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REASSESSMENT OF THE BRAZILIAN SPECIES OF *AMPHIDOXA* ALBERS, 1850 (GASTROPODA: STYLOMMATOPHORA: PUNCTOIDEA)

RODRIGO BRINCALEPE SALVADOR[1]*, FERNANDA S. SILVA[2], KRASIMIRA SEIZOVA[3], FABRIZIO SCARABINO[4,5]

[1] Finnish Museum of Natural History, University of Helsinki, Finland (e-mail: salvador.rodrigo.b@gmail.com); https://orcid.org/0000-0002-4238-2276
[2] Museu de Zoologia, Universidade de São Paulo, Brazil
[3] Center for Systematic Biology and Evolution, The Academy of Natural Sciences of Drexel University, United States
[4] Centro Universitario Regional del Este, Universidad de la República, Uruguay
[5] Zoología, Museo Nacional de Historia Natural, Uruguay
* corresponding author

ABSTRACT: *Amphidoxa* Albers, 1850 is a genus of minute charopid land snails known primarily from Chile. However, two species from southern Brazil have been allocated to it, *Amphidoxa flammulata* Ihering, 1922 and *Amphidoxa inexpectata* Ihering, 1922. Curiously, after their original description, these species were never again mentioned in the literature. They were recently "rediscovered" during work to produce the latest checklist of terrestrial gastropods in Brazil and their classification needs to be reassessed. Herein, we reclassify those species as *Lilloiconcha inexpectata* (Ihering, 1922) comb. nov. and *Lilloiconcha flammulata* (Ihering, 1922) comb. nov. (Punctoidea, Cystopeltidae). Moreover, considering the former confusion involving *L. inexpectata* and *L. pleurophora* (Moricand, 1846), we also clarify the known distribution of the latter.

KEY WORDS: Charopidae; Cystopeltidae; land snails; *Lilloiconcha*

INTRODUCTION

Amphidoxa Albers, 1850 is a genus of minute terrestrial gastropods belonging to the family Charopidae. Its type species, *Amphidoxa marmorella* (Pfeiffer, 1846), is endemic to Juan Fernández Archipelago (Chile) in the southeastern Pacific (PFEIFFER 1846, MIQUEL & ARAYA 2015). All other species in the genus are also endemic to Chile (PFEIFFER 1846, PHILIPPI 1855, HYLTON SCOTT 1969, STUARDO & VEGA 1985, MIQUEL & ARAYA 2015, COAN & KABAT 2017): *A. helicophantoides* (Pfeiffer, 1846) from Juan Fernández Archipelago; *A. ochsenii* (Philippi, 1855) from Valdivia province and Chiloé Island; and *A. haesselae* Hylton Scott, 1969 from La Unión commune. The genus is considered to belong to the subfamily Flammulininae within Charopidae, a group of Australian and New Zealand snails (SCHILEYKO 2001). Recent molecular phylogenetic analyses, however, have shown that Flammulininae is a synonym of Charopinae (SALVADOR et al. 2020, COLGAN & STANISIC 2023). Nevertheless, as no members of *Amphidoxa* were analysed, the genus' relationship to other Charopidae remains uncertain. That is a familiar pattern with South American punctoids; despite many studies on them over the decades (e.g., HYLTON SCOTT 1969, WEYRAUCH 1965, FONSECA & THOMÉ 1993, HAUSDORF 2005, MIQUEL & ARAYA 2015), a lot of questions remain about the generic status and relationships of most taxa.

Despite being largely a Chilean endemic genus, there are two additional species from south and

southeast Brazil that have been described and allocated to it, *Amphidoxa flammulata* Ihering, 1922 and *Amphidoxa inexpectata* Ihering, 1922. Curiously, after their original description (Ihering 1922), these species were never again featured in the literature. They are absent from Thiele (1927), from all the punctoid-focused studies of Weyrauch and Hylton Scott, from the compilations of the Brazilian molluscan fauna (Lange de Morretes 1949, 1953, Salgado & Coelho 2003, Simone 2006), and also from the type catalogues of the institution where Ihering's types are deposited (Dornellas & Simone 2011, Cavallari et al. 2016). At last, these "phantom" species were recently "rediscovered" during the work to produce the latest checklist (Salvador et al. 2024), although their original descriptions had already been unearthed some years ago, thanks to the extensive malacological library of the Muséum National d´Histoire Naturelle (Paris, France). Considering such problematic taxonomic history, herein we reassess the classification of the purported Brazilian *Amphidoxa* spp.

