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To cite this article: Arielli Straube, Priscila Izabel Tremarin & Thelma Alvim Veiga Ludwig (2017): Species of *Luticola* D.G. Mann (Bacillariophyceae) in the Atlantic Forest rivers from southern Brazil, *Diatom Research*, DOI: [10.1080/0269249X.2017.1389771](https://doi.org/10.1080/0269249X.2017.1389771)

To link to this article: <http://dx.doi.org/10.1080/0269249X.2017.1389771>



Published online: 10 Nov 2017.



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Species of *Luticola* D.G. Mann (Bacillariophyceae) in the Atlantic Forest rivers from southern Brazil

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The genus *Luticola* is characterized mainly by valves with an internal longitudinal channel located at the valve face/mantle junction, rounded areolae and an isolated pore (stigma) near the central area. Studies on *Luticola* species that occur in Brazil are scarce. Therefore, this paper illustrates and describes the morphology of 18 species of *Luticola* under optical and scanning electron microscopy, from 15 rheophilic environments of an Atlantic Forest in southern Brazil. Two new species are proposed: *Luticola moreirae* Straube, Tremarin et T. Ludwig and *Luticola papilioformis* Straube, Tremarin et T. Ludwig, and are compared with morphologically similar species. Furthermore, the ultrastructure of *Luticola camopiensis* is revealed and described from SEM. *Luticola beyensii*, *L. camopiensis* and *Luticola saprophila* are recorded for the first time from Brazil.

Keywords: diatoms, freshwater, lotic environments, taxonomy, southern Brazil

Introduction

Species of the genus *Luticola* D.G. Mann (Round et al. 1990) can be found in several freshwater and estuarine aquatic environments, as well as soil, snow and subaerial habitats (Hustedt 1966, Poulicková & Hasler 2007, Van de Vijver & Mataloni 2008, Pavlov et al. 2009, Kopalová et al. 2011). About 180 *Luticola* species are known and recently a considerable number of new taxa, mainly from Antarctica and Macedonia, were proposed for this genus (Van de Vijver et al. 2002, 2006, 2011, Kopalová et al. 2011, Levkov et al. 2013, Kohler et al. 2015). Other important taxonomic studies on the genus include Poulicková (2008), who analysed the morphology, cytology and sexual reproduction of *Luticola dismutica* (Hustedt) D.G. Mann for the Czech Republic, and Pavlov et al. (2009), who described *Luticola grupcei* A. Pavlov, Nakov et Levkov from Macedonia and United States. Levkov et al. (2013) conducted a detailed study of the genus, in which about 200 different *Luticola* species were informally recognized in 18 groups, illustrated and characterized in specific tables. This work described 92 new taxa based on samples from several world regions, including eight taxa from Brazilian samples.

In Brazil, *Luticola* species have largely been recorded in floristic studies or catalogues (e.g., Torgan et al. 1999, 2009, Wetzel et al. 2002, Schneck et al. 2008, Tremarin et al. 2009, Silva et al. 2011, Bes et al. 2012), without a more detailed analysis of their ultrastructural features. One exception was the description of *Luticola deniseae*

C.E. Wetzel, Van de Vijver & Ector from the Amazon region by Wetzel et al. (2010).

Our study documents *Luticola* species from rivers of the littoral region of Paraná, southern Brazil, with optical (LM) and scanning electron microscopy. Two new species are proposed: *Luticola moreirae* Straube, Tremarin et T. Ludwig and *Luticola papilioformis* Straube, Tremarin et T. Ludwig, and the morphology of these species is compared with that of similar taxa.

Material and methods

Species were studied based on samples obtained from 15 rivers (Table 1, Fig. 1) from the State of Paraná, Southern Brazil. This region has a humid subtropical climate and is located in the Atlantic Forest (Maack 1981, Vanhoni & Mendonça 2008). The rivers in the sierra are fast-flowing, clear water streams (São João, Mãe Catira, Cachoeira, Nhundiaquara, do Nunes, Iporanga, Cacatu and Quintilha rivers), whereas the rivers in the plain have low current speeds and dark waters (Guraraguaçu, das Pombas, Sertãozinho, da Onça, Cambará, do Salto and Colônia Pereira rivers) (Bigarella 2001).

