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Neoluticola (Bacillariophyceae) a new genus of colonial diatoms from tropical America

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Abstract: In the framework of a study of the genus *Luticola* Mann we collected and processed samples from different ecoregions of Argentina, analyzed them with light microscopy (LM) and scanning electron microscopy (SEM). In aerophilous samples collected in Misiones Province, Argentina, we found colonial specimens. The aim of this work is to elucidate the identity of the colonial forms found in aerophilous samples in NE Argentina. In the present study, we describe the genus *Neoluticola* Simonato, Sala et Kociolek and four species: *Neoluticola spinosa* Simonato, Sala et Kociolek sp. nov., *Neoluticola arrechensis* Simonato, Sala et Kociolek sp. nov., *Neoluticola alegrensis* Simonato, Sala et Kociolek sp. nov., and *Neoluticola salvadoriana* Simonato, Sala et Kociolek. *Neoluticola* comprises a group of aerophilous colonial species that share with *Luticola* a conspicuous isolated pore in the central area, distinctly punctate striae, and marginal channels. The new genus differs from *Luticola* in the location of the isolated pore on the valve face/mantle junction, colonial life habit, special structures (spines or silica projections) that join cells together, very thin slit–like areolae on the valve mantle, an elevated fascia expanded side to side, internal proximal raphe ends strongly curved, and fimbriate girdle bands. We compare the species of the new genus with morphologically similar ones from *Luticola* and discuss the geographic distribution of *Neoluticola* gen. nov.

Keywords: aerophilous, fine morphology, geographic distribution, *Luticola*, SEM, taxonomy

Introduction

Luticola D.G. Mann in Round et al. (1990) is characterized by the presence of an isolated conspicuous pore in the central area that has a complex internal structure. Round et al. (1990) included 30 taxa when the genus was first proposed. Levkov et al. (2013) made a revision of the genus and included 200 taxa, most of which were described originally in the genus *Navicula* Bory (Hustedt 1955; Frenguelli 1924, 1941, 1953; Bock 1963, 1970). After this revision numerous species new to science were described, demonstrating the great diversity presented by the genus (Zidarova et al. 2014; Kohler et al. 2015; Bustos et al. 2017; Straube et al. 2017; Bak et al. 2017, 2019; Kale et al. 2017; Chattová et al. 2017; Levkov et al. 2017; Glushchenko et al. 2018; Liu et al. 2018; da Silva–Lehmkuhl et al. 2019; Simonato et al. 2020; Kochman–Kedziora et al. 2020, 2022; Lokhande et al. 2020; Peszek et al. 2021; Hindáková & Noga 2021; Rybak et al. 2021, 2022, 2024; Yang et al. 2022; Shea et al. 2022; Bagmet et al. 2023). All species of the genus share the presence of a conspicuous isolated pore in the central area with a complex internal structure, distinctly punctate striae and internal, longitudinal, marginal canals on each side of the valve. Despite these shared features, there is remarkable heterogeneity in valve outline, valve margins, and the shape of the valve apices (Levkov et al. 2013).

The geography of Misiones Province in NE Argentina is characterized by a landscape mainly composed of plateaus and mountain ranges. The abundant rainfall of the area (up to 2,000 annual mm) generates numerous fluvial courses that overcome the altitude differences through waterfalls (Cranwell 1974). The largest of them is Iguazú Falls, located within Iguazú National Park. The area is covered by a tropical forest known as the Paranaense rainforest, a major subdivision of the Atlantic Rain Forest ecoregion of South America (Di Bitetti et al. 2003). This biome is one of the most important biodiversity hotspots in the world, hosting a high number of endemic plants and animals (Avigliano et al. 2019). Previous work on the diatom flora of Misiones

(Frenguelli 1953; Maidana 1981, 1983, 1985; Bartozek et al. 2013; Nardelli et al. 2016) elucidated the high diversity of diatoms in this area, including those from subaerial microhabitats associated with the waterfalls (Vouilloud et al. 2022).

In aerophilous microhabitats mainly associated with waterfalls in Misiones Province, we found specimens similar to *Luticola* forming straight–chain colonies. Previously, only two species of the genus were described as forming colonies, *Luticola lagerheimii* (Cleve) D.G.Mann described from tropical America and *Luticola spinifera* (Bock) Denys et De Smet described from England and cited in Italy and Turkey (Bock 1970; Denys & de Smet 1996).

The aim of this paper was to elucidate the identity and valve ultrastructure of the chain–forming species found in Misiones and compare them to members of the genus *Luticola.*

Materials and Methods

Samples were collected at aerophilous microhabitats mainly associated with waterfalls during two expeditions carried out to Misiones Province, in December 2017 and May 2019. The samples were mostly taken from mosses and rock scrapings at waterfall sites, from the falls proper and their spray zones. Sampling sites were georeferenced with a Garmin eTrex 20x GPS. Studied samples, their collection number (LPC), geographic coordinates, and type of sample are listed in Table 1. An aliquot of each sample was treated to eliminate organic matter following the methods described in van der Werff (1953) and the protocol outlined in www.queensu.ca/pearl/methods/diatoms.php.

For Light Microscopy (LM) observations, materials were mounted onto permanent slides with Naphrax®, examined with a Leica DM2500 microscope equipped with DIC optics, and photographed with a Leica DFC425 digital camera. The position in the slides of the specimens designated as holotypes was recorded with a S7 England Finder slide (Graticules Pyser–SGI Ltd.). For Scanning electron microscopy (SEM) observations, aliquots of the cleaned material were air–dried onto glass coverslips, attached to bronze stubs, and sputter–coated with ca. 1.5 nm gold or gold–palladium. Observations were made using a Carl Zeiss NTS SUPRA 40 SEM (Centro de Microscopías Avanzadas, Universidad de Buenos Aires, Argentina), a FEI Quanta 200 (Servicio de Microscopía Electrónica de Barrido y Microanálisis, Laboratorio de Investigaciones de Metalurgia Física, Argentina), a Carl Zeiss Sigma (Laboratorio de Análisis de Materiales por Espectrometría de Rayos X, Universidad Nacional de Córdoba), and a Zeiss GeminiSEM 360 (Servicio de Microscopía Electrónica de Barrido, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia").

Raw samples, treated subsamples, and permanent slides are deposited at the Herbarium of the División Ficología "Dr. Sebastán A. Guarrera" (LPC), Museo de La Plata, Argentina. Isotypes are deposited in the J.P. Kociolek Diatom Collection at the University of Colorado, Boulder (COLO).

Cells were isolated following the single–cell isolation methodology with a micropipette (Andersen, 2005). The unialgal cultures were established/maintained in WC medium (Guillard & Lorenzen 1972) at controlled temperature and light conditions (12:12 h light: dark) following the methodological prescriptions of Andersen (2005).

The terminology of frustule features follows that in Barber & Haworth (1981), Cox (2012), and Levkov et al. (2013).

Results

***Neoluticola* Simonato, Sala et Kociolek gen. nov.**

Description: Cells forming colonies composed of 3–18 frustules (up to 200 frustules in culture). Frustules rectangular in girdle view. Valves rhombic with subcapitate–capitate apices. Axial area linear. Central area rectangular, bordered with round areolae or short striae. Slit–like, transapically elongated isolated pore present on

Table 1. List of samples with collection number (LPC) and sampling data.