MATERIAL AND METHODS

For the present study, we located the type specimens of the two Brazilian species of *Amphidoxa*, and consulted the other scarce available specimens, including those studied by Pilsbry (1900) and Suter (1900). We also considered the new phylogenetic studies (Salvador et al. 2020, Salvador 2022) and the changes they implemented in the classification of Punctoidea, which directly impact the Brazilian "charopids".

The material studied herein is deposited in the following museum collections: ANSP – Academy of Natural Sciences of Drexel University (Philadelphia, PA, USA); FMNH – Field Museum of Natura History (Chicago, IL, USA); MNHG – Muséum d'histoire naturelle Genève (Geneva, Switzerland); MZSP – Museu de Zoologia da Universidade de São Paulo (São Paulo, SP, Brazil); NHMUK – Natural History Museum (London, UK); NMNZ – Museum of New Zealand Te Papa Tongarewa (Wellington, New Zealand). The specimens were imaged under stereomicroscopes coupled with computer-assisted cameras and stacking software at the ANSP, NMNZ, and MZUSP, and under a scanning electron microscope (SEM) at the ANSP (images taken by Phenom G2 Pro). Specimens from the other collections were studied via photographs.

SYSTEMATICS

Ihering's species were originally assigned to the genus *Amphidoxa* and never reassessed afterwards. *Amphidoxa* is diagnosed by a shell with a depressed spire, and a nearly identical proto- and teleoconch sculpture consisting of numerous axial prosocline ribs interspersed with up to five fine riblets (Schileyko 2001, Miquel & Araya 2015). Additionally, the fact that shells of *Amphidoxa* spp. have transverse stripes probably guided the generic allocation of Ihering (1922), although the use of *Amphidoxa* was then much broader, as shown by the discussion of the genus by Pilsbry (1894) and his allocation of *Zilchogyra costellata* (d´Orbigny, 1835) within it (Pilsbry 1894).

As presently understood, and considering many uncertainties regarding the anatomy and protoconch sculpture of some species and a high likelihood of polyphyly, *Lilloiconcha* (a senior synonym of *Trochogyra* Weyrauch, 1965) includes South American punctoids that have depressed to high conical shells with reddish-brown transverse stripes (lacking in *L. zulmae*), with axial riblets that are straight in apical view, and a smooth protoconch (Weyrauch 1965, Schileyko 2001, Hausdorf 2005, Miquel et al. 2007) (though microscopical spiral threads have been observed under SEM in some species; Hausdorf 2005, Salvador et al. 2018). Notably, the protoconchs of well-preserved specimens of its type species *L. tucumana* (Hylton Scott, 1963) have not yet been examined under SEM to assess their sculpture (Hausdorf 2005); under light microscopy, however, the protoconch appears smooth (Hylton Scott 1963, pers. obs.). Furthermore, members of *Lilloiconcha* have multicuspid marginal radular teeth, a backwards shifted mesocone of the lateral radular teeth, a hardly differentiated epiphallus, and, in comparison to other South American punctoids, a reduced penis (Hausdorf 2005, Miquel et al. 2007).

The above-mentioned conchological features are in accord with the type material of Ihering's species (see below). Thus, here we transfer them from *Amphidoxa* (Charopidae) to *Lilloiconcha* (Cystopeltidae). *Lilloiconcha* was established long after the original descriptions by Ihering (1922), so it would not be possible for that author to use such a classification. Even so, it is worth noting that Ihering (1922) compares his new species with *Amphidoxa pleurophora* (Moricand, 1846) from eastern Brazil, which is presently classified in *Lilloiconcha* (Simone 2006, Salvador et al. 2024).

Lilloiconcha was previously classified in Charopidae, but it was recently shown that it belongs instead to Cystopeltidae, an independent lineage within Punctoidea that contains one Australian branch and one South American branch (Salvador et al. 2020, Salvador 2022). As previously mentioned, it is possible that *Lilloiconcha* as presently understood is non-monophyletic, so the generic allocation of Ihering's species might change in the future as further studies are conducted.

