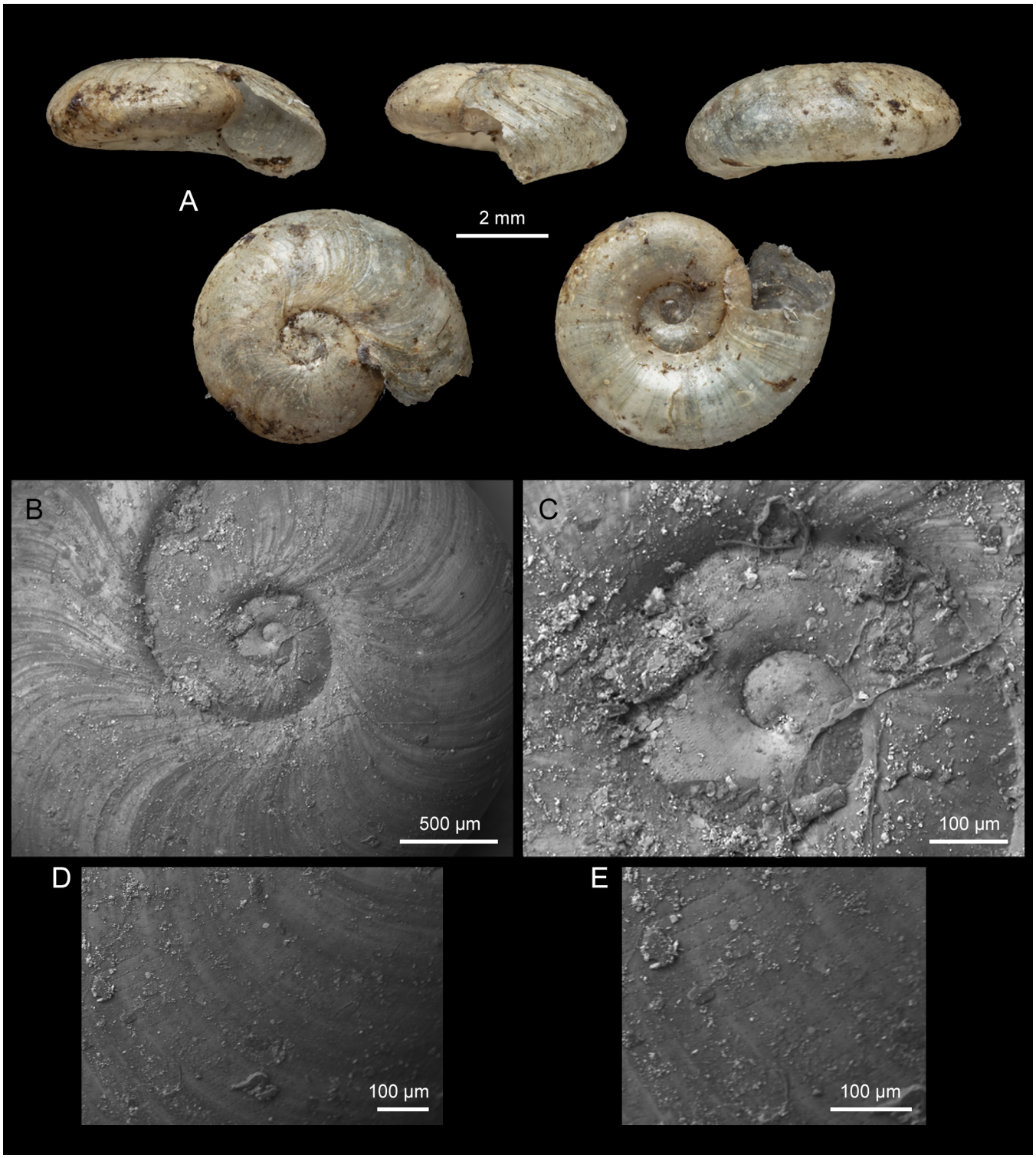

Figure 1. *Happia ammonoceras* (Reeve, 1854). **A–E**, NHMUK 20210342, syntype. **B–E** apical surface of same shell.

adopted by Ramírez (1993). Because of all of the above, several scolodontid genera became entangled with *Happia*, which resulted in all those species, including type species of other genera, being lumped together in *Happia*.

Happia ammonoceras (Reeve, 1854)

Figure 1

Helix ammonoceras Reeve 1854: pl. 191 fig. 1338; Pfeiffer 1855a: 54; Pfeiffer 1859: 104.

Helix (*Ammonoceras*) *ammonoceras* Pfeiffer—Pfeiffer 1855b: 122.
Streptaxis (*Ammonoceras*) *ammonoceras* (Pfeiffer)—Pfeiffer & Clessin 1881: 15.; Tryon 1885: 65, pl. 13, fig. 52.
Scolodonta ammonoceras (Pfeiffer)—Bourguignat 1890: 41.
Happia ammonoceras (Pfeiffer)—Gude 1902: 235.
Drepanostomella ammonoceras (Pfeiffer)—?Baker 1925: 23.; Ramírez 1993: 21.
Misidentification:
Streptaxis (*Ammonoceras*) *ammonoceras* (Pfeiffer)—Smith 1895: 315 (= unknown species).

Studied material. NHMUK 20210342 (syntypes, 3 shells, dry), "New Grenada".

Type locality. "Santa Anna, New Grenada".

Measurements. "Diam. maj. 4½, min. 3¾, alt. vix 1½ mill." (Pfeiffer 1855a: 55).

Redescription. Shell medium-sized, discoid, translucent, with a sunken spire. Embryonic whorl smooth. After one whorl, eight slightly oblique spiral rows consisting of densely spaced punctuations develop on last quarter of shell between suture and periphery. Spiral rows visible on entire shell and continue over periphery and onto base, only to disappear on last quarter whorl in umbilicus. Flexuous growth striae also present on entire shell but stronger towards aperture. Aperture deflected, rounded-trapezoidal in shape, with a small incision at suture. Peristome simple. Umbilicus wide, up to 32% of shell width.

Geographic range. Colombia.

Comparisons. Only "*Ammonoceras*" *lyzarzaburui* Jousseaume, 1887 is similar in shape and microsculpture. This species differs from *H. ammonoceras* by its smaller size, less distinct microsculpture that is only visible in high-resolution SEM images, and the absence of an incision in the upper left corner of the aperture. In some respects "*Ammonoceras*" *lyzarzaburui* is more similar to *Miradiscops*, but it differs from this genus by its smaller microsculpture and completely sunken spire. A new genus might have to be established for this species, but this requires further study of the type material and freshly collected shells from the "Un poco del Chocó" nature reserve (Roosen 2019). For differences with *H. andia* (Pilsbry, 1932) comb. nov., see that species.

Remarks. *Happia* sensu stricto is figured here for the first time since Reeve (1854). This is also the first time that spiral rows of papillae are documented for a scolodontid genus other than *Miradiscops*. It is unclear whether the record of this species by Baker (1925b) belongs to this taxon. If it does, its periostracum has spiral rows of papillae.

***Happia andia* (Pilsbry, 1932) comb. nov.**
Figure 2

Drepanostomella andia Pilsbry 1932: 400, fig. 5–5b—Baker 1963: 239; Richardson 1989: 118; Ramírez 1993: 21.

Studied material. ANSP 159924 (holotype, one shell, dry), "Leymebamba, Department of Amazonas, Peru, at 7,000 ft".

Type locality. "Leymebamba, Department of Amazonas, Peru, at 7,000 ft" (Pilsbry 1932).

Redescription. Shell minute, transparent-whitish, with a slightly sunken spire. Protoconch 1¼ whorl, without sculpture. Teleoconch sculpture starts with a patch of 16 small, densely crowded axial ribs and numerous indistinct spiral grooves. Spiral grooves cover entire teleoconch, but axial ribs become less crowded and distance between them more variable. Aperture ovate-drop-shaped, with thin, simple peristome. Umbilicus wide, up to 45% of shell width.

Dimensions. "Height 1 mm, Diam. 2.45 mm, 3¼ whorls" (Pilsbry 1932).

Differential diagnosis. It is most similar to *Happia ammonoceras* (Reeve, 1854), which differs from *H. andia* by its sculpture consisting of spiral rows of papillae and larger size.

Distribution. Peru: Amazonas department.