Site	LPC	Date	Latitude	Longitude	Altitude (m asl)	Collector	Observations
Núñez fall	15436	09/12/2017	25°41'01.7"S	54°26'33.4"W	135	Julian Simonato	Composite sample
Dos Hermanas fall	15442	10/12/2017	25°41'01.9"S	54°26'44.5"W	137	Julian Simonato	Composite sample
Chávez fall	15602	19/05/2019	27°16'18.7"S	54°55'22.1"W	n/d	Julian Simonato	Dry Mosses on dry wall
Alegre fall	15616	20/05/2019	27°07'53.0"S	54°49'39.8"W	319	Julian Simonato	Rock scrape on wet wall
Arrechea fall	15639	21/05/2019	25°39'18.5"S	54°27'25.7"W	153	Julian Simonato	Dry mosses downstream
Núñez fall	15644	22/05/2019	25°41'01.7"S	54°26'33.4"W	135	Julian Simonato	Rock scrape
Núñez fall	15646	22/05/2019	25°41'01.7"S	54°26'33.4"W	135	Julian Simonato	Mosses

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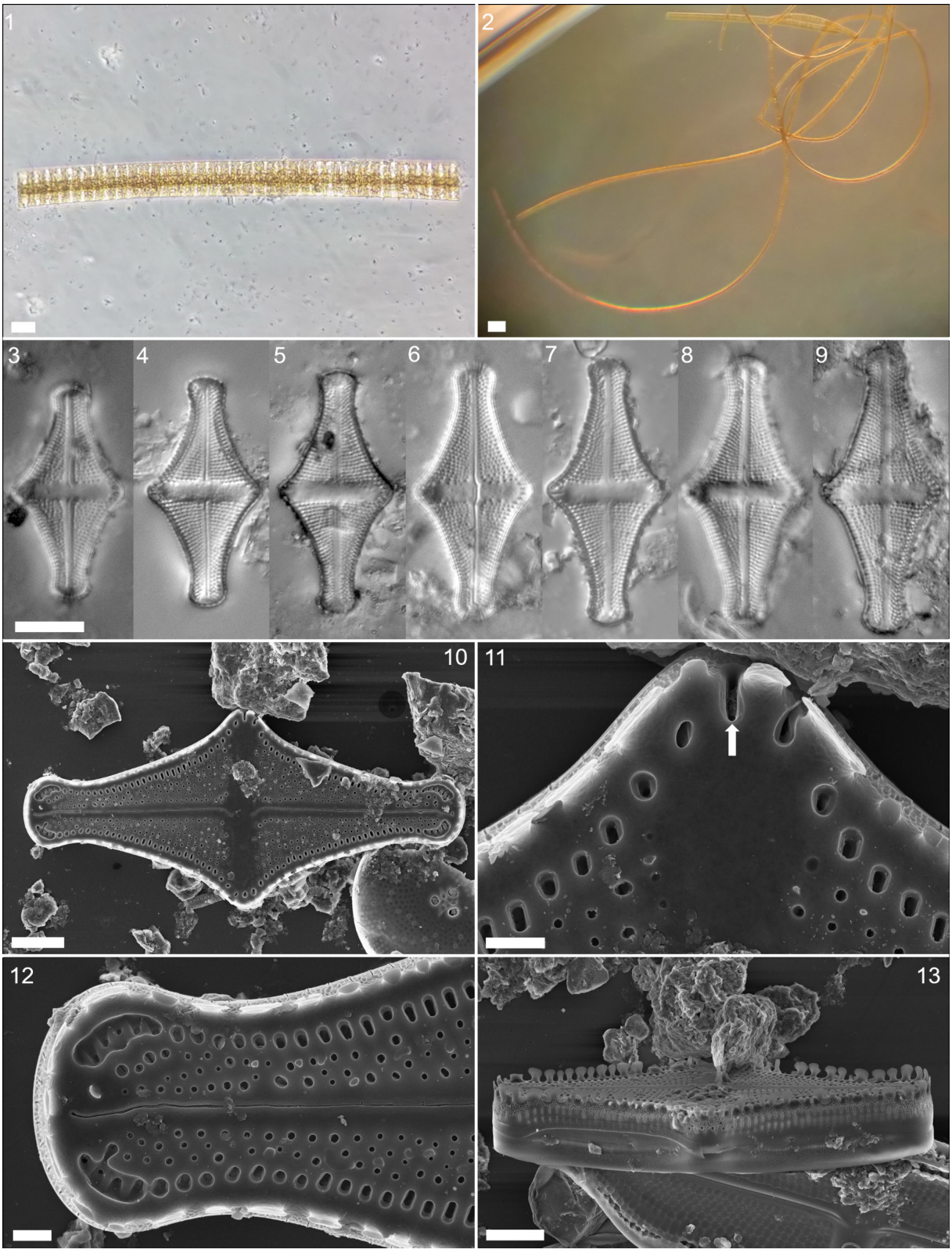

Figs 1–13. *Neoluticola spinosa* sp. nov.: (1–9) LM; (1–2) colonies in culture (scale bar 20 µm and 100 µm respectively); (3–9) valve views showing size diminution series (scale bar 10 µm); (7) holotype; (10–13) SEM, external views; (10) valve view (scale bar 5 µm); (11) detail of the central area showing the isolated pore (arrow) (scale bar 1 µm); (12) valve apices showing distal raphe fissures (scale bar 1 µm); (13) tilted specimen showing valve mantle and the spines (scale bar 5 µm).

valve face/mantle junction. Raphe straight with external proximal ends deflected away from isolated pore. Terminal raphe fissures short, linear, not extending onto the valve mantle. Striae composed of round areolae, radiate near mid–valve, becoming strongly radiate towards apices. Valve mantle with very thin slit–like areolae. Triangular to irregular–shaped spines or silica projections located along valve face/mantle junction. Fimbriate girdle bands open with a row of poroids.

Internally, axial area expanded into rectangular side to side elevated fascia. Proximal raphe ends strongly curved to the isolated pore side. Isolated pore without distinct opening, surrounded by circular, lipped structure. Striae with segmented hymenate occlusions. Marginal channel, located on the valve face/mantle junction, occluded with hymens; at the opposite side of the isolated pore; a thin and small silica flap covers the end of the central areolae.

Etymology: the name of the genus refers to the similarity with the genus *Luticola* and the neotropical distribution.
Generitype: *Neoluticola spinosa* Simonato, Sala et Kociolek, sp. nov.

***Neoluticola spinosa* Simonato, Sala et Kociolek sp. nov. (Figs 1–21)**

Description

LM (Figs 1–9): Cells forming colonies composed of 3–18 frustules (Fig. 1), more than 200 frustules in culture (Fig. 2). Frustules rectangular in girdle view (Fig. 1). Valve rhombic, strongly expanded at mid–valve with broad subcapitate apices (Figs 3–9). Length 28.5–42.5 µm, width 15.0–19.5 µm (n=62). Axial area linear, slightly wider near valve center. Central area rectangular, bordered with 3–5 round areolae. One slit–like, transapically elongated isolated pore present at the valve face/mantle junction. Raphe straight with external proximal ends deflected away from isolated pore. Terminal raphe fissures short, linear, not extending onto the valve mantle. Striae radiate near mid–valve, becoming strongly radiate towards apices, each composed of 7–8 round areolae, numbering 16–19/10 µm. Marginal spines 9–10/10 µm.
SEM (Figs 10–21): Externally, proximal raphe ends deflected away from the slit–like, transapically elongated isolated pore. Pore opening on the valve face/mantle junction (Fig. 11). Terminal raphe fissures short, linear, not extending onto the valve mantle (Fig. 12). Distinct, unornamented rim at the valve margin (Figs 10–12). Valve mantle with a single row of very thin, slit–like areolae or one very thin slit–like areola and one rounded areola; near the valve face with irregular depressions bordered with narrow silica ridges (Fig. 16). Triangular to irregular shaped spines located along valve face/mantle junction (Figs 13–16). Fimbriate open girdle bands with a row of poroids (Fig. 21).