Superfamily Punctoidea Morse, 1864

Family Cystopeltidae Cockerell, 1891

Genus *Lilloiconcha* Weyrauch, 1965

Type species: *Austrodiscus superbus tucumanus* Hylton Scott, 1963, by original designation.

Lilloiconcha pleurophora (Moricand, 1846)

(Figs 1–3)

Helix pleurophora Moricand 1846: 150, pl. 5, figs 6–9.
Helix pleurophora – Hupé 1857: 18.
Helix (*Microconus*) *pleurophora* – Tryon 1885: 53, pl. 9, figs 8–9.
Patula pleurophora – Tryon 1885: 277, pl. 9, figs 8–9.
Amphidoxa (*Stephanoda*) *pleurophora* – Pilsbry 1894: 41.
Stephanoda pleurophora [in part] – Pilsbry 1900: 387; Lange de Morretes 1949: 135.
Zilchogyra (*Trochogyra*) *pleurophora* – Weyrauch 1965: 123.
Trochogyra (*Trochogyra*) *pleurophora* [in part] – Fonseca & Thomé 1993: 102.
Trochogyra pleurophora [in part] – Salgado & Coelho 2003: 154.
Lilloiconcha pleurophora [in part] – Hausdorf 2005: 2796; Simone 2006: 234, fig. 894A.
Lilloiconcha pleurophora – Breure & Tardy 2016: 122, figs 86–88; Salvador et al. 2024: 154.

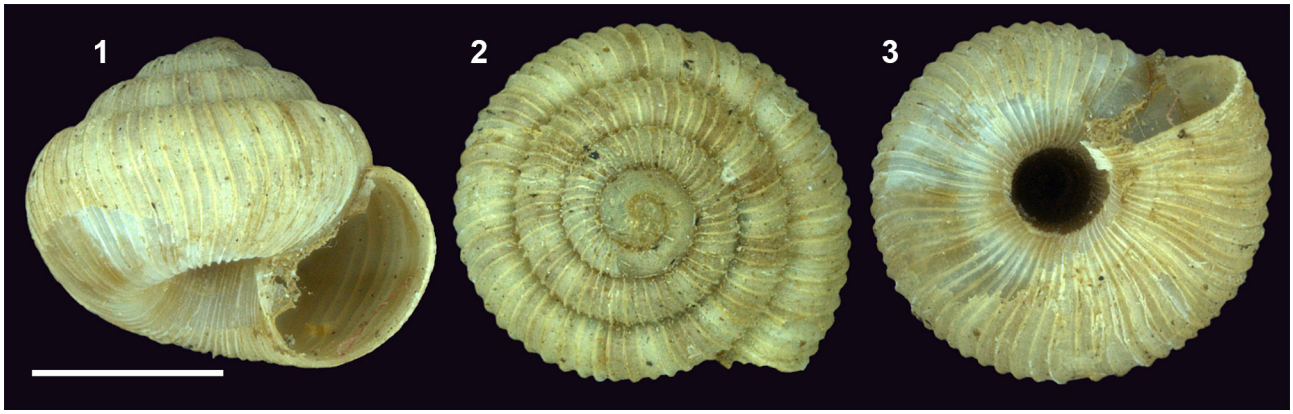
Type material. Syntypes MHNG-INVE-69077 (18 shells) (see also Breure & Tardy 2016). Simone (2006), and later Miquel et al. (2007), incorrectly considered specimen NHMUK 1900.7.5.8 as the holotype of *L. pleurophora*. Specimen NHMUK 1900.7.5.8 was collected much later, in São Paulo state (i.e., far away from the type locality), and then donated to the NHMUK by Ihering; it represents *Lilloiconcha inexpectata* (Ihering, 1922) comb. nov., as argued by Ihering (1922) and explained below.

Type locality. "la province de Bahia" (Moricand 1846: 150). Bahia state, Brazil.

Distribution. Bahia state. No further valid record of this species has emerged since Moricand (1846), so *L. pleurophora* remains known with certainty only from its type material.