Remarks. Although the spiral sculpture and small size were documented by Pilsbry (1932), at that time these characters were not recognised as a significant in distinguishing *H. andia* from *Drepanostomella*.

Genus *Drepanostomella* Bourguignat, 1890

Drepanostomella Bourguignat 1890: 42. Type species *Helix ammoniformis* d'Orbigny, 1835 by monotypy.

Diagnosis. Shell large for family, discoid to subdiscoid, with concave to slightly elevated spire. Younger whorls partially cover older ones. Protoconch smooth; teleoconch with only growth lines. Aperture ovate, not deflected. Peristome simple, with an acute incision in parietal angle.

Species included in the genus. *Drepanostomella ammoniformis* (d'Orbigny, 1835), *D. tucma* Hylton Scott, 1948.

Species tentatively included in the genus. ?*Drepanostomella pinchoti* Pilsbry, 1930.

Species not evaluated. *Drepanostomella circumscripta* Hylton Scott, 1948, *D. stolli* (E. von Martens, 1892), *D. uruguayana* Hylton Scott, 1979.

Geographic range. Panama, Brazil, Bolivia, Uruguay, and Argentina.

Comparisons. Species belonging to *Happia* have often erroneously be assigned to *Drepanostomella*, probably because of the invalid subsequent type designation of *Helix ammoni-*

Figure 2. *Happia andia* (Pilsbry, 1932). **A–C**, ANSP 159924, holotype. **B, C**, apical surface of same shell.

formis d'Orbigny, 1835 as type species of *Ammonoceras* L. Pfeiffer, 1854 (= *Happia* Bourguignat, 1890) by Tryon (1885) (see the discussion of *Happia*). However, *Drepanostomella* differs from *Happia* by its larger size and the absence of punctate or striate microsculpture on the protoconch and/or teleoconch.

As shown by Roosen (2023), a species of *Hirtudiscus* Hylton Scott, 1973 was used to provide a diagnosis of *Drepanostomella* in several major papers on Scolodontidae (e.g. Baker 1925a). Because of this, *Hirtudiscus* might be confused with *Drepanostomella*. This genus differs from *Hirtudiscus* by its much larger size, smooth protoconch and simple periostracum (e.g. Hausdorf 2003; Hausdorf & Medina 2006; Roosen 2023).

Remarks. Recently *Drepanostoma nautiliforme* Porro, 1836, was reported from Ecuador as *Drepanostomella nautiliforme* in a paper on iridescence in terrestrial gastropods (González & Teruel 2022). However, this is likely a misidentification, as *Drepanostoma* Porro, 1836 is an unrelated European genus. We noticed shells of *Guestieria* cf. *powisiana* (L. Pfeiffer, 1848) misidentified as *Drepanostomella nautiliforme* (Porro, 1836) on Femorale.com, the website of a Brazilian shell vendor showcasing shells for sale (Femorale 2023). Perhaps González & Teruel (2022) and the Femorale website used the same erroneous source to identify *Guestieria* Crosse, 1872 species as *Drepanostoma nautiliforme*. If so, this source was not found by us. That said, it could also be a simple error based on a misinterpretation of the similarity of *Drepanostoma* to *Drepanostomella*, the tendency of authors to describe the shape *Guestieria* species as "nautiliform" (e.g. Jousseaume 1887) and the comparison of *Guestieria* to *D. nautiliforme* in the original description of *Guestieria* (Crosse 1872). The genus *Guestieria* will be discussed in a later paper.

Drepanostomella ammoniformis (d'Orbigny, 1835)

Figure 3

Helix (*Helicella*) *ammoniformis* d'Orbigny 1835: 5.
Helix ammoniformis—Férussac & Deshayes 1850: pl. 69B, fig. 1; Gray 1854: 11.
Ammonoceras ammoniformis—Doering 1875: 441; Pfeiffer 1876: 41; Pfeiffer & Clessin 1881: 15.

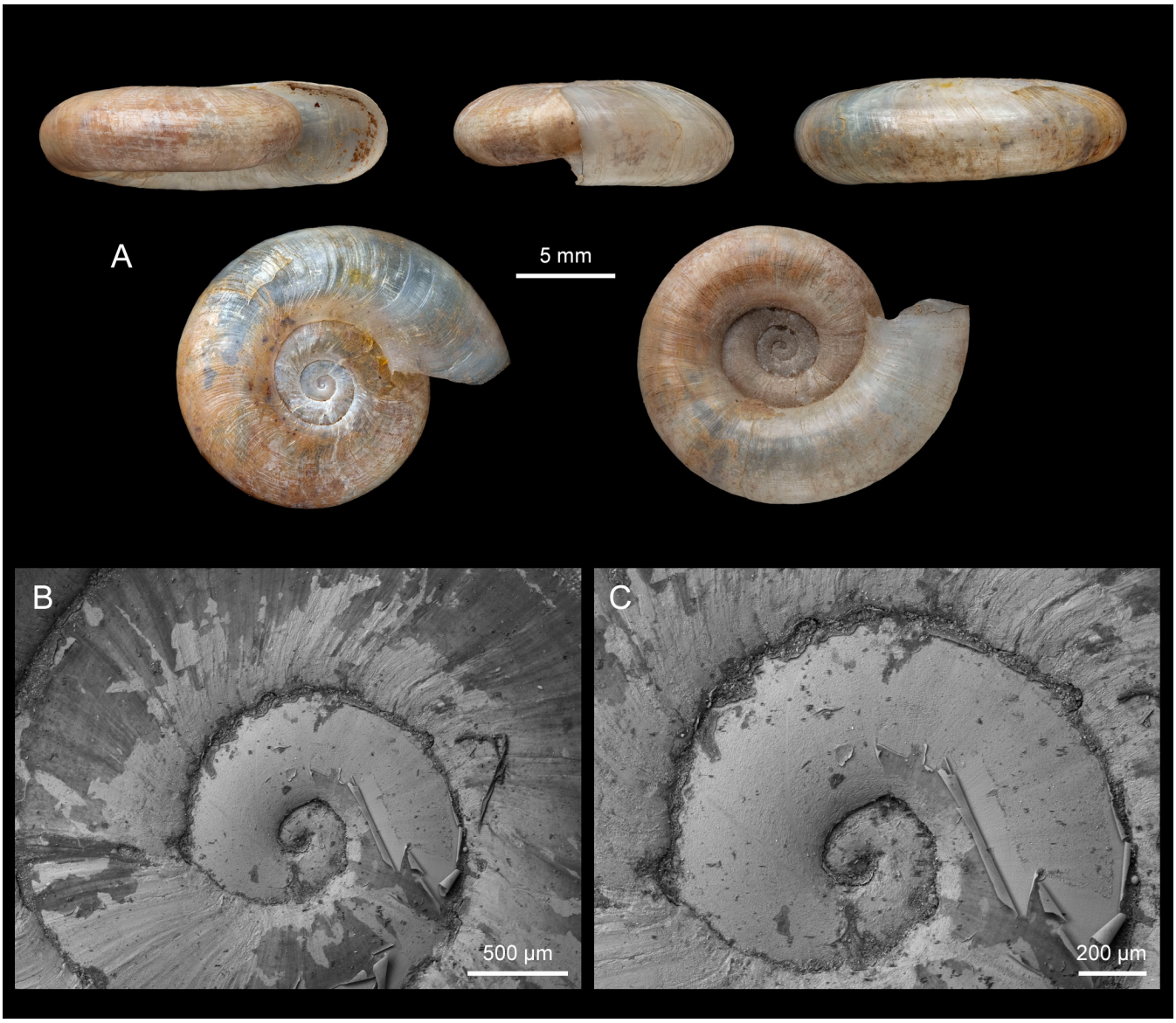

Figure 3. *Drepanostomella ammoniformis* (d'Orbigny, 1835). **A–C**, NHMUK 1854.12.4.105, syntype. **B, C**, apical surface of same shell.

Hyalinia ammoniformis—Clessin 1888: 166.
Drepanostomella ammonitiformis—Bourguignat 1890: 43 (incorrect subsequent spelling).
Happia (*Drepanostomella*) *ammoniformis*—Haas 1949: 243.
Drepanostomella ammoniformis—Ramirez 1993: 19; Roosen 2023: 108, fig. 5

Studied material. NHMUK 1854.12.4.105 (syntypes, 5 shells, dry), Yungas Province, Bolivia; MNHN-IM-2000-25753 (syntype, 1 shell, dry), Yungas Province, Bolivia.