Internally, axial area expanded into a rectangular side to side elevated fascia (Fig. 17). Proximal raphe ends curved to the pore side (Fig. 17), while distally the raphe terminates in small helictoglossae (Fig. 19). Isolated pore without distinct opening, surrounded by circular, lipped structure (Fig. 18). Striae with segmented hymenate occlusions (Fig. 20). Marginal channel, located on valve face/mantle junction, occluded with hymens; at the opposite side of the isolated pore a thin and small silica flap covers the end of the central areolae of the opposite side (Fig. 17).

Holotype: Slide, LPC 15436 in Herbarium of the División Ficología "Dr. Sebastán A. Guarrera", Museo de La Plata, Argentina, Finder H 32 (2) Fig. 7.
Isotype: COLO 652042 in J.P. Kociolek Diatom Collection at the University of Colorado, Boulder, USA.
Type locality: Argentina, Misiones Province, Salto Núñez, 25°41'01.7"S, 54°26'33.4"W, collected by Julian Simonato, 09/12/2017.
Etymology: The specific epithet refers to the presence of spines on the valve rim.
Distribution: This species was found at Dos Hermanas and Núñez falls, Misiones, Argentina. LPC: 15436, 15442, 15644, 15646.

Comments: *Neoluticola spinosa* can be compared to the other species of the genus. The most similar species is *N. salvadoriana* which has spines located along valve face/mantle junction but differs in striae number density (20–22 in 10 µm in *L. salvadoriana*), in the areolae number per stria (5–6 in *N. salvadoriana*) and having undifferentiated apices and the presence of silica thickenings on valve face. The other species of the genus (*N. alegrensis* and *N. arrechensis*) differ from *N. spinosa* by the absence of spines (see Table 2).

***Neoluticola arrechensis* Simonato, Sala et Kociolek sp. nov. (Figs 22–38)**

Description

LM (Figs 22–29): Cells forming colonies composed of 3–17 frustules (Fig. 29). Frustules rectangular in girdle view (Fig. 29). Valves rhombic, transapically slightly curved to the opposite side to the isolated pore, subcapitate apices (Figs 22–28). Length 15.0–35.0 µm, width 7.5–11.0 µm (n=53). Axial area linear. Central area rectangular, bordered with 2–4 round areolae. Slit–like, transapically elongated isolated pore present on the valve face/mantle junction. Raphe straight with external proximal ends deflected away from the isolated pore. Terminal raphe fissures short, linear, not extending onto the valve mantle. Striae radiate near mid–valve, becoming strongly radiate towards apices, each composed of 4–6 round areolae, numbering 16–18/10 µm.
SEM (Figs 30–38): Externally, proximal raphe ends deflected away from the pore opening, present at the valve face/mantle junction (Fig. 32). Distinct, unornamented rim at the valve margin with silica projections (Figs 30, 32). Mantle and silica projections with reticulated thickenings, more evident at the apices (Figs 32–33). Valve mantle with a single row of very thin slit–like areolae

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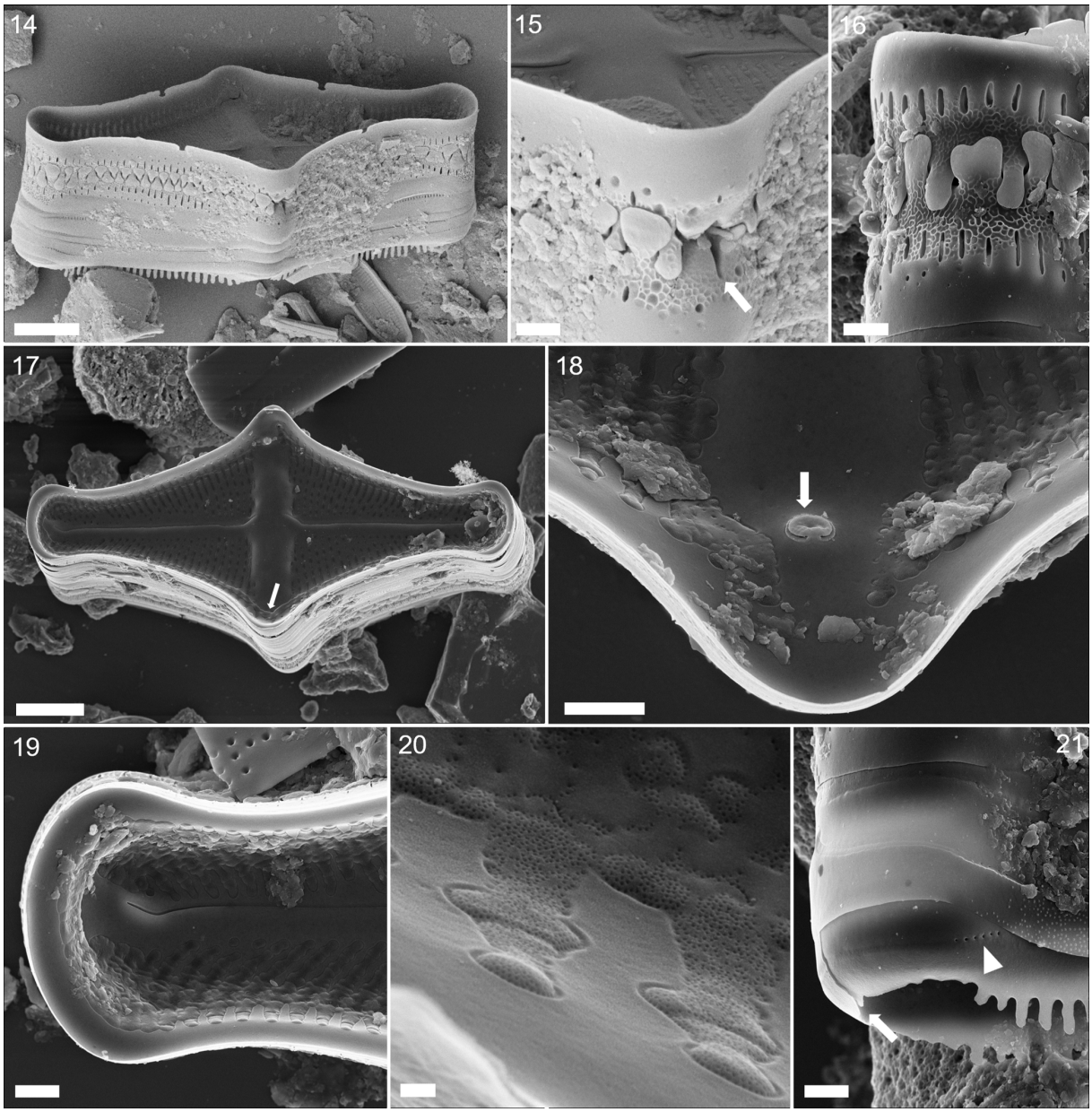


Figs 14–21. *Neoluticola spinosa* sp. nov.: (14–21) SEM, internal views; (14) tilted specimen showing valve mantle and union of two valves through the spines (scale bar 5 µm); (15) detail of the central area showing the isolated pore (arrow) (scale bar 1 µm); (16) detail of the mantle showing the spines and mantle very thin slit–like areolae (scale bar 1 µm); (17) valve view showing elevated fascia, proximal raphe ends, and silica flap (arrow) (scale bar 5 µm); (18) detail of the central area showing the isolated pore surrounded by a lipped structure (arrow) (scale bar 1 µm); (19) detail of the valve apex showing the raphe terminated in a small helictoglossa (scale bar 1 µm); (20) detail of the areolae occlusions (scale bar 0.1 µm); (21) detail of the open fimbriate girdle bands (arrow) with a row of poroids (arrowhead) (scale bar 1 µm).