Discussion. *Lilloiconcha pleurophora* was considered as a single species ranging from Bahia to southern Brazil (Pilsbry 1900, Suter 1900). Nevertheless, Ihering (1922) assigned its southern "population" (from São Paulo state to Rio Grande do Sul state) to a separate new species, *Amphidoxa inexpectata*. That action restricted *L. pleurophora* to the population from Bahia state, known only from Moricand's (1846) records. As explained above, Ihering's (1922) study fell under the radar of malacologists working in South America and the earlier views of Pilsbry (1900) and Suter (1900) have been reproduced ever since in South American malacology (Lange de Morretes 1949, Fonseca & Thomé 1993, Simone 2006, Miquel et al. 2007).

Ihering (1922) argued that the actual *L. pleurophora* from Bahia could be distinguished from his two new southern species by some conchological features based on Moricand's (1846) description and accompanying figure, as the type material was unavailable to him. The syntypes of *L. pleurophora* have since been located (Breure & Tardy 2016) and Ihering's (1922) assessment is substantiated by analysis of the types. *Lilloiconcha pleurophora* can be distinguished from Ihering's (1922) southern species by its smaller size, taller and narrower aperture, narrower umbilicus, and fewer and stronger ribs on the teleoconch, and presence of riblets between pairs of the ribs.



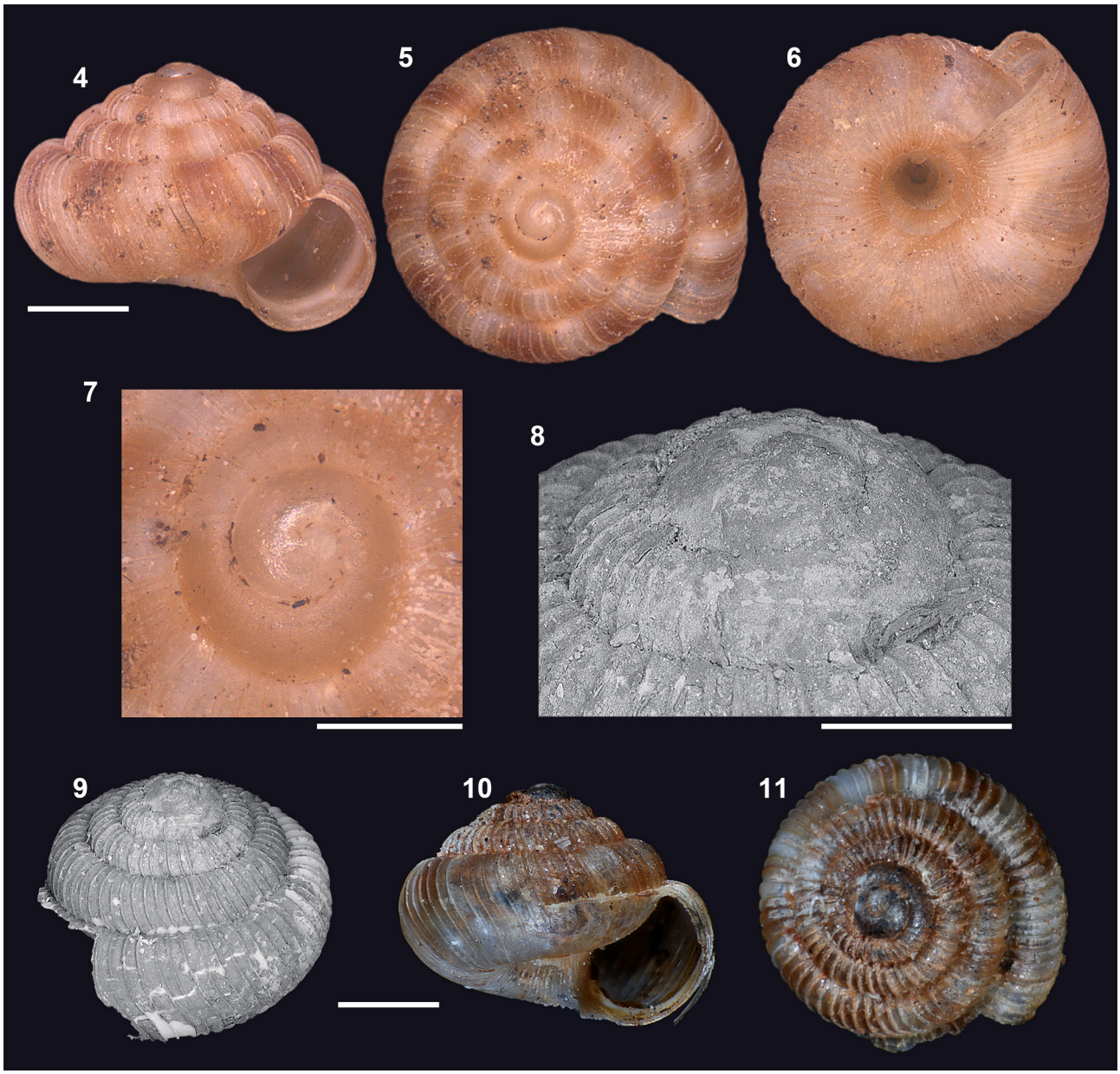
Figs 1–3. *Lilloiconcha pleurophora* (Moricand, 1846), syntype MHNG-INVE-69077 (shell width – 2.15 mm). Scale bar 1 mm