Phytoplankton samples were obtained with a plankton net (25 µm mesh size) and periphyton samples by scraping submerged macrophyte stalks, rocks and sand. Organic matter was oxidized with potassium permanganate and hydrochloric acid according to Simonsen's method (1974)

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Associate Editor: Sarah Spaulding

(Received 7 November 2016; accepted 24 July 2017)

Table 1. Sampling points, environmental conditions and type of samples obtained from the rivers of the coastal region of Paraná, held at the Herbarium of Universidade Federal do Paraná (UPCB).

Site	Municipality	Coordinates	Abiotic data	Sample	Date of sampling	Record number (UPCB)
Guaraguaçu river	Pontal do Paraná	25°43'57''S/48°33'26.8''W to 25°34'58.8''S/48°28'43.5''W	...	plankton	16/04/2003	47493-47503, 47506
				epiphyton	24/10/2003	47509-47526
São João river	Morretes	25°22'50.4''S/48°51'50.1''W	pH 6.93 T 19°C C 21.1 $\mu\text{S cm}^{-1}$	plankton epiphyton epilithon	02/12/2011	72994 72997 72998
Mãe Catira river	Morretes	25°21'52.7''S/48°52'26.4''W	pH 6.11 T 18°C C 18.2 $\mu\text{S cm}^{-1}$	plankton epiphyton epilithon epipsammon	02/12/2011	72978 72975 72976 72977
Nhundiaquara river	Morretes	25°26'01.7''S/48°52'25.6''W	pH 7.34 T 18.5°C C 19.9 $\mu\text{S cm}^{-1}$	plankton epiphyton	02/12/2011	72979 72980
Iporanga river	Morretes	25°29'14.5''S/48°51'9.6''W	pH 9.72 T 19°C C 17 $\mu\text{S cm}^{-1}$	plankton epiphyton epilithon	02/12/2011	72972 72973 72974
do Nunes river	Antonina	25°20'43.2''S/48°46'14.0''W	pH 6.25 T 19°C C 16.7 $\mu\text{S cm}^{-1}$	plankton epiphyton epilithon	02/12/2011	72984 72985 72986
Cachoeira river	Antonina	25°19'9.9''S/48°42'26.8''W	pH 6.98 T 20°C C 39.4 $\mu\text{S cm}^{-1}$	plankton epiphyton	02/12/2011	72981 72982
Cacatu river	Antonina	25°19'26''S/48°45'7.7''W	pH 6.33 T 19°C C 11.3 $\mu\text{S cm}^{-1}$	plankton epiphyton	02/12/2011	76000 73000
da Onça river	Matinhos	25°43'54.3''S/48°30'32.2''W	pH 7.9 T 23°C C 2.76 $\mu\text{S cm}^{-1}$	plankton epiphyton	03/12/2011	72969 72970

(Continued).

Table 1. Continued.

Site	Municipality	Coordinates	Abiotic data	Sample	Date of sampling	Record number (UPCB)
Sertãozinho river	Matinhos	25°48'0.58''S/48°33'19.1''W	pH 5.72 T 21°C C 69.7 $\mu\text{S cm}^{-1}$	epiphyton	03/12/2011	72971
Colônia Pereira river	Matinhos	25°41'15.6''S/48°34'30.3''W	pH 6.22 T 21°C C 151 $\mu\text{S cm}^{-1}$	plankton	03/12/2011	75227
				epiphyton		75225
				epilithon		75229
				epipsammon		75230
das Pombas river	Matinhos	25°39'13.0''S/48°35'12.7''W	pH 6.11 T 22°C C 167 $\mu\text{S cm}^{-1}$	plankton	03/12/2011	73001
				epiphyton		73002
				epilithon		73003
				episammon		73004
Cambará river	Paranaguá	25°43'59.8''S/48°35'26.2''W	pH 7.19 T 21°C C 34.3 $\mu\text{S cm}^{-1}$	plankton	03/12/2011	72965
				epiphyton		72966
				epilithon		72967
				epipsammon		72968
do Salto river	Paranaguá	25°36'43.6''S/48°36'18.6''W	pH 6.61 T 22°C C 78.4 $\mu\text{S cm}^{-1}$	plankton epiphyton	03/12/2011	76001 73005
Quintilha river	Paranaguá	25°38'28''S/48°37'14.1''W	pH 7.24 T 21°C C 29.4 $\mu\text{S cm}^{-1}$	plankton	03/12/2011	72993
				epiphyton		72989
				epilithon		72991
				epipsammon		72992

Note: T, water temperature; C, conductivity.