(Figs 32–33). Fimbriate girdle bands open with a row of small poroids (Figs 33–34).

Internally, axial area expanded into rectangular side to side elevated fascia (Fig. 35). Proximal raphe ends curved to the isolated pore side (Figs 36–37), while distally the raphe terminates straight or deflected to the same side (Fig. 38). Pore without distinct opening, surrounded by circular, lipped structure (Fig. 36). Striae with segmented hymenate occlusions (Figs 37–38). Marginal channel, located on valve face/mantle junction, occluded with hymens (Fig. 35). At the opposite side of the isolated pore a thin and small silica flap covers the end of the central areolae (Fig. 37).

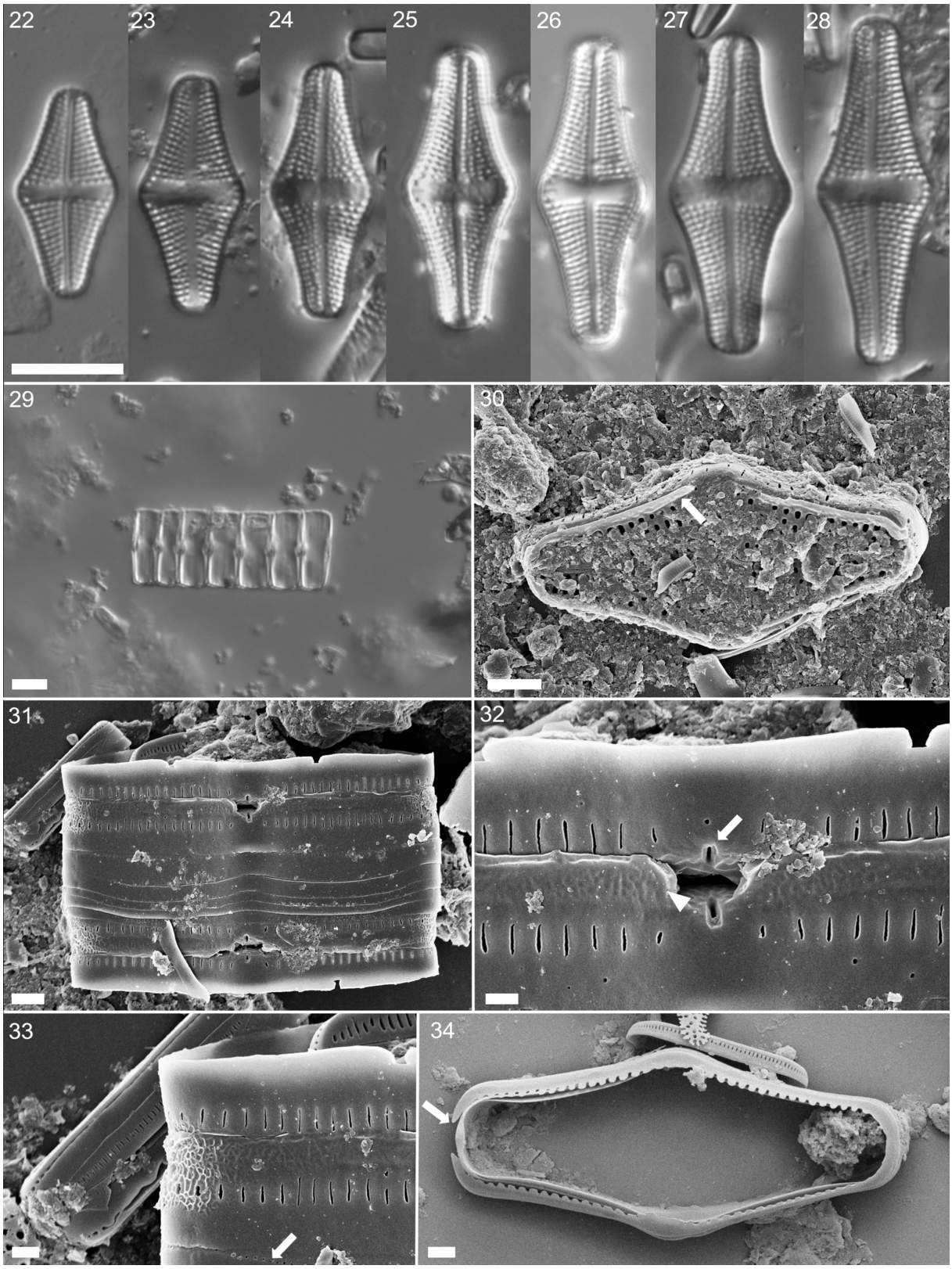
Holotype: Slide, LPC 15639 in Herbarium of the División Ficología "Dr. Sebastán A. Guarrera", Museo de La Plata, Argentina, Finder P 36 (1) Fig. 26).

Isotype: COLO 652043 in J.P. Kociolek Diatom Collection at the University of Colorado, Boulder, USA.

Type locality: Argentina, Misiones Province, Salto Arrechea, 25°39'18.5"S 54°27'25.7"W, collected by Julian Simonato, 21/05/2019.

Etymology: The specific epithet refers to the type locality, Arrechea fall.