The protoconch of the type specimens are largely eroded, but some ambiguous vestiges of axial ribs seem to be present, although that cannot be ascertained with confidence. If fresher specimens become available and such protoconch sculpture pattern is indeed present, this species would have to be excluded from the cystopeltid genus *Lilloiconcha* and likely transferred to a genus in Charopidae.

Lilloiconcha inexpectata (Ihering, 1922) comb. nov.

(Figs 4–11)

Amphidoxa inexpectata Ihering 1922: 153.
Stephanoda pleurophora [in part, non Moricand, 1846] – Pilsbry 1900: 387, pl. 12, figs 4–5; Lange de Morretes 1949: 135.
Amphidoxa pleurophora [non Moricand, 1846] – Suter 1900: 333, pl. 3, fig. 9.
Amphidoxa (*Stephanoda*) *pleurophora* [non Moricand, 1846] – Haas 1953: 205.
Austrodiscus (*Zilchogyra*) *pleurophora* [in part, non Moricand, 1846] – Vaz 1987: 12.
Austrodiscus (*Zilchogyra*) *pleurophorus* [in part, non Moricand, 1846] – Vaz 1991: 278, fig. 1.



Figs 4–11. *Lilloiconcha inexpectata* (Ihering, 1922): 4–6 – holotype, MZSP 7634 (shell width – 3.5 mm); 7 – holotype, protoconch detail; 8–11 – Pilsbry's (1900) specimen, ANSP 71244 (shell width – 3.1 mm) (8 – protoconch detail, in oblique view, under SEM 10kV single image, 9 – under SEM stitched image, 10–11 – under light microscopy). Scale bars: 500 μm (7–8), 1 mm (4–6, 9–11)

Lilloiconcha pleurophora [non Moricand, 1846] – Simone 2006: 234, fig. 894B.
Amphidoxa inexpectata – Salvador et al. 2024: 153.