Type locality. "provincia Yungasensi (republica Boliviana)".

Measurements. "Long. 6 millim.; latit. 18 millim., amplit. 27 millim." (d'Orbigny 1835).

Redescription. Shell discoid, rather large for the family (up to 27 mm wide), with a sunken spire. Protoconch–teleoconch transition unclear. Microsculpture of minute growth striae on teleoconch. Some specimens with vestigial spiral sculpture on earlier whorls. Aperture ovate; peristome thin, with an incision in upper left corner of aperture. Umbilicus wide, up to 37% of shell width.

Geographic range. Bolivia and Argentina.

Comparisons. This species is most similar to *Drepanostomella tucma* Hylton Scott, 1948, which is distinguished from *D. ammoniformis* by its smaller size. *Drepanostomella tucma* Hylton Scott, 1948 was recently revised by Cuezzo & Miranda (2009).

Genus *Hirtudiscus* Hylton Scott, 1973

Hirtudiscus Hylton Scott 1973: 128. Type species *Hirtudiscus hirtus* Hylton Scott, 1973 by original designation.

Redescription. Shell small, up to 6 mm wide, subdiscoid to discoid, with a flat or only slightly raised spire. Protoconch often with more or less distinct, scalloped spirals; teleoconch sculpture of thin, wavy axial ribs. Periostracum brownish, with thin, often spirally arranged periostracal hairs. Aperture drop-shaped to trapezoidal, with an acute incision in parietal angle.

Species included in the genus. *Hirtudiscus antioquiensis* Hausdorf & Medina, 2006, *H. boyacensis* Hausdorf, 2003, *H. comatus* Hausdorf, 2003, *H. curei* Hausdorf, 2003, *H. excisa* (Reeve, 1854), *H. hirtus* Hylton Scott, 1973, *H. triserialis* Hausdorf & Medina, 2006.

Geographic range. Colombia, Ecuador, and Peru.

Comparisons. *Hirtudiscus* can be distinguished from all other Scolodontidae by its small shell size, waved spirals on the protoconch and complex periostracal structures.

Remarks. Until recently *Hirtudiscus excisa* (Reeve, 1854) was regarded as a typical species of *Drepanostomella*. This was resolved by Roosen (2023), by redescribing the species while comparing it to *Hirtudiscus hirtus* Hylton Scott, 1973 and *Drepanostomella ammoniformis* (d'Orbigny, 1835). For the differences between *Hirtudiscus* and *Drepanostomella*, see the discussion of *Drepanostomella*.

The record from Peru is based on an unnamed species reported by Wendebourg & Hausdorf (2019) from the Panguana reserve in the Peruvian Amazon. Even though the species is likely undescribed, this record is worth mentioning, as it presents a significant range extension for the genus.

Hirtudiscus hirtus Hylton Scott, 1973

Figure 4

Hirtudiscus hirtus Hylton Scott 1973: 129, fig. 2—Hausdorf 2003: 179, fig. 4A, 5A, B, 6; Hausdorf & Medina 2006: 211; Roosen 2023: fig. 4.

Studied material. MLP 3965, holotype, "Monte Redondo, Colombia oriental, entre Bogotá y Villavicencio, 3800 m alt." (images only).

Type locality. "Monte Redondo, Colombia oriental, entre Bogotá y Villavicencio, 3800 m alt." (Hylton Scott 1973; Hausdorf 2003).

Measurements. "D: 3.9; D3: 3.1; H: 1.8 mm" (Hausdorf 2003).

Redescription. Shell small, nearly discoid, with a flat spire. Protoconch of 1¾ whorls, separated from teleoconch by a distinct scar. Spiral striae distinct on protoconch. Teleoconch with dense growth striae and, on damaged base, spirally arranged periostracal hairs. Body whorl rounded,

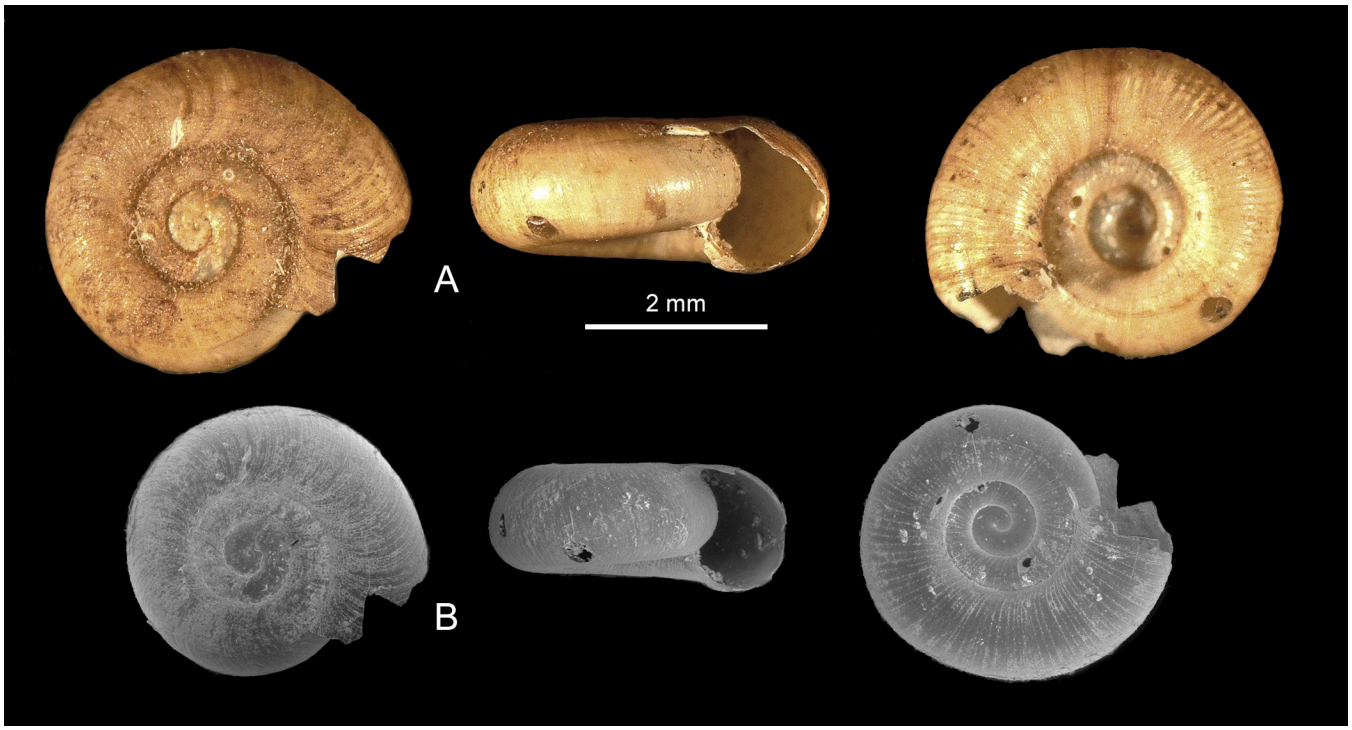

Figure 4. *Hirtudiscus hirtus* Hylton Scott, 1973. **A, B**, MLP 3965, holotype. **B**, SEM images of same shell, not at the same scale as A.

aperture broadly lunulate. Peristome sharp, neither expanded nor thickened, with an incision in parietal angle of aperture near suture. Umbilicus wide, occupying about 42% of shell width.

Geographic range. Colombia.

Comparisons. *Hirtudiscus hirtus* differs from other species by its flat spire, comparatively smaller axial ribbing and comparatively shorter periostracal hairs. *Hirtudiscus triserialis* Hausdorf & Medina, 2006 is somewhat similar in shape, but *H. hirtus* has more and shorter periostracal hairs (*H. triserialis* only has three spirally rows of periostracal hairs) and has a smaller adult size. For an in-depth description and comparison of all *Hirtudiscus* species, see Hausdorf (2003), Hausdorf & Medina (2006), and Roosen (2023).

Remarks. Periostracal hairs seem to worn of on the type, but they were present when Hylton Scott (1973) examined the specimen and are visible on the original figures.

Genus *Systrophiella* H.B. Baker, 1925

Systrophiella H.B. Baker 1925a: 15, 31. Type species: *Scolodonta* (*Systrophiella*) *eudiscus* H.B. Baker, 1925 by original designation.