Fig. 1. Location of the rivers sampled along the coast of Paraná state, southern Brazil.

modified by Moreira-Filho & Valente-Moreira (1981). Permanent slides were mounted with Naphrax (R.I. = 1.74) for light microscopy. Images were taken using an Olympus BX40 microscope equipped with Olympus DP71 capture equipment. Part of the cleaned material was dried and coated with gold on aluminium stubs for scanning electron microscopy observation in a JEOL JSM 6360LV microscope (operated at 15 kV voltage, 8 mm working distance). Abiotic data (water temperature, pH and conductivity) were measured on site with a multiparameter analyser CONSORT C535.

The samples were stored in the Herbarium of the Universidade Federal do Paraná (UPCB) and the Natural History Museum, London (BM). The terminology used in the descriptions followed Round *et al.* (1990), Hendey (1964) and Levkov *et al.* (2013).

Results and discussion

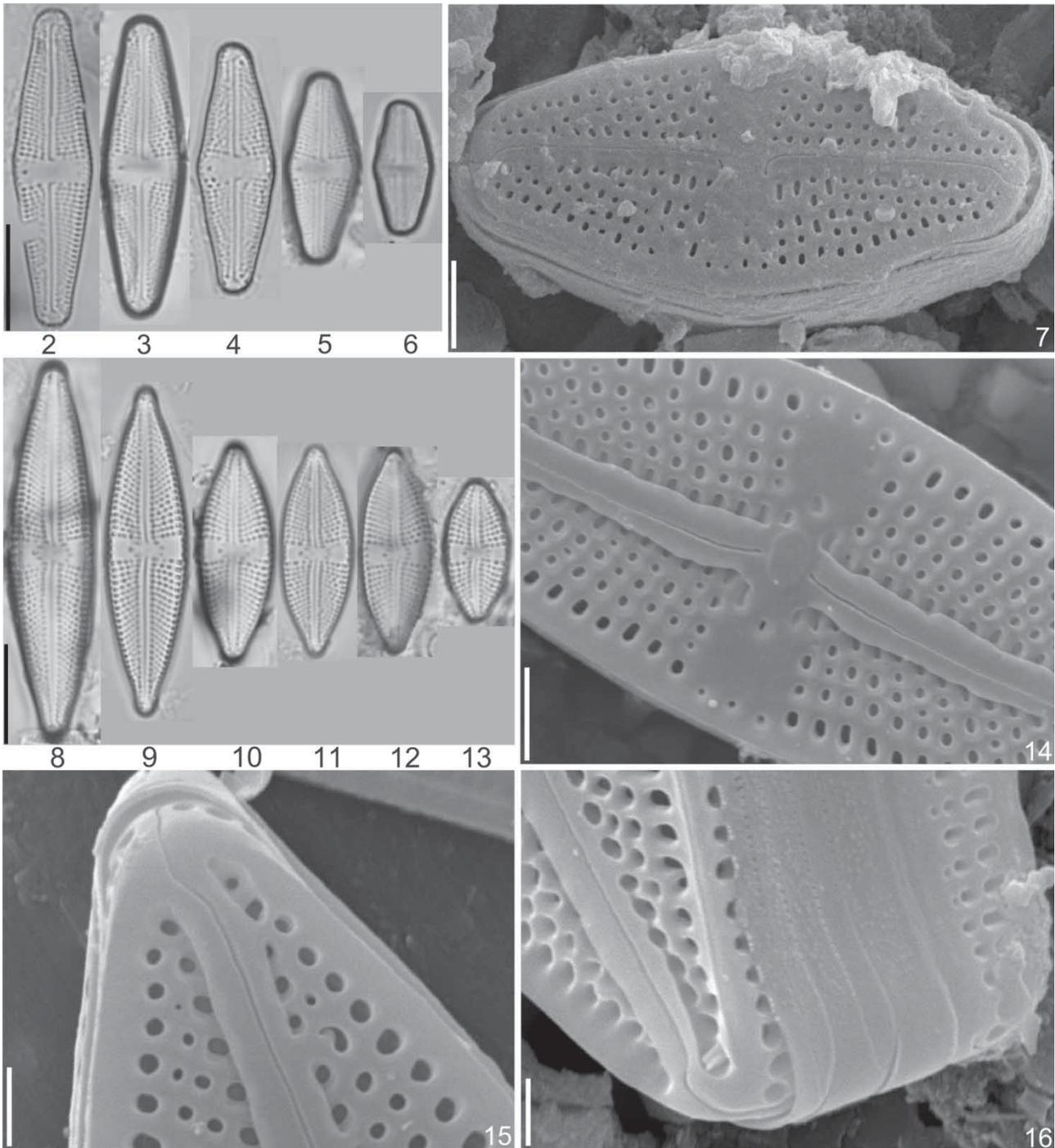
***Luticola beyensii* Van de Vijver *et al.* (2002: 236–238, figs 2–13)**