Type material. Holotype MZSP 7634 (São Leopoldo).
Type locality. "S. Leopoldo, im Staat Rio Grande do Sul" (Ihering 1922: 154). São Leopoldo municipality, Rio Grande do Sul state, Brazil.
Diagnosis. Shell discoid with raised spire; aperture rounded, somewhat D-shaped, inserted closer to the middle section of body whorl; colour pattern consisting of ca. 13 irregular brownish-red band-like blotches per whorl; umbilicus wide (~25% of shell width), with preceding whorls visible.
Description. Shell minute (width ca. 3.5 mm, height ca. 2.8 mm), discoid, with ca. 5 whorls. Spire raised; spire top rounded. Whorls regularly increasing in size. Whorls with a lightly marked shoulder. Suture well-marked. Shell base colour whitish, marked by few irregular reddish brown axial blotches that fade out towards basal (abapical) region of whorl (13 in body whorl of holotype). Protoconch (1½ whorl) smooth (assessed from both apical and umbilical views), of base shell colour; transition to teleoconch clear. Teleoconch sculptured by multiple fine sinuous prosocline ribs, regularly spaced along whorls (ca. 80 on body whorl); space between ribs about four times rib width. Aperture rounded, nearly D-shaped; aperture insertion on preceding whorl located close to the middle section of that whorl. Peristome simple. Umbilicus wide (~25% of shell width), deep, with early whorls visible. Details on the species' anatomy, including radular morphology, can be found in Vaz (1991, as *Austrodiscus pleurophorus*); no specimens with soft parts available could be obtained for the present study.
Additional material. São Paulo: undetermined locality, ANSP 71244 (1 shell, juvenile; H. v. Ihering leg., 1894), NHMUK 1900.7.5.8 (1 shell, fragmented; H. v. Ihering leg.); Perus: NMNZ M.205846 (1 shell; H. v. Ihering leg.). Paraná: Caiobá: FMNH IZ 78671(2 shells, xii.1958). Rio Grande do Sul: Taquara: FMNH IZ 216234 (1 shell, juvenile).
Distribution. São Paulo state (and potentially southern Rio de Janeiro state) to Rio Grande do Sul state; apparently restricted to the eastern and coastal areas of these states. Besides the type locality in São Leopoldo and the nearby Taquara municipality (Rio Grande do Sul state), the species is known from one locality in Paraná state (Caiobá, newly reported here) and a few localities in São Paulo state (records previously assigned to *L. pleurophora*): Perus municipality (Suter 1900); Mogi Guaçu municipality (Ihering 1922); Cotia and Iguape municipalities (Vaz 1987); Miracatu municipality (Vaz 1991). The latter two records (Vaz 1987, 1991) could not be checked with voucher specimens, but they are within reasonable expectations considering the species' geographic distribution. The record of *L. pleurophora* from Ilha Grande, Rio de Janeiro state (Haas 1953, specimen FMNH IZ 43814) is a misidentification of *Radioconus amoenus* (Thiele, 1927) (Charopidae).
Discussion. Moricand (1846) described *L. pleurophora* from Bahia state; specimens later found by Ihering in São Paulo state in southeastern Brazil were assigned to that same species (Pilsbry 1900, Suter 1900). Nevertheless, when further adult specimens became available from Rio Grande do Sul, the southernmost state in Brazil, Ihering (1922) described the new species *Amphidoxa inexpectata*, including the populations in São Paulo and Rio Grande do Sul. As explained in the entry for *L. pleurophora* above, our analysis of the type material and additional specimens from Pilsbry (1900) and Suter (1900), agrees with Ihering's (1922) conclusion that *L. inexpectata* is a distinct species.

Among its congeners, *L. inexpectata* is most similar to the other species that have more discoid (i.e., less conical) shells: *L. clara* (Thiele, 1927), from Santa Catarina state (Simone 2006), and *L. gordurasensis* (Thiele, 1927), distributed from eastern Brazil to Argentina and likely Paraguay (Miquel et al. 2007, Salvador et al. 2018). Records from Colombia and Peru (Hausdorf 2005) have been attributed to *L. gordurasensis*, even though they are completely removed from the species' actual distribution (see above); we consider they were misattributed and represent another yet unidentified species, with a narrower and flatter shell.

Lilloiconcha inexpectata can be easily distinguished from *L. clara* (syntypes figured by Simone 2006: fig. 888) by its finer and more numerous ribs, as well as by its larger and more D-shaped aperture. *L. inexpectata* is more closely similar to *L. gordurasensis* (syntype figured by Miquel et al. 2007: fig. 30) but can be distinguished from it by its slightly taller whorls and more raised spire, as well as the larger and nearly D-shaped aperture.
Remarks. Miquel et al. (2007) identified some specimens from Rio Grande do Sul state as *L. pleurophora*. Considering the species' geographic range, those specimens could belong to *L. inexpectata*, although that does not seem to be the case. The shells studied by those authors are discoid and display a protoconch sculptured by both spiral and axial striae (Miquel et al. 2007: p. 223), which is inconsistent with present understanding of *Lilloiconcha* (see above) and the holotype of *L. inexpectata* (Figs 4–7). Therefore, those specimens do not seem to represent either *L. pleurophora* or *L. inexpectata* and need to be revisited. Similarly, records of *L. pleurophora* from Paraguay (Schade 1965, Quintana 1982) possibly do not represent either *L. pleurophora* or *L. inexpectata* and ought to be reassessed.