Redescription. Shells small to medium-sized, subdiscoid to discoid, with a flat or only slightly elevated spire and thin, yellow-brown to brown periostracum. Protoconch without sculpture; teleoconch with some vestigial spiral sculpture most often present on the teleoconch. Whorls slowly increase in diameter. The umbilicus wide to very wide, aperture subcircular, peristome simple. The last section of the body whorl can be slightly deflected.

Species included in the genus. *Systrophiella alicea* (Guppy, 1871), *S. altivaga* (Crawford, 1939) comb. nov., *S. cayennensis* (L. Pfeiffer, 1842) comb. nov., *S. eudiscus* (H.B. Baker, 1925), *S. lobaterita* (H.B. Baker, 1925) *S. pygmea* (Spix *in* Spix & Wagner, 1827) comb. nov., *S. snethlagei* (F. Baker, 1913) comb. nov., *S. starkei* (H.B. Baker, 1925), *S. viridis* (H.B. Baker, 1925), *S. vitrina* (J.A. Wagner *in* Spix & Wagner, 1827) comb. nov., *S. weyrauchi* (F. Haas, 1951).

Geographic range. Venezuela, French Guinea, Brazil, and Peru.

Comparisons. Conchologically *Systrophiella* is most similar to *Scolodonta*, but it differs from this genus by its larger size and presence of vestigial spiral sculpture on the teleoconch. For more information on *Scolodonta*, see Hausdorf (2006).

Remarks. Based on current information, this genus cannot be separated from the *Helix vitrina* group (= the dominant definition of *Happia* since the incorrect subsequent designation of *H. vitrina* as type species by Gude (1902)). No properly identified specimen of *H. vitrina* was available to us for dissection and comparison to the anatomy of *S. eudiscus* as reported by Baker (1925a).

Baker (1925a) regarded the presence of vestigial spiral sculpture on the teleoconch as the distinguishing character in separating shells of the *H. vitrina* group from *Systrophiella*. However, we found some vestigial spiral sculpture on the teleoconch of the syntypes of *Systrophiella eudiscus*, *H. vitrina*, and *H. nana*, so this character cannot be used to separate these taxa at the generic level. Therefore, we tentatively include the *H. vitrina* group in *Systrophiella*, while acknowledging they might be different. Pending further study, all orphaned species previously included in *Happia* based on their similarities with *Systrophiella vitrina* comb. nov. are moved to *Systrophiella*, except for *Prohappia besckei* (Dunker, 1847), which likely should be maintained in a separate genus (Roosen & Breure in prep.).

Baker (1925a) noted that *Helix thomasi* L. Pfeiffer, 1855 from Marmato (Colombia) and some allied species are similar to *Systrophiella*, but they differ in their minute spiral sculpture. We have seen images of the syntypes of *H. thomasi* and tentatively agree with Baker that these shells require further study. The syntypes of this species will be discussed in a later paper, along with some striate shells currently included in *Miradiscops* and poorly known scolodontids described by Preston (1914).

Systrophiella eudiscus (H.B. Baker, 1925)

Figure 5

Scolodonta (*Systrophiella*) *eudiscus* Baker 1925a: 31 pl. 8 fig. 43; Baker 1926: 5.

Systrophiella eudiscus—Tillier 1980: 68, 194, 286, 292, figs 399–403.

Systrophia eudisca—Richardson 1989: 128.

Systrophia (*Systrophiella*) *eudiscus*—Ramírez: 68, fig. 14B.

Studied material. ANSP 140959, holotype, near La Fría, Venezuela.

Type locality. "near La Fría", Venezuela.

Measurements. "alt. 5.0, Shell maj. diam. 16.3, min. diam. 15.3, Aperture alt. 4.4, diam. 4.4 mm, Whorls 6¼" (Baker 1925a).

Redescription. Shell large for genus, discoid, semitranslucent, greenish brown. Protoconch of circa two whorls, with only rather indistinct growth wrinkles. Teleoconch whorls evenly rounded, slightly flattened above; suture shallow but distinct. Sculpture on teleoconch consists of rather prominent growth wrinkles. Aperture broadly lunulate, with thin, simple peristome. Umbilicus wide, up to 47% of shell width.

Figure 5. *Systrophiella eudiscus* (H.B. Baker, 1925), ANSP 140959, paratype.

Geographic range. Venezuela.

Comparisons. This species differs from others by its wide umbilicus and low spire. *Systrophiella weyrauchi* comb. nov. from the Peruvian Andes is most similar but has a higher spire and thicker, dark-brown periostracum.

Remarks. The anatomy of this species was described by Baker (1925a).

Systrophiella vitrina (J.A. Wagner *in* Spix & Wagner, 1827) comb. nov.

Figure 6

Solarium imperforatum Spix *in* Spix & Wagner 1827: 25, pl. 17 fig. 6; Gray 1847: 170.

Helix vitrina Wagner *in* Spix & Wagner 1827: 25, pl. 17, fig. 6—Pfeiffer 1848: 109.

Helix (*Helicella*) *imperforata* (Spix)—Beck 1837 *in* 1837–1838: 7.

Helix (*Patula*) *vitrina* Wagner—Albers 1850: 65.

Ammonoceras vitrina (Wagner)—Pfeiffer & Clessin 1881: 15.

Streptaxis (*Ammonoceras*) *vitrina* (Wagner)—Tryon 1885: 64.

Happia vitrina (Wagner)—Bourguignat 1890: 40; Gude 1902: 234; Thiele 1927: 318; Baker 1928: 125; Haas 1953: 205; Ramírez 1993: 35; Salgado & Coehlo 2003: 169; Agudo-Padrón 2008: 165; Viana & Santos 2008: 104; Santos *et al.* 2010: 514, 536; Nunes & Santos 2012: 82; Oliveira 2015: 40, 43, fig. A2; Birckolz *et al.* 2016: 150; Salvador 2019: 93; Salvador 2020: 64, figs 7–9.

Streptaxis (*Happia*) *tumescens* Suter 1900: 330, pl. 3 fig. 4–4b.

Scolodonta (*Happia*) *vitrina* (Wagner)—Kobelt 1905 *in* 1905–1906: 49, pl. 48 figs 13, 14.

Happia (*Happia*) *vitrina* (Wagner)—Schileyko 2000: 756–757, fig. 986A.

Misidentifications:

Helix vitrina Wagner—Hidalgo 1870: 36 (= "*Helix*" *circumplexa* Deshayes, 1839 *in* Férussac & Deshayes, 1820–1851?).

Helix vitrina Wagner—Hidalgo 1893: 84 (= "*Helix*" *circumplexa* Deshayes, 1839 *in* Férussac & Deshayes, 1820–1851?).

Happia vitrina (Wagner)—Simone 2006: 228, fig. 871 (=

Figure 6. *Systrophiella vitrina* (J.A. Wagner *in* Spix & Wagner, 1827), ZSM 20020666, holotype.

"*Helix*" *circumplexa* Deshayes, 1839 *in* Férussac & Deshayes, 1820–1851?); Barbosa 2014: 58-65, fig. 5–7 (= Scolodontidae sp.?); Breure & Araujo 2017: 110, fig. 40D–F (="*Helix*" *circumplexa* Deshayes, 1839 *in* Férussac & Deshayes, 1820–1851?); Salvador *et al.* 2018: 116–119, fig. 11A–C (=?); Silva *et al.* 2019: 179, fig. 2L–N (= Scolodontidae sp.); Rangel *et al.* 2021: 4–6, fig 7e (= Scolodontidae sp.).

Streptaxis tumescens—Simone 2006: 194, fig. 722 (= Streptaxidae sp.?).

Studied material. ZSM 20020666, holotype, "Brasilien", leg. Spix 1827.

Type locality. "Habitat cum precedente [Provinciis australioribus Brasiliae]".

Measurements. "Longitudo 2½ lin.; lat. 5 lin." (Spix & Wagner 1827).

Redescription. Shell medium-sized for genus, whitish-transparent, with some remnants of a brownish periostracum and a slightly raised spire. Suture rather deep, protoconch–teleoconch transition indistinct. Sculpture of indistinct, slightly flexuous growth lines. Vestigial spiral sculpture absent. Aperture rather large, subcircular, peristome too damaged for description. Umbilicus of medium width, up to 30% of shell width.