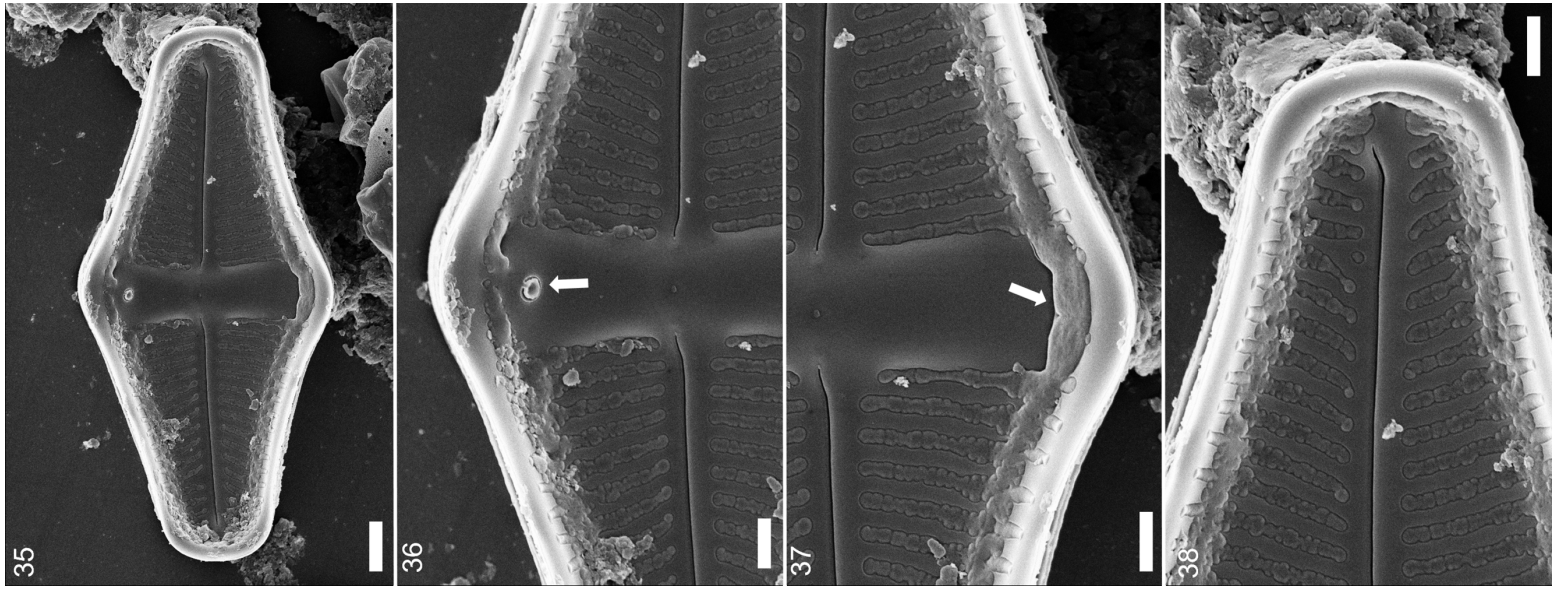
Distribution: This species was found at Arrechea fall,



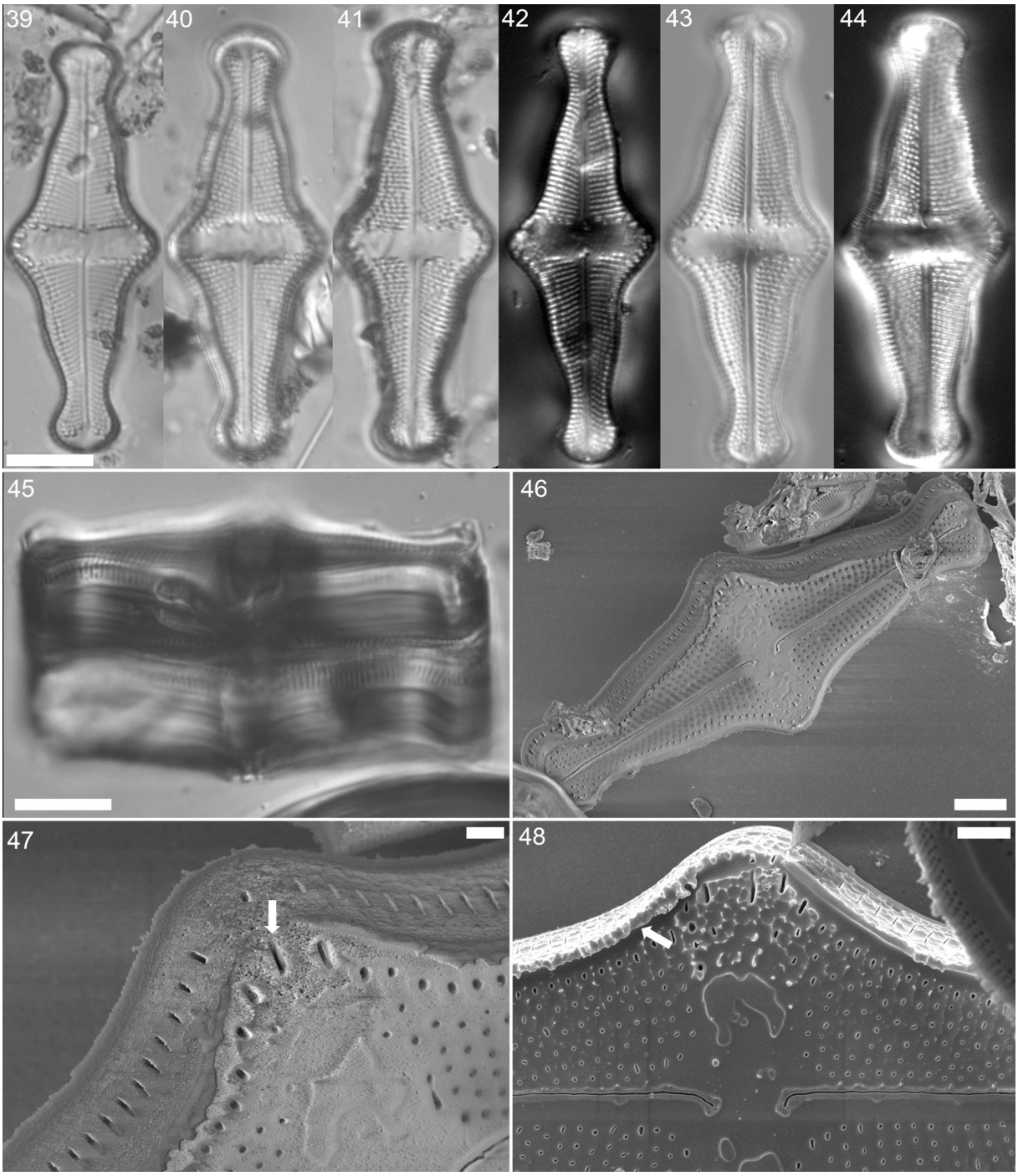
Figs 22–34. *Neoluticola arrechensis* sp. nov.: (22–29) LM; (22–28) valve views showing size diminution series (scale bar 10 µm); (26) holotype; (29) colony (scale bar 10 µm); (30–34); SEM, external views; (30); valve view showing the silica projections (arrow) (scale bar 2 µm); (31); girdle view showing a colony joined through silica projections, the mantle, and the girdle bands (scale bar 2 µm); (32); detail of the central area showing the isolated pore (arrow), the silica projections (arrowhead), and mantle very thin slit–like areolae (scale bar 1 µm); (33) detail of one apex showing the poroids of the girdle bands (arrow) and mantle very thin slit–like areolae (scale bar 1 µm); (34) open fimbriate girdle bands (arrow) (scale bar 2 µm).

Table 2. Comparison of *Neoluticola* species with the allied species.

Species	Length (µm)	Width (µm)	Striae/10 µm	Areolae per striae	Spines	Isolated pore in internal view	Cells forming colonies	Bibliography
Neoluticola salvadoriana	25–48	14–18	20–22	5–6	Present	Mantle	Yes	Levkov et al. (2013, figs 168: 1–6; 169: 1–6)
Neoluticola arrechensis	15–35	7.5–11	16–18	4–6	Absent	Central area/ mantle	Yes	This study
Neoluticola spinosa	28.5–42.5	15–19.5	16–19	7–8	Present	Mantle	Yes	This study
Neoluticola alegrensis	46.5–53	16.5–20	14–16	5–7	Absent	Mantle	Yes	This study
Luticola hustedtii	12–32	6.5–9.5	18–22	4–5	Absent	Central area	No	Levkov et al. (2013, figs 24: 49; 166: 24–37; 168: 7–26; 170: 1–7)



Figs 35–38. *Neoluticola arrechensis* sp. nov.: (35–38) SEM, internal views; (35) valve view, showing the marginal channel (scale bar 2 µm); (36) detail of the central area showing the isolated pore surrounded by a lipped structure (arrow) (scale bar 1 µm); (37) detail of the central area showing the silica flap (arrow) (scale bar 1 µm); (38) detail of the valve end showing the raphe terminate in a small helictoglossa (scale bar 1 µm).