Lilloiconcha flammulata (Ihering, 1922) comb. nov.

(Figs 12–15)

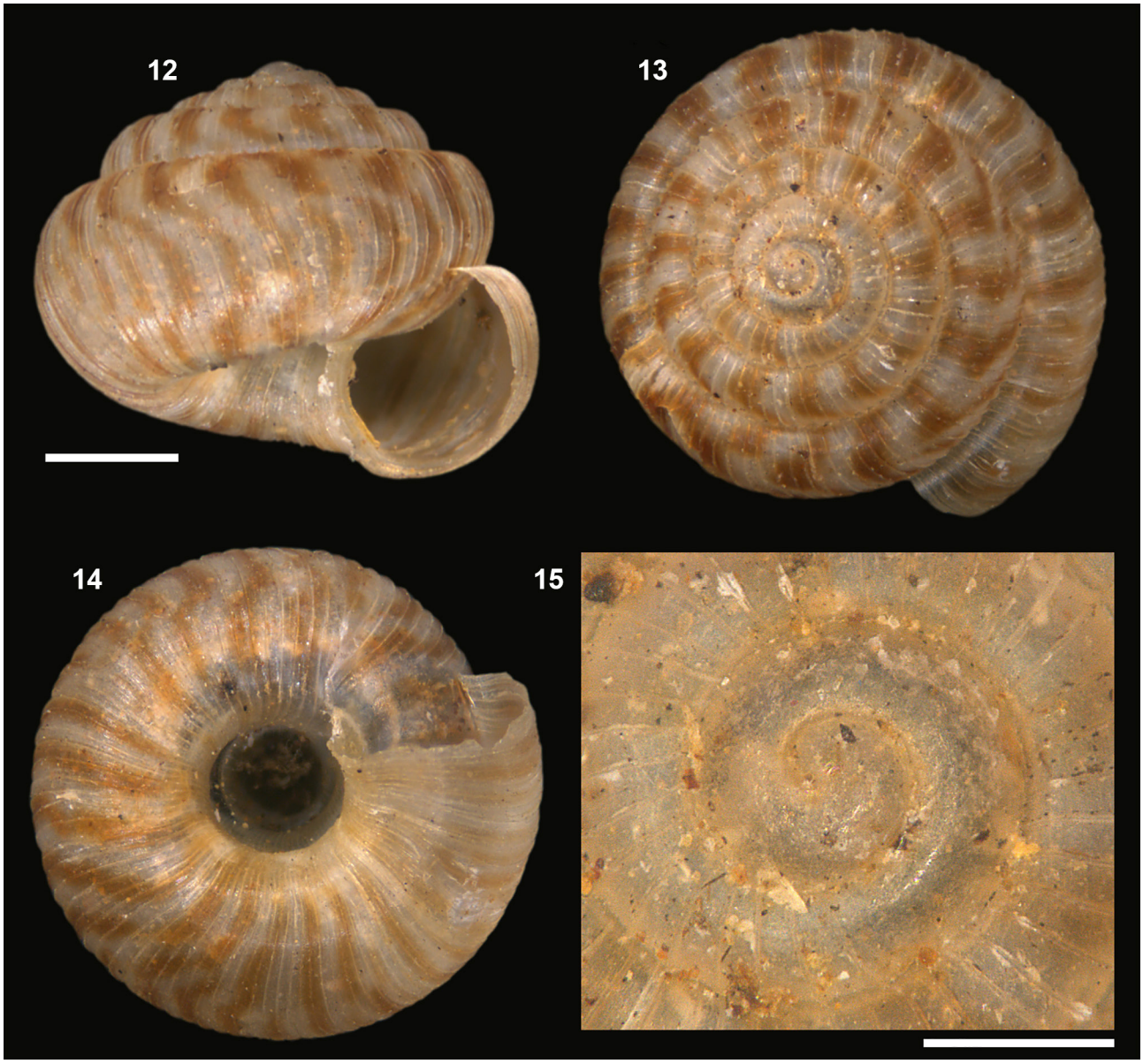
Amphidoxa flammulata IHERING 1922: 154.
Amphidoxa flammulata – SALVADOR et al. 2024: 153.