Geographic range. Brazil.

Comparisons. It is similar to *S. pygmea* (Spix *in* Spix & Wagner, 1827), but that species has a much smaller size at the same whorl count and a less circular aperture.

Aside from *S. pygmea*, *S. vitrina* has been confused with several poorly known and possibly undescribed species of Scolodontidae from Brazil. For instance, Simone (2006), Barbosa (2014), Silva *et al.* (2019), and Rangel *et al.* (2021) figured several species with a flatter spire and broadly lunulate aperture under the name "*Happia vitrina*". These species can be separated from each other by the shape of the aperture, colour, and differences in size. Moreover, Salvador *et al.* (2018) figured a small species unknown to us under the name "*Happia vitrina*"; it has a narrow umbilicus, flat to concave spire, and a last whorl that partially covers the preceding whorls.

"*Helix*" *circumplexa* Deshayes, 1839 is a species from the Atlantic rainforest of Brazil, which differs from *S. vitrina* by its low spire that is partially covered by the last whorl (Férussac & Deshayes 1820–1851, **1** (30): 19, pl. 84 figs 5, 6). Therefore, it is not a synonym of *S. vitrina*, as suggested by several authors, including Gude (1902) and Ramírez (1993). The specimens listed as *H. vitrina* by Hidalgo (1870, 1893), Simone (2006), and Breure & Araujo (2017) might be "*H.*" *circumplexa*, but we have not had the opportunity to compare these shells with the type material. The re-identification in this paper of the specimens described by Hidalgo (1870, 1893) was based on the figure by Breure & Araujo (2017), who imaged the specimen used in Hidalgo's publication.

Another species often listed as a synonym of *S. vitrina*, "*Helix valvaeformis* 'Nyst'", seems to be an unpublished manuscript name first used by Pfeiffer (1847 *in* 1847–1848: 110) in the synonymy of *Helix vitrina*. Here we regard it as a *nomen nudum*.

Remarks. Beck (1837 *in* 1837–1838) used *Solarium imperforatum* Spix, 1827 as the valid name for this species. Beck met all the requirements of first reviser according to ICZN Article 24.2. Cowie et al. (2004) also considered Spix's names to take precedence over Wagner's. However, Spix's *Solarium imperforatum* has not been used as valid since Gray (1847), so replacing Wagner's *Helix vitrina* with Spix's name would threaten the stability of the taxon in our opinion. As the conditions of ICZN Article 23.9.1. are not met, we cannot make the decision to maintain the name ourselves but must refer the case to the International Commission on Zoological Nomenclature (Roosen & Breure submitted). Meanwhile, we tentatively use *Helix vitrina* following prevailing usage in recent papers.

Gray (1847) designated *Solarium imperforatum* Spix, 1827 as type species for *Solarium* "Spix". However, Spix never made this name available, but seems to have misapplied *Solarium* Lamarck, 1799 (= *Architectonica* Röding, 1798). As the genus itself is not valid, neither is the type designation.

Systrophiella pygmea (Spix *in* Spix & Wagner, 1827) comb. nov.

Figure 7

Solarium pygmeum Spix *in* Spix & Wagner 1827: 25, pl. 17 fig. 7.

Helix nana Wagner *in* Spix & Wagner 1827: 25, pl. 17 fig. 7 (*non* Pennant, 1777).

Happia nana—Barbosa 2014: 66–73, figs 8–10; Oliveira 2015: 40, 44, fig. A3.

Studied material. ZSM 20020657, syntypes (two shells, dry), "Brasilien".

Type locality. "Habitat cum precedentibus [Provinciis australioribus Brasiliae]".

Measurements. "Longitudo 1½ lin.; lat. 3½ lin." (Spix & Wagner 1827).

Redescription. The type material is likely juvenile, so not all diagnostic characteristics could be studied. Shell small for genus, subdiscoid, with a slightly raised spire, semitransparent, yellowish brown. Distinction between protoconch and teleoconch not clear. First whorls smooth, without visible sculpture. Later whorls with indistinct growth lines; base

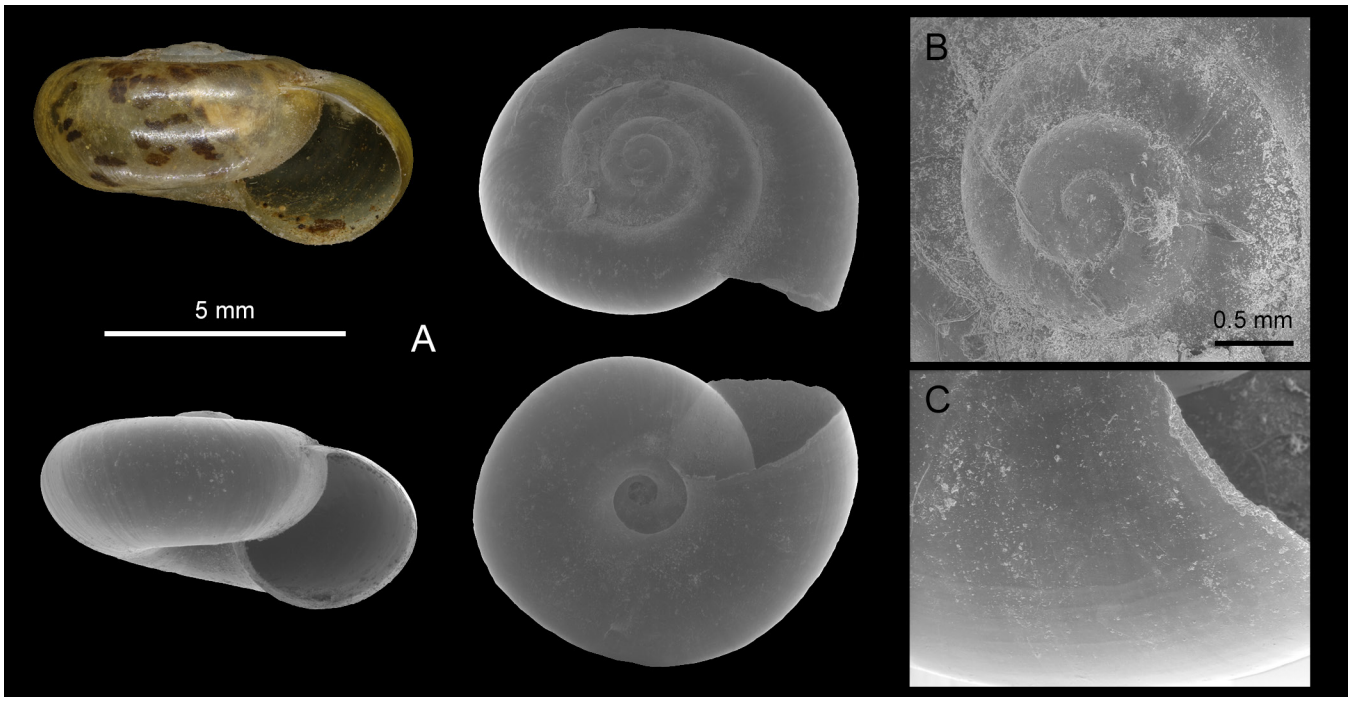

Figure 7. *Systrophiella pygmea* (Spix *in* Spix & Wagner, 1827). **A–C**, ZSM 20020657, syntype. **B**, apical surface of same shell. **C**, basal surface of same shell, in umbilicus (not to scale).

of last whorl with indistinct vestigial spiral sculpture. Aperture subcircular, with thin, simple peristome. Umbilicus of medium width, up to 20% of shell width.

Geographic range. Brazil.

Comparisons. *Systrophiella vitrina* is similar, but it is larger at the same number of whorls and has a more elevated spire and a nearly circular aperture.

Remarks. This species has most often been regarded as a synonym of *S. vitrina*, but re-examination indicates that it is likely a valid species, so some nomenclatural issues need to be addressed. Both *Helix nana* J.A. Wagner, 1827 and *Solarium pygmeum* Spix, 1827 were made available by Spix & Wagner (1827), and as there is no official first revisor—*Helix nana* was only treated as valid in unpublished theses (Barbosa 2014; Oliveira 2015)—that decision is made here. As Cowie *et al.* (2004) explained at length, Spix's names should get priority over Wagner's names in most cases. Moreover, Wagner's *Helix nana* is a junior primary homonym of *Helix nana* Pennant, 1777 (= *Planorbarius corneus* (Linnaeus, 1758)). Therefore, we follow Cowie *et al.* (2004) and ICZN Article 57.2 and select *Solarium pygmeum* Spix *in* Wagner & Spix, 1827 as the valid name for this species.