Figs 39–48. *Neoluticola alegrensis* Simonato, Sala et Kociolek sp. nov.: (39–45); LM; (39–44) valve views showing size diminution series (scale bar 10 µm); (43) holotype; (45) colony (scale bar 10 µm); (46–48) SEM, external views; (46) valve view showing proximal and distal raphe ends (scale bar 5 µm); (47) detail of the central area showing the isolated pore (arrow) and mantle very thin slit–like areolae (scale bar 1 µm); (48) detail of the central area showing the silica projections (arrow) (scale bar 2 µm).

Misiones, Argentina. LPC: 15639.

Comments: The most similar species to *Neoluticola arrechensis* is *N. alegrensis,* a taxon which has silica projections located along valve face/mantle junction but mainly differs in valve shape (with undulations in the latter) and valve dimensions (length 46.5–53.0 µm and width 16.5–20.0 µm in the latter). The other species of the genus (N. *spinosa* and *N. salvadoriana*) differ from *N. arrechensis* by possessing spines. *Luticola hustedtii* Levkov, Metzeltin et Pavlov has a solitary growth habit but has a similar valve shape and valve measurements (length 12.0–32.0 µm, width 6.5–9.5 µm); it also differs by the isolated pore being located on the valve face and the absence of silica projections along the valve face/mantle junction (Levkov et al. 2013; see Table 2).

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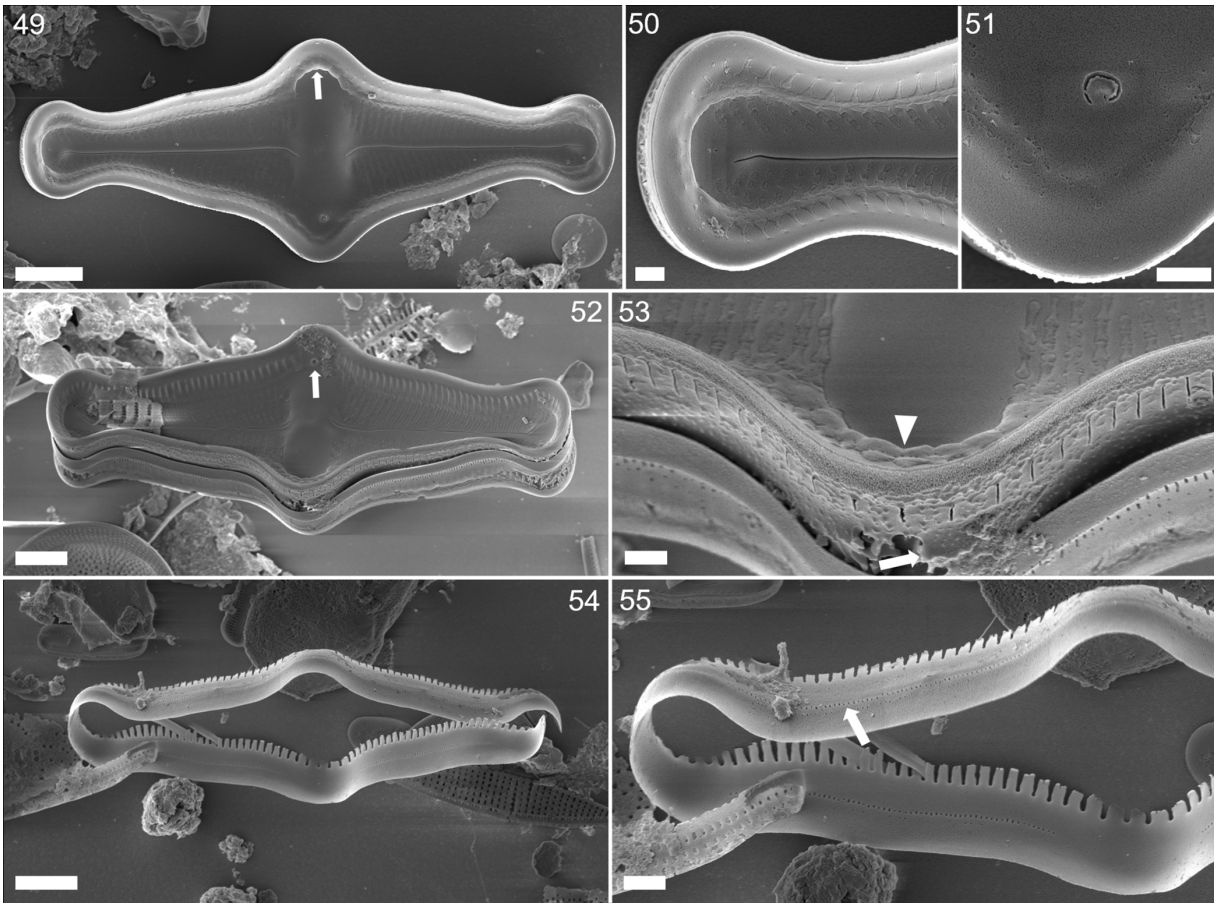

Figs 49–55. *Neoluticola alegrensis* sp. nov.: (49–55) SEM, internal views; (49) valve view showing raphe ends and silica flap (arrow) (scale bar 5 µm); (50) detail of the valve apex showing the raphe terminated in a small helictoglossa (scale bar 1 µm); (51) detail of the central area showing the isolated pore surrounded by a lipped structure (scale bar 1 µm); (52) tilted specimen showing the pore on the mantle (arrow) (scale bar 5 µm); (53) detail of the central area showing the silica projections (arrow), the silica flap (arrowhead), and mantle very thin slit–like areolae (scale bar 1 µm); (54) fimbriate open girdle bands (scale bar 5 µm); (55) detail of the girdle bands with a row of poroids (arrow) (scale bar 2 µm).

***Neoluticola alegrensis* Simonato, Sala et Kociolek sp. nov. (Figs 39–55)**

Description

LM (Figs 39–45): Cells forming straight–chain colonies (Fig. 45). Frustules rectangular in girdle view. Valves rhombic, with marginal undulations and capitate apices (Figs 39–44). Length 46.5–53.0 µm, width 16.5–20.0 µm (n=37). Axial area linear. Central area rectangular, bordered with 5–7 round areolae or short striae. Slit–like, transapically elongated isolated pore present on the valve face/mantle junction (Fig. 43). Raphe straight with external proximal ends deflected away from the pore. Terminal raphe fissures short, linear, not extending onto the valve mantle. Striae radiate near mid–valve, becoming strongly radiate towards apices, each composed of 5–6 round areolae, numbering 14–16/10 µm.

SEM (Figs 46–55): Externally, pore opening present on the valve face/mantle junction (Fig. 47). Proximal raphe ends deflected away from the pore (Figs 45–47) and terminal raphe fissures short, linear, not extending onto the valve mantle (Fig. 45). Distinct, unornamented rim with silica projections located along valve face/mantle junction (Figs 47, 53). Valve mantle with one or two rows of very thin slit–like areolae (Figs 46, 53). Fimbriate girdle bands open with a row of poroids (Figs 54–55). Internally, axial area expanded into a rectangular side to side elevated fascia (Figs 49, 52). Proximal raphe ends curved to the pore side (Fig. 49), while distally the raphe terminates deflected to the pore side (Fig. 50). Pore without distinct opening, surrounded by a circular, lipped structure (Figs 51–52). Striae with segmented hymenate occlusions (Fig. 53). Marginal channel, located at the valve face/mantle junction, occluded with hymens (Fig. 49); at the opposite side the isolated pore a thin and small silica flap covers the end of the central areolae (Figs 49, 52).