Type material. Holotype, MZSP 146539 (old nr. MZSP 7632; Hammonia, H. LÜDERWALDT col., ix/1910).

Type locality. "Kolonie Hammonia im Staat Sta. Catharina im Walde" (IHERING 1922: 154). The former settlement of Hammonia (also known as 'Colônia Hammonia' or 'Hansa Hammonia') is now the municipality of Ibirama, in Santa Catarina state, south Brazil.

Diagnosis. Shell discoid with raised step-like spire and conical aspect; whorls with marked shoulder; aperture large, rounded, inserted more abapically in body whorl; colour pattern consisting of multiple (ca. 23) sinuous brownish-red bands.

Description. Shell minute (width ca. 3.8 mm, height ca. 3.2 mm), conical-discoid, with ca. 5¼ whorls. Spire high, step-like; spire top rounded. Whorls regularly increasing in size. Whorls tall, with a marked shoulder. Suture well-marked, deep. Shell base colour whitish, marked by regular reddish brown sinuous axial bands that go all the way from suture to umbilicus; there are 23 such bands on body whorl of holotype. Protoconch (1½ whorls) smooth (assessed from both apical and umbilical views), of base shell colour; transition to teleoconch clear. Teleoconch sculptured



Figs 12–15. *Lilloiconcha flammulata* (Ihering, 1922): 12–14 – holotype MZSP 146539 (shell width 3.8 mm); 15 – detail of the holotype protoconch. Scale bars: 500 μm (15), 1 mm (12–14)

by multiple fine sinuous prosocline ribs, regularly spaced along whorls (ca. 115 on body whorl); space between ribs about four times rib width. Aperture large, rounded, nearly circular; aperture insertion on preceding whorl located below median section of that whorl. Peristome simple. Umbilicus (~25% of shell width) deep, with early whorls visible.

Distribution. Known only from type locality.

Discussion. *Lilloiconcha flammulata* can be easily distinguished from most congeners due to its more conical shell and high step-like spire. It is most similar to *Lilloiconcha superba* (Thiele, 1927), a species distributed from NE Brazil to Rio de Janeiro state (Simone 2006, Miquel et al. 2007, Salvador et al. 2018), and to *Lilloiconcha zulmae* (Miquel, Ramírez et Thomé, 2004) from Rio Grande do Sul state (Simone 2006, Miquel et al. 2007). The shell of *L. superba* is also conical, with a high spire, but *L. flammulata* can be distinguished from it by a lower spire, the marked shoulder of the whorls, the wider shell, having fewer whorls, the more apically positioned aperture, and the larger number of coloured axial stripes on the shell. The shell of *L. flammulata*, while more similar in shape to *L. zulmae*, can still be easily distinguished by its teleoconch sculpture, which displays finer and more numerous axial ribs, and a slightly narrower umbilicus in which the preceding whorls are not so easily visible. Furthermore, no "flammulae" (i.e., coloured axial stripes) are described for *L. zulmae*.

CONCLUSION

Here we reassessed two forgotten species of Brazilian microgastropods, *Amphidoxa inexpectata* and *Amphidoxa flammulata* (Punctoidea, Charopidae). They were reclassified as *Lilloiconcha inexpectata* (Ihering, 1922) comb. nov. and *Lilloiconcha flammulata* (Ihering, 1922) comb. nov. (Punctoidea, Cystopeltidae), acknowledging the need of a revision of this likely non-monophyletic genus.

Considering the former confusion involving *L. inexpectata* and *L. pleurophora*, we also took the opportunity to clarify the known distribution of each. So far, *L. pleurophora* is only known with certainty from Bahia state (Ihering 1922), represented by the type specimens of Moricand (1846). *Lilloiconcha inexpectata* is known from São Paulo, Paraná, and Rio Grande do Sul states. *Lilloiconcha flammulata* is known only from its type locality in Santa Catarina state (Ihering 1922).

Brazilian microgastropods, notably the Punctoidea, are still scarcely studied due to a historical bias towards larger snails such as the Orthalicoidea and Strophocheilidae (Salvador 2019, Machado et al. 2023). Thus, the current known diversity of microgastropods in Brazil is vastly underestimated and it is expected that many new taxa will come to light as these molluscs become more thoroughly studied (Salvador et al. 2018).

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