The specimen from Ilha Grande (Rio de Janeiro State, Brazil) figured by Barbosa (2014) differs only slightly from the type material.

Genus *Luteostriatella* gen. nov.

ZooBank identifier. urn:lsid:zoobank.org:act:3971CFD2-C22A-46CC-9FA6-B828A5AAD314

Type species. *Austroselenites variegatus* F. Haas, 1949.

Description. Shell strongly depressed, conical-globular, medium-sized for family. Periostracum with thin, yellowish-white and reddish-brown axial streaks, three per 1 mm. Sculpture of weak growth lines. Aperture subcircular, with thin, simple peristome. Umbilicus of moderate width, c. 30% of shell width.

Species included in the genus. *Luteostriatella variegata* (F. Haas, 1949) comb. nov.

Geographic range. Peru.

Derivation of the name. The name of the genus is composed of the Latin word *luteo* and *striata*, which means yellow-striped. Its gender is feminine.

Comparisons. This species has been questionably included in *Austroselenites*, but species of *Austroselenites* can be separated from *Luteostriatella* gen. nov. by their stronger axial sculpture, larger size, lower spire, and uniformly coloured periostracum. Ramírez (1993) placed the species in *Systrophiella* H.B. Baker, 1925, which differs from *Luteostriatella* gen. nov. by its vestigial spiral sculpture, uniformly coloured periostracum and lower spire.

Remarks. Over 70 years after the original description of *L. variegatus*, an additional specimen was photographed in the Peruvian Amazon. As it is unlikely more material will become available soon, so we are describing the genus here based on the available information. We are placing it in the Scolodontidae based on its conchological similarities to *Systrophiella*, but we acknowledge that studies of its DNA and anatomy may reveal that it belongs to the Streptaxidae.

***Luteostriatella variegata* (F. Haas, 1949) comb. nov.**
Figure 8

Austroselenites (subgenus?) *variegatus* Haas 1949: 247, fig. 59.
Systrophia variegata—Richardson 1989: 140.
Systrophia (*Systrophiella*) *variegata*—Ramirez 1993: 72.

Studied material. FMNH 30037, holotype (dry), Peru, Loreto department, near Rio Ucayali.

Type locality. Peru: "Cerro Azul, on Rio Ucayali, Department of Loreto".

Measurements. "Diameter 10.3 mm, height 5.5 mm, diameter of umbilicus 3.9 mm" (Haas 1949).

Redescription. Shell strongly depressed, conical-globular, medium-sized for family; suture shallow. Periostracum with thin, yellowish-white and reddish-brown axial streaks, three per 1 mm. Spire whorls slightly damaged, without sculpture. Teleoconch sculpture with minute growth lines. Aperture subcircular, with thin, simple peristome. Umbilicus of medium width, up to 31% of shell width.

Geographic range. Peru: Loreto Department: near Rio Ucayali and Maynas Province (iNaturalist observation 15694700, https://www.inaturalist.org/observations/15694700).

Comparisons. There are no similar species currently known.

Remarks. The placement of *L. variegata* in Scolodontidae is tentative and should be corroborated by anatomical and genetic research.

Genus *Austroselenites* Kobelt, 1905

Scolodonta (*Austroselenites*) Kobelt 1905 *in* 1905–1906: 49, 70. Type species: *Helix euspira* Reeve, 1854 by subsequent designation (Baker 1925a: 15).

Redescription. Shell medium-sized to large, discoid to subdiscoid, broadly umbilicate. Spire strongly depressed to slightly elevated. Protoconch smooth, no clear distinction between protoconch and teleoconch. Teleoconch with narrow, dense axial ribs, which become weaker on later whorls. Periostracum yellow-brown. Whorls usually convex or flattened above. Aperture broadly lunulate to rounded-trapezoidal, with simple peristome. Living animal yellowish, with red antennae (Nicole Büttner pers. comm. 2020; Fig. 9).

Species included in the genus. *Austroselenites euspira* (Reeve, 1854), *A. flora* (L. Pfeiffer, 1850), *A. moyobambensis* (J. Moricand, 1858), *A. pichinchense* sp. nov.

Species tentatively included in the genus. ?*Austroselenites cyclina* (Cousin, 1887)

Geographic range. Venezuela, Brazil, Peru, and Ecuador.

Comparisons. Species included in *Austroselenites* were often assigned to *Happia* (e.g. Breure *et al.* 2022). However, *Happia* contains discoid species that, to our knowledge, only reach 4.5 mm wide when adult. Moreover, all *Happia*

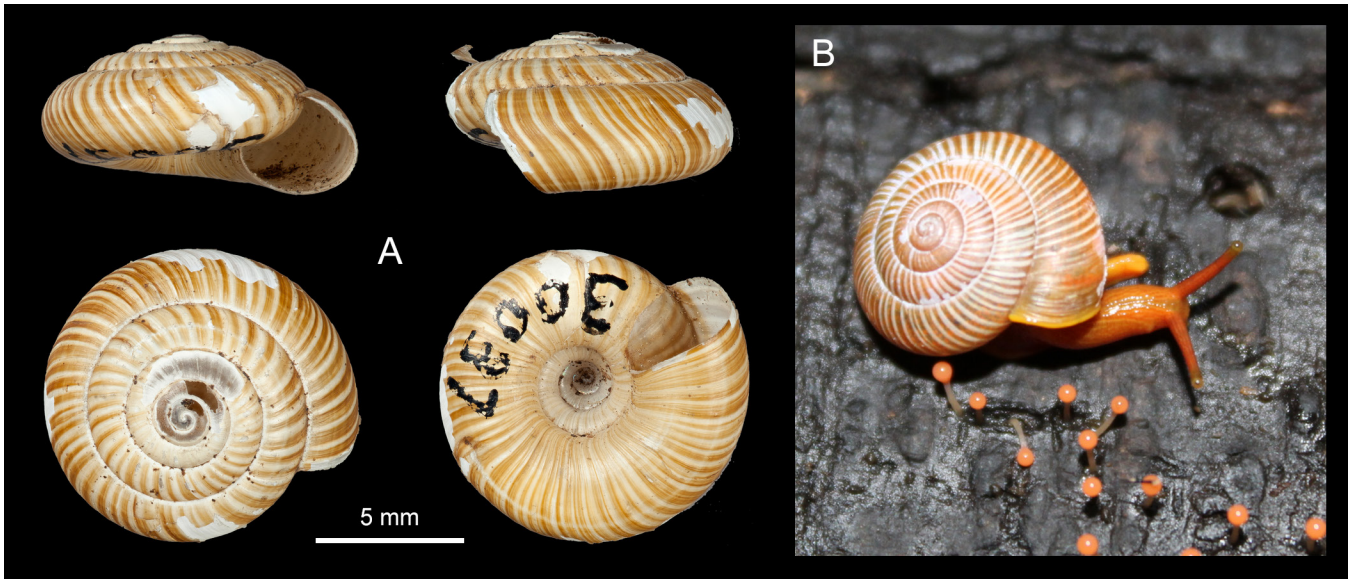

Figure 8. *Luteostriatella variegata* (Haas, 1949). **A**, FMNH 30037, holotype. **B**, living specimen (iNaturalist observation 15694700).

Figure 9. *Austroselenites* sp., living specimen, on road around Las Tolas (Gualea), Pichincha Province, Ecuador, at 1700 m (Nicole Büttner pers. comm. 2020).

species have spiral rows of microscopic papillae, which do not occur in *Austroselenites*. *Austroselenites* are most similar to *Systrophiella*, which differs by its smaller, semitransparent shells lacking strong axial sculpture.

Austroselenites flora was included in *Mesomphix* Rafinesque, 1819 in MolluscaBase (2023c). However, *Mesomphix* is known from North America, and all species have smaller shells with a narrow to nearly closed umbilicus. In addition, *Mesomphix* is not known to have the yellowish body, as in *Austroselenites*. The source which persuaded MolluscaBase editors to move the species to *Mesomphix* is unknown.