Holotype: Slide, LPC 15616 in Herbarium of the División Ficología "Dr. Sebastán A. Guarrera", Museo de La Plata, Argentina, Finder M 27(3) Fig. 43.

Isotype: COLO 652044 in J.P. Kociolek Diatom Collection at the University of Colorado, Boulder, USA.

Type locality: Argentina, Misiones Province, Salto Alegre, 27°07'53.0"S 54°49'39.8"W, collected by Julian Simonato, 20/05/2019.

Etymology: The specific epithet refers to the type locality, Alegre fall.

Distribution: This species was found at Alegre fall, Misiones, Argentina. LPC: 15616.

Comments: The most similar taxon to this species is *N. arrechensis* which has silica projections located along valve face/mantle junction but mainly differs in valve shape (rhombic, slightly transapically convex to the isolated pore side, without undulations) and valve measurements (length 15–35 µm and width 7.5–11 µm). The other species of the genus *N. spinosa* and *N. salvadoriana* differ in the presence of spines.

***Neoluticola salvadoriana* Simonato, Sala et Kociolek sp. nov.**

Holotype: El Salvador, Los Chorros. Hustedt (BRM 10/18, old number 918).

Synonyms: *Navicula lagerheimii* Cleve sensu Hustedt 1955, Neue und wenig bekannte Diatomeen VII. Bericht der Deutschen Botanischen Gessellschaft. 68(3): 121–132.

Luticola lagerheimii (Cleve) D.G.Mann sensu Levkov et al. 2013, *Luticola* and *Luticolopsis*. In: Diatoms of Europe. Diatoms of the European inland waters and comparable habitats. Volume 7, p. 149, figs 168: 1–6; 169: 1–6.

Lit.: Hustedt (1955, p. 121, figs 21–23), Hustedt (1964, p. 624, fig. 1621), Levkov et al. (2013, p. 149, figs 168: 1–6; 169: 1–6).

Description

LM (Hustedt 1955, figs 21–23; Hustedt 1964, fig. 1621; Levkov et al. 2013, pl. 168: 1–6): Cells forming straight–chain colonies. Frustules rectangular in girdle view. Valves rhombic, strongly expanded at mid–valve with undifferentiated apices. Length 25.0–48.0 µm, width 14.0–18.0 µm. Axial area linear, slightly wider near the valve center. Central area rectangular, bordered with 2–3 round areolae. Slit–like, transapically elongated isolated pore present at the valve face/mantle junction. Raphe straight with external proximal ends deflected away from the isolated pore. Terminal raphe fissures short, linear, not extending onto the valve mantle. Striae radiate near mid–valve, becoming strongly radiate towards apices, each composed of 5–6 round areolae, numbering 20–22/10 µm. Marginal spines 8–10/10 µm.

SEM (Levkov et al. 2013, pl. 169: 1–6): Valve face with silica thickenings. Externally, proximal raphe ends deflected away from the transapically elongated pore. Isolated pore opening on the valve face/mantle junction. Terminal raphe fissures short, linear, not extending onto the valve mantle. Valve mantle with a single row of very thin, slit–like areolae or one very thin slit–like areola and one rounded areola. Mantle near the valve face with irregular depressions bordered with narrow silica ridges. Triangular to irregular shaped spines located along the valve face/mantle junction. Girdle bands open with a row of poroids.

Internally, axial area expanded into a rectangular side to side elevated fascia. Proximal raphe ends curved to the isolated pore side, while distally the raphe ends terminate in small helictoglossae. Isolated pore without distinct opening, surrounded by a circular, lipped structure. Striae with segmented hymenate occlusions. Marginal channel, located on the valve face/mantle junction, occluded with hymens; at the opposite side of the isolated pore a thin and small silica flap covers the end of the central areolae.

Comments: Morphometric data given here correspond to Hustedt (1955) and Levkov et al. (2013).

Navicula lagerheimii was described by Cleve based on material collected in Ecuador (Cleve 1894a, p. 131; Cleve 1894b, p. 101, fig. 7: 11). In the original description Cleve noticed the absence of an isolated pore in the central area. Hustedt in 1921 cited this species for Africa but pointed out that Cleve made a mistake when he claimed that it does not have an isolated pore in the central area. After Hustedt's comment, this species was erroneously cited in several locations in Africa and Asia, and several varieties with an isolated pore were erected. In 1955, Hustedt found specimens in El Salvador that resembled Cleve's taxon and said that all those taxa cited in Africa and Asia were wrongly determined, and designated El Salvador's material as a neotype since there was no type material for the taxon. In the specimens from El Salvador Hustedt observed that they had an isolated pore located on the mantle (Hustedt 1955, p. 121, figs 21–23; Hustedt 1964, p. 624, fig. 1621). In 2013 Levkov et al. analyzed with SEM the material from Hustedt's collection. Comparing description and illustration given by Cleve with those given by Hustedt and Levkov we conclude that the material observed by Hustedt does not correspond to *N. lagerheimii* Cleve. We base our conclusion on the absence of an isolated pore and spines, differences in central area shape and morphometric data. The lack of the pore in the central area indicated that Cleve's taxon does not belong to either *Luticola* or *Neoluticola*.

Several forms and varieties of *N. lagerheimii* have been described. *Navicula lagerheimii* var. *intermedia* Hustedt 1937 was recently analyzed and transferred to the genus *Luticola* as *Luticola intermedia* (Hustedt) Levkov, Metzeltin et A.Pavlov 2013.

Other varieties of *Navicula lagerheimii* were transferred to *Luticola*, including:

Luticola lagerheimii var. *hongkongensis* (Skvortzov) Li et Qi = *Navicula lagerheimii* var. *hongkongensis* Skvortzov 1975.

Luticola lagerheimii var. *capitata* (Skvortzov) Li et Qi = *Navicula lagerheimii* var. *capitata* Skvortzov 1938.

Luticola lagerheimii var. *lanceolata* (Skvortzov) Li et Qi = *Navicula lagerheimii* var. *lanceolata* Skvortzov 1938.

Luticola lagerheimii var. *ovata* (Skvortzov) Li et Qi = *Navicula lagerheimii* var. *ovata* Skvortzov 1937 (listed as *Luticola lagerheimii* (Skvortzov) J.Y.Lin et Y.Z.Qi 2018 in Guiry and Guiry 2024).

These four taxa appear to belong to *Luticola*, but further research is needed to verify their systematic position.

On the other hand, *Navicula lagerheimii* var. *nomismatiformis*

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Manguin, 1964 from Perú, has not been analyzed since it was described. According to Manguin´s description and drawing, this taxon belongs to the genus *Luticola* and there are no other species that match it, thus we propose its transfer to the genus:

***Luticola nomismatiformis* (Manguin) Simonato comb. nov. stat. nov.**
Basionym: *Navicula lagerheimii* var. *nomismatiformis* Manguin in Manguin 1964. Contribution à la connaissance des diatomées des Andes du Pérou. Mémoires du Muséum National d'Histoire Naturelle, nouvelle série, série B, Botanique, 12(2): 98 pp., 25 pls. page(s): p. 72; pl. 11, fig. 2.