(Figs 2–7)

Description: Valves rhombic-lanceolate, slightly undulate, 12.5–29.2 μm long and 5.5–7.5 μm wide, with rounded apices. Raphe sternum linear. Central area expanded towards the valve margin, delimited by 4–5 areolae. Stigma in central area, rounded, submarginal. Marginal channel not evident in LM. Raphe straight; external proximal endings of raphe deflected to side opposite the stigma; external distal endings hooked away from the stigma, expanded onto valve mantle. Striae radiate, 20–24 in 10 μm , composed of rounded to elliptic areolae, 18–22 in 10 μm .

Material examined: UPCB 47496, UPCB 72975, UPCB 73001, UPCB 73005.

Remarks: *Luticola beyensii* resembles *Luticola dismutica* (Hustedt) D.G. Mann recorded by Poulícková (2008) from cave material in the Czech Republic. However, the specimens studied by Poulícková (2008) differ from the type material of *L. dismutica*, which has slightly undulate valves and coarser areolae (Hustedt 1966). *Luticola dismutica* differs from *L. beyensii* in its greater valve dimensions (length 15–44 μm , width 6–11 μm), lower stria density (16–20 in



Figs. 2–7. *Luticola beyensii*, Figs 2–6. Valves in LM. Fig. 7. Valve face in external view, SEM. Figs 8–16. *Luticola camopiensis*. Figs 8–13. Valves in LM. Fig. 14. External view of median region of valve, SEM. Fig. 15. External view showing distal raphe ending, SEM. Fig. 16. Apex of frustule showing the distal raphe ending, mantle and girdle bands, SEM. Scale bars = 10 μm (Figs 2–6, 8–13), 2 μm (Figs 7, 14), 1 μm (Figs 15, 16).

10 μm), stigma close to the proximal raphe ends and the depressions in the central area (Hustedt 1966, Simonsen 1987). This is the first record of *L. beyensii* from Brazil and the population agrees with the material from the island of Saint Paul, southern Indian Ocean (Van de Vijver et al. 2002, Levkov et al. 2013).

Luticola beyensii is an aerophilous, subtropical diatom recorded from subantarctic islands (Van de Vijver et al. 2002, Levkov et al. 2013). In Brazil, this species was found in the epiphyton and epilithon of subtropical rivers with mildly acidic waters (pH 6.1–6.6).

***Luticola camopiensis* Levkov *et al.* (2013: 80, pl. 71, figs 1–19)**

(Figs 8–16)

Description: Valves lanceolate, 14.2–38.5 µm long and 6.8–8.5 µm wide, with cuneate-rostrate to cuneate-rounded apices. Raphe sternum linear, separated from striae by a narrow deep groove. Central area expanded towards valve margin and delimited by 2–4 areolae. Presence of ‘ghost areolae’ in central area. Stigma close to central area, externally linear. Marginal channel evident in LM. Raphe straight to slightly curved; external proximal endings dilated and slightly deflected to side opposite the stigma; external distal endings hooked away from the stigma, expanded onto valve mantle. Striae radiate, 18–24 in 10 µm, composed of rounded to irregular areolae, 18–21 in 10 µm. Valve mantle with one to three rows of rounded to elliptic areolae. Open girdle bands with one row of small poroids.