Remarks. *Austroselenites* Kobelt, 1905 was described for *A. euspira* (Reeve, 1854) and *A. moyobambensis*, but Baker (1941) and Schileyko (2000) included only *A. euspira* in this genus. However, based on re-examination of several shells of *A. euspira*, *A. flora*, *A. pichinchense* sp. nov., and *A. moyobambensis*, they are all similar in microsculpture on the early whorls, shape of the aperture, and colour of the periostracum. The only shell characteristic hinting towards separation of *A. euspira* and the other taxa at the generic level is the slightly smaller size of *A. euspira*.

Its yellow mantle, along with a few shell characteristics, suggests true *Austroselenites* belongs to the Scolodontidae rather than Haplotrematidae. This agrees with the inclusion of its species in *Happia sensu lato* by most authors. The species studied by Baker (1941) seem to differ from *Austroselenites sensu stricto* and were correctly referred to *Zophos* Gude, 1911 by him. In our opinion, Baker (1941) provided sufficient evidence to place *Zophos* in the Haplotrematidae. Therefore, we follow Schileyko (2000) in treating *Zophos* as a genus in the Haplotrematidae. As Austroselenitinae Baker, 1941 was largely based on the examination of *Zophos* species (Baker 1941), we refrain from using it here pending further study.

To better illustrate the microsculpture of this genus, we include SEM photomicrographs of an unidentifiable juvenile *Austroselenites* sp. from Cotopaxi province, Ecuador (Fig. 10; QCAZ-I-274879).

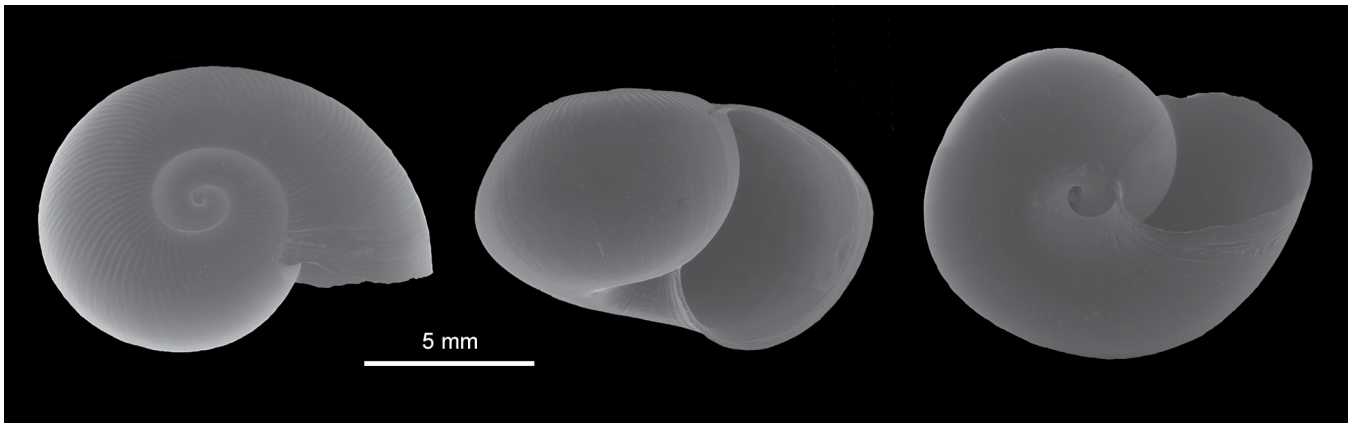

Figure 10. *Austroselenites* sp., QCAZ-I-274879.

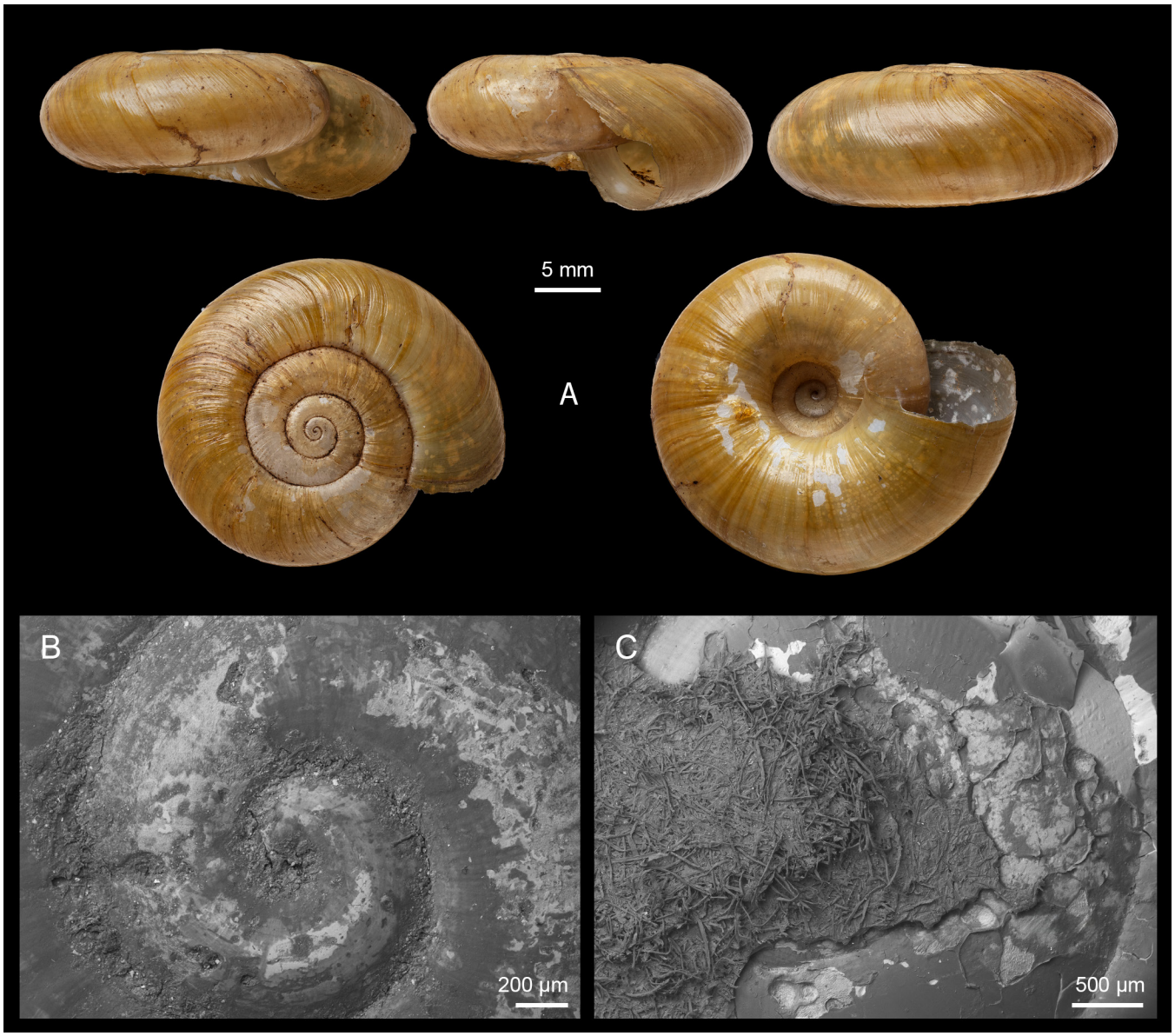

Figure 11. *Austroselenites euspira* (Reeve, 1854). **A–C**, NHMUK 20230164, syntype. **B, C**, apical surface of same shell.

***Austroselenites euspira* (Reeve, 1854)**

Figure 11

Helix euspira Reeve 1854: pl. 185, fig. 1277—Pfeiffer 1855a: 54; Brown 1866: 15.
Ammonoceras euspira (Pfeiffer, 1855)—Albers & Martens 1860: 72.
Hyalina (*Ammonoceras*) *euspira* Pfeiffer—Martens 1873: 167.
Macrocyclis euspira (Pfeiffer)—Binney 1876: 247.
Happia euspira (Pfeiffer)—Gude 1902: 233; Simone 2006: 226, fig. 863.
Scolodonta (*Austroselenites*) *euspira* (Pfeiffer)—Kobelt 1905 *in* 1905–1906: 70, pl. 52 figs 1–3.
Haplotrema (*Austroselenites*) *euspira* (Pfeiffer)—Baker 1941: 423.
Haplotrema euspira (Pfeiffer)—Richardson 1988: 22.
Austroselenites euspira (Pfeiffer)—Bouchet *et al.* 2017: 44.