Description (according to description and illustrations in Manguin 1964): Valves rhombic, strongly expanded at mid–valve with broad subcapitate apices. Length 24.0–28.0 µm, width 11.5–13.0 µm. Axial area linear, wider near valve center. Bow–tie–shaped central area, bordered with 6–7 short striae. Isolated pore present near the valve center. Raphe straight with external proximal ends deflected away from the pore. Terminal raphe fissures hooked, first deflected towards the same side as the proximal endings and then hooked towards the opposite side. Striae radiate composed of 6–7 areolae, numbering 11–13/10 µm.
Syntype: General Collection ANSP: G.C. 26657, G.C. 26658, G.C. 26660 (Mahoney & Reimer 1997)
Distribution: This species was reported in 3 different localities from Peru (Carhumayo, Cordillera Negra, and Capricosa) all of them at high altitude sites (3800 to 4800 m asl).

Navicula lagerheimii var. *robusta* Skvortzov 1938, *Navicula lagerheimii* var. *ovalis* Manguin 1938, and *Navicula lagerheimii* f. *rotundata* Cholnoky 1954 were not treated after their initial descriptions; their systematic positions are uncertain. Further revision is required to ascertain the genera to which they should be assigned.

Discussion and conclusions

The genus *Neoluticola* comprises a group of aerophilous colonial species that share with *Luticola* the presence of a conspicuous isolated pore in the central area, distinctly punctate striae, and marginal channels. Nevertheless, the new genus differs from *Luticola* in:

- the colonial growth habit, due to the presence of special structures to join the cells. (spines or silica projections)
- the location of the isolated pore on the valve face/mantle junction
- very thin, slit–like areolae on the valve mantle
- fascia in internal view strongly silicified and elevated side to side
- internal proximal raphe ends strongly curved towards the isolated pore
- presence of fimbriate girdle bands

Before this study, only two species of *Luticola* were described as forming colonies, specimens referred to as *Luticola lagerheimii* (=*Neoluticola salvadoriana*), and *Luticola spinifera* (Bock) Denys et De Smet. The latter species does not belong to *Neoluticola* based on the position of the isolated pore, the absence of very thin slit–like mantle areolae, a fascia not elevated or slightly elevated in the center, the straight internal proximal raphe ends and the absence of fimbriate girdle bands (Levkov et al. 2013). *Luticola georgzizkae* Witkowski, Lange–Bertalot, M. Rybak et Peszek 2021, also has spines but was not described as forming colonies; furthermore, it also differs from *Neoluticola* in the position of the isolated pore, mantle areolae, fascia, internal proximal raphe ends and girdle bands.

In the genus *Luticola* the position of the isolated pore is used to differentiate species. It has been reported to be either: 1) halfway between the valve center and the valve margin, 2) near the valve center, or 3) near the margin. It has never been reported on the valve face and mantle junction (Levkov et al. 2013) for *Luticola* species. Cox & Van de Vijver (2024) analyzed the structure of the isolated pores in raphid diatoms, relating the genus *Luticola* with *Olifantiella* Riaux–Gobin et Compère. In this work the authors misunderstood the description of the genus *Luticolopsis* Levkov, Metzeltin et A.Pavlov confusing it with the description of *Luticola lagerheimii*. This species differs from other *Luticola* species by forming colonial chains and having its isolated pore displaced to the valve margin.

Some *Luticola* species have transapically elongated areolae on the mantle. Species with this condition include *L. burmensis* Metzeltin et Levkov, *L. dapaloides* (Frenguelli) Metzeltin et Lange–Bertalot, or *L. obligata* (Hustedt) D.G.Mann (Levkov et al. 2013). This feature in *Luticola* species, however, differs from those in *Neoluticola* due to them being wider.

Internally, the fascia is elevated side to side in *Neoluticola* while that characteristic is not reported for *Luticola*, which, when an elevated fascia is present, is elevated only in the center and not expanded to the sides. Also, the proximal raphe ends are strongly curved to the isolated pore side in *Neoluticola* in contrast to what has been observed in *Luticola* species where the raphe ends are straight, although in some cases they look slightly curved due to the elevation of the fascia (e.g. *Luticola grupcei* Pavlov, Nakov et Levkov, *L. hlubicovae* Levkov, Metzeltin et Pavlov, *L. mitigata* (Hustedt) D.G.Mann) (Levkov et al. 2013).

The specimens of *Luticola* have open girdle bands, with one or two rows of poroides (Mayama & Kobayasi 1984; Round 1990). These characteristics are observed in the genus *Neoluticola*, but the girdle bands are fimbriated, a feature never observed in *Luticola*.

Luticola is a genus with a worldwide distribution, although generally individual species have restricted distributions. South America and Antarctica have a high diversity with 20 % of the species in each area (Hanišová

2016). Of the *Luticola* species reported in Antarctica 98% are endemic and only one is cosmopolitan (Kociolek et al. 2017).

On the contrary, *Neoluticola* has a geographic distribution restricted to Central and South America, and its ecological niche appears to be aerophilous habitats in tropical regions.

Another genus related to *Neoluticola* is *Luticolopsis* Levkov, Metzeltin et A.Pavlov 2013. This genus also has an isolated pore, marginal channels, and areolae occluded by hymens. Still, it differs from *Neoluticola* in valve morphology, internal opening of the isolated pore, areolae morphology, proximal raphe endings, and solitary life habit. This monospecific genus also has a restricted distribution (to date only found at the type locality in Vietnam).

Within the context of a detailed revision of the genus *Luticola* in Argentina that we are currently undertaking, after examination of nearly 1,000 samples collected throughout the country (Simonato 2025), *Neoluticola salvadoriana* was not found in these samples. In Argentina, *Navicula lagerheimii* was recorded by Zanon (1949) who pointed out that his taxon corresponds to the drawing in Schmidt's Atlas (1930 figs 370: 19–21) from Java that does not correspond to *Navicula lagerheimii* Cleve (Cleve1894) nor *Neoluticola salvadoriana* considering valve outline and presence of a pore on the valve face. Besides, Levkov et al. (2013) transferred the specimens illustrated in figs (370: 19–20) to *L. hustedtii*. On the other hand, Martinez de Marco et al. (2011) reported *Luticola lagerheimii* in Tucuman province. This taxon is similar to *Navicula lagerheimii* in the absence of isolated pore but differs in the shape of the central area and morphometric data and does not correspond to the new genus. *Luticola lagerheimii* was also reported from Paraná State, Brazil (which borders Misiones province) by Tremarin et al. (2009). However, these specimens correspond to *Luticola hustedtii* according to the analysis of Straube et al. (2017).

According to our results, the genus *Neoluticola* is restricted to aerophilous habitats from tropical America. *Neoluticola salvadoriana* is only known from El Salvador while *N. spinosa*, *N. alegrensis*, and *N. arechensis* are presently known only from Misiones Province, Argentina.

We isolated cells of *Neoluticola spinosa* in culture, but unfortunately, these did not prosper, and thus molecular analysis was ruled out. It is important to point out that molecular information about *Luticola* and related genera is scarce (BAGMET et al. 2023), perhaps due to culturing difficulties. Future phylogenetic analyses are warranted to review species relationships within the new genus and with other, closely allied taxa.

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Competing interests

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