Material examined: UPCB 47513, UPCB 72975, UPCB 72982.

Remarks: The species was recorded from French Guyana and now from Brazil. The valves analysed were similar to the type of *L. camopiensis* (Levkov *et al.* 2013), and the ultrastructure of this species is revealed for the first time. The ‘ghost areolae’ present in the central region of *L. camopiensis* are depressions in the valve face and also occur in *L. dismutica* and *L. rionegrensis* Wetzel, Ector *et al.* (Levkov *et al.* 2013). The raphe sternum of *L. camopiensis* forms a partial conopeum that almost covers the rows of areolae closest to the raphe on both sides. This feature was also seen in *L. obligata* (Hustedt) D.G. Mann, *L. higleri* Van de Vijver, Van Dam *et al.* (Levkov *et al.* 2013), *L. katkae* Van de Vijver *et al.* (Zidarova, *L. desmetii* Kopalová *et al.* (Van de Vijver *et al.* 2006, 2011, Kopalová *et al.* 2011, Levkov *et al.* 2013). The most similar species to *L. camopiensis* is *L. grupcei* Pavlov, Nakov *et al.* (Levkov *et al.* 2013). However, *L. grupcei* differs in having larger valves (length 23–46 µm, width 8.5–10.5 µm), lower density of striae and areolae (15–17 in 10 µm and 16–20 in 10 µm, respectively), punctiform stigma, and absence of conopeum and depressions in the central area (Pavlov *et al.* 2009).

Luticola camopiensis was more common in the epiphyton of Cachoeira river, with fast-flowing clean waters with neutral pH (6.98).

***Luticola cristinae* Levkov *et al.* (2013: 93, pl. 181, figs 37–46, pl. 183, figs 1–5)**

(Figs 17–26)

Description: Valves linear to linear-lanceolate with undulate margin, 15.8–29.2 µm long and 6.8–7.5 µm wide, with

rostrate to subcapitate apices. Raphe sternum linear. Central area linear, expanded towards valve margin, delimited by 3–4 areolae. Stigma externally linear, internally covered by a ‘C’-like structure near central area. Marginal channel not evident in LM. Raphe straight with external proximal endings as in small pores deflected to side opposite the stigma and internally simple; external distal ends hooked towards the stigma side and extending onto the mantle, internally ending in small helictoglossa. Striae radiate, 24–26 in 10 µm, composed of rounded to irregular areolae, 20 in 10 µm. Valve mantle with two rows of rounded to elliptic areolae.

Material examined: UPCB 72965, UPCB 72979, UPCB 73005.

Remarks: *Luticola* spec. No. 87/29, recorded by Metzeltin and Lange-Bertalot (1998, pl. 87, fig. 29), is similar to *L. cristinae* in valve outline and apices, but has larger valves (length 33.3 µm, width 10 µm) and a punctiform stigma (Metzeltin & Lange-Bertalot 1998).

Luticola cristinae was mistakenly identified as *L. nivalis* (Ehrenberg) D.G. Mann in several Brazilian studies (Tremarin *et al.* 2009) because of the undulate valve margins. This species was described from the Mogiguaçu river, Brazil (Levkov *et al.* 2013) (no other records). *Luticola cristinae* occurred in the plankton and epiphyton of slightly acidic to neutral waters (pH 6.6–7.3). The presence of this species in the plankton is probably consequence of the rapid current in some localities, which removes the diatoms from the sediment and marginal areas to the water column.