Studied material. NHMUK 20230164, syntypes (3 shells, dry), "Brazil".

Type locality. "Brazil".

Measurements. "Diam. maj. 26, min. 22½, alt. 9 mill." (Pfeiffer 1855a).

Redescription. Shell small for genus (but large for family), subdiscoid, with a distinct suture and a yellow-brown periostracum. Protoconch–teleoconch transition unclear. Sculpture of rather strong, slightly flexuous growth wrinkles, that weaken on base of shell. Aperture broadly lunulate, with

thin, simple peristome. Umbilicus wide, up to 26% of shell width.

Geographic range. Venezuela (Martens 1873) and Brazil.

Comparisons. *Austroselenites euspira* (Reeve, 1854) differs from all other *Austroselenites* species by its smaller size. The axial ribbing of the teleoconch is stronger in Andean taxa, like *A. flora* and *A. pichinchense* nov. sp.

Remarks. We have been unable to check the Venezuelan shells in the ZMB to verify the record of Martens (1873). Examination of the type material in the NHM may help researchers rediscover this species, so the systematic position of *Austroselenites* and the distribution of *A. euspira* can be clarified.

***Austroselenites pichinchense* sp. nov.**

Figure 12

ZooBank identifier. urn:lsid:zoobank.org:act:09ED417F-772A-4952-9617-EF8677FC8B2A

Type locality. Ecuador: Pichincha Province, between Calacalí and Nanegalito at 2100 m.

Type material. Holotype: dry shell, QCAZ-I 274877; from the type locality.

Paratype: 1 dry shell, QCAZ-I 274878; Ecuador: Pichincha Province: La Favorita, "under log".

Measurements.

	H (mm)	W (mm)	HA (mm)	WA (mm)	Whorls
Holotype	14.6	25.4	12.2	11.9	4¼
Paratype	17.8	30.6	14.7	14.4	4½

Description. Shell large (Table 2), depressed, with a slightly elevated spire; whorls convex; periostracum yellow. Nucleus small, partially covered by succeeding whorl. Protoconch smooth, with transition between protoconch and teleoconch indistinct. Teleoconch sculpture of slender, densely spaced, slightly flexuous growth lines, which are more distinct on apical surface and fade away in umbilicus. Umbilicus of medium width, up to 20% of shell width. Aperture subcircular, with peristome simple.

Derivation of the name. The new species is named after the province of Pichincha, where the specimens were found.

Geographic range. Ecuador: Pichincha province, known form the type locality and La Favorita.

Comparisons. The new species is most similar to large individuals of *Austroselenites flora* and ?*A. cyclina* from which it differs by its higher spire, more circular aperture, smaller umbilicus, and less excavated suture. Other species lack periostracum, are much smaller at the same number of whorls, and/or have a more elongate aperture.

Remarks. *Austroselenites flora* might occur in somewhat the same area as *A. pichinchense* sp. nov.

A living specimen photographed near Las Tolas (Gualea) in Pichincha Province, Ecuador, likely belongs to *A. pichinchense*, but its identity cannot be confirmed from the photographs (Fig. 9).

Discussion

Pfeiffer, Reeve, Spix, or Wagner?

One issue that needs to be addressed is the authorship of some of the type species and other taxa in this paper. Several taxa were previously attributed to Pfeiffer based on what seems to be the intended order of publication (e.g. Roosen 2023), for instance *Austroselenites flora* (Reeve, 1854), *Happia ammonoceras* (Reeve, 1854), and *Hirtudiscus excisa* (Reeve, 1854). During our study we concluded that Reeve (1854) was published before Pfeiffer (1855), even though

Figure 12. *Austroselenites pichinchense* sp. nov., QCAZ-I 274878, holotype.

Reeve (1854) clearly cited Pfeiffer (1855) as the original source. As all taxa by Pfeiffer (1855) are also treated by Reeve (1854), Reeve is the first person to describe these species and, thus, has priority over Pfeiffer.

Determining correct authorship and applying the principle of priority to the names published by Spix & Wagner (1827) is more difficult. First, Spix and Wagner's paper is often attributed to only Wagner, although from the title and further analysis it is clear Spix made substantial contributions. Therefore, the paper should be cited as Spix & Wagner (1827), as done by Salgado & Coelho (2003) and suggested to us by Francisco Welter-Schultes (pers. comm. 2023). We can assume that the names on the plates of Spix & Wagner (1827) were contributed by Spix, as Wagner finished the paper after the plates were already made (Cowie *et al.* 2004). We agree with Cowie *et al.* (2004) that new names and spellings introduced in the main text of Spix & Wagner (1827) can be attributed to Wagner. All names are made available in the same paper, so the first revisor decides which name should be treated as valid (ICZN Article 24.2.1; Francisco Welter-Schultes pers. comm. 2023).

Decisions regarding *Happia*

Some of our decisions regarding *Happia* Bourguignat, 1890 need further explanation. Most authors consider *Helix vitrina* Wagner, 1827 as the type species (e.g. Ramírez 1993; Salvador *et al.* 2018). Although, if we do not accept Pfeiffer's (1855b) type designation by absolute tautonomy for *Ammonoceras* (= *Happia*), the subsequent designation of *Helix euspira* Reeve, 1854 as type species for *Ammonoceras* by Bland (1863) would have priority over later designations. This would make *Austroselenites* Kobelt, 1905 a junior objective synonym of *Happia*, leaving *Helix ammonoceras* without a valid genus and still causing *Helix vitrina* to be moved to *Systrophiella*. If *Helix ammonoceras* is retained as type species for *Ammonoceras* Pfeiffer, 1855, and by extension *Happia*, at least *Austroselenites* and *Helix ammonoceras* remain stable.

That said, until now, many more species have been included in *Happia*. Discussing all these species is beyond the scope of our study, but they do need to be placed in a genus. As the dominant definition for *Happia* was the current definition of *Systrophiella* in this paper, we propose that all "orphaned" *Happia* species are placed in *Systrophiella sensu lato* pending further study.

Systrophiella vitrina (Wagner *in* Spix & Wagner, 1827)

Strict adherence to the ICZN would mean that *Helix vitrina* Wagner, 1827 should be replaced with *Solarium imperforatum* Spix, 1827, because Beck (1837 *in* 1837–1838: 7) used the latter name as valid and his paper meets all requirements to be First Revisor. However, as shown in the systematic section, this name was not used since Gray (1847). All subsequent authors regarded *Helix vitrina* as the valid name, but not enough papers have been published to trigger an automatic reversal of precedence. As we believe using *Solarium imperforatum* would cause unnecessary confusion and threaten the stability of this already often confused taxon, we will petition the ICZN to retain the name.

Austroselenites and the Austroselenitinae

Another decision with high impact made in this paper is the tentative move of *Austroselenites sensu stricto* to the Scolodontidae. However, its conchological similarity to *Systrophiella* and yellow body colour support this view. Even the variation within the genus, which seems largely limited to microsculpture, aperture shape, and spire height, fits within our current expectations of the Scolodontidae.

That said, it is unlikely that the entire Austroselenitinae of Baker (1941) should be a subfamily of the Scolodontidae. *Zophos*, a genus often regarded as a subgenus of *Austroselenites* and the genus on which Austroselenitinae was based, has a grey body and its anatomy, as described by Baker (1941), does seem to support placement in the Haplotrematidae. Because of all this, we propose to regard *Zophos* as a separate haplotrematid genus and not to use the Austroselenitinae until the DNA and anatomy of the type species of *Austroselenites* are known.

General discussion and conclusion

In this paper we redescribe several, often poorly known, genera of Scolodontidae and their type species, and where necessary also redescribe or describe additional species to further stabilise the genera. However, this is only one small step. The anatomy of the type species, except for *Systrophiella eudiscus* (Baker, 1925), is still unknown, and their DNA has not been sequenced yet. Although many authors have tried to find relationships by shell and radular morphology (e.g. Gude 1902; Ramírez 1993; Thiele 1927; Tillier 1980), we refrain from doing so, as another potentially wrong interpretation of Scolodontidae is not needed. Besides, such a study is also beyond the scope of this paper.

We sincerely hope that our redescriptions provide a baseline for further research and are useful for malacologists working on this taxonomically difficult group.

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