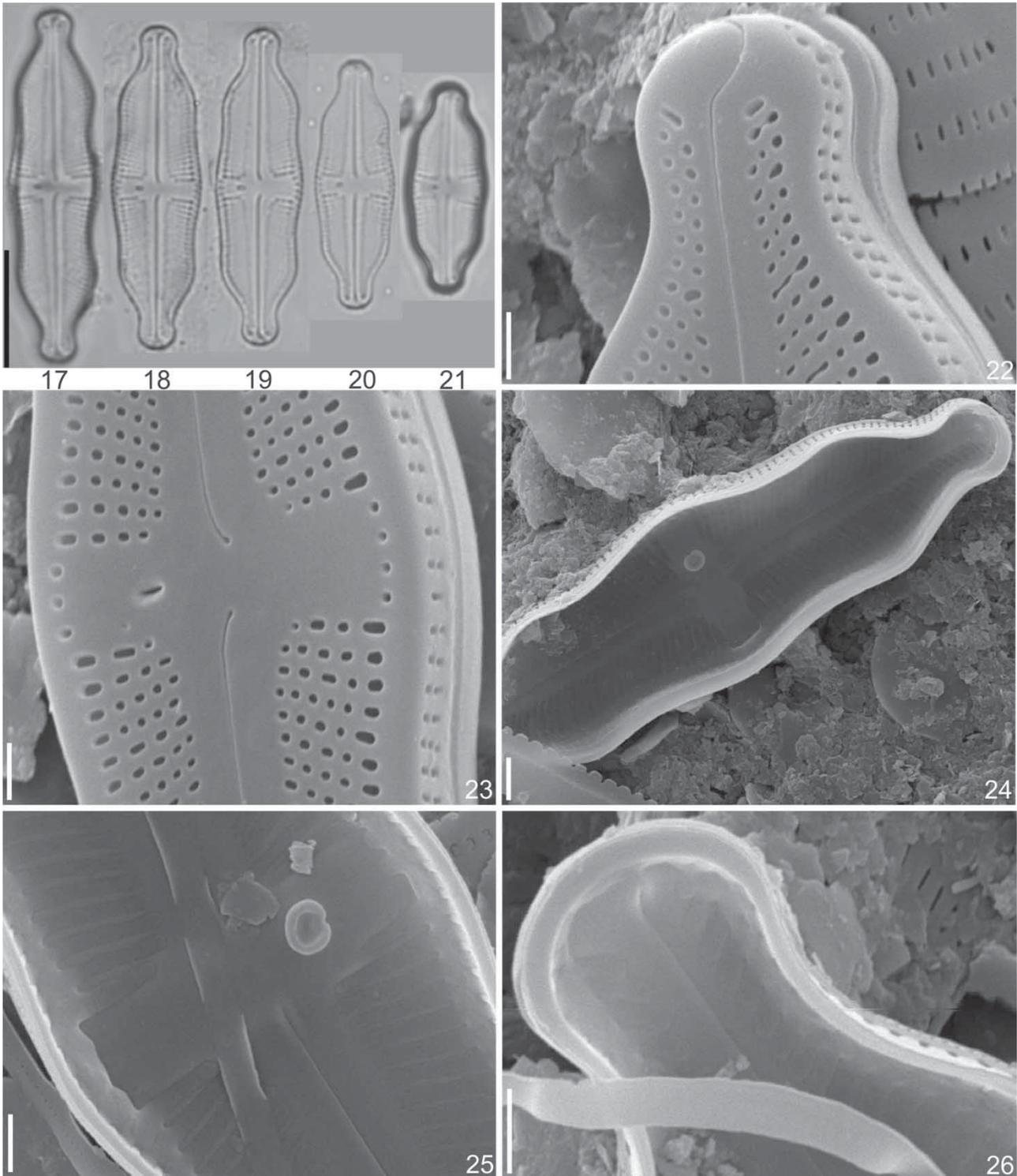
***Luticola dapaoides* (Frenguelli) Lange-Bertalot in Metzeltin and Lange-Bertalot (1998: 137)**

(Figs 27–33)

Description: Valves linear-elliptic with margins slightly undulate in larger specimens and slightly constricted at the centre in smaller specimens, 49–88 µm long and 19–25 µm wide, with attenuate-rounded to subrostrate apices. Raphe sternum linear. Central area delimited by 3–4 shortened striae. Stigma in central area located close to valve margin, externally linear and internally covered by ‘C’-like structure. Marginal channel wide and evident in LM. Raphe straight with external proximal ends dilated, deflected to side opposite the stigma; distal raphe ends slightly hooked over the mantle. Striae radiate, 12–13 in 10 µm, composed of rounded to irregular areolae, 8–12 in 10 µm. Valve mantle with single row of elongated areolae with fimbriate edges. Valvocopula perforated by two rows of rounded pores.

Material examined: UPCB 72981, UPCB 72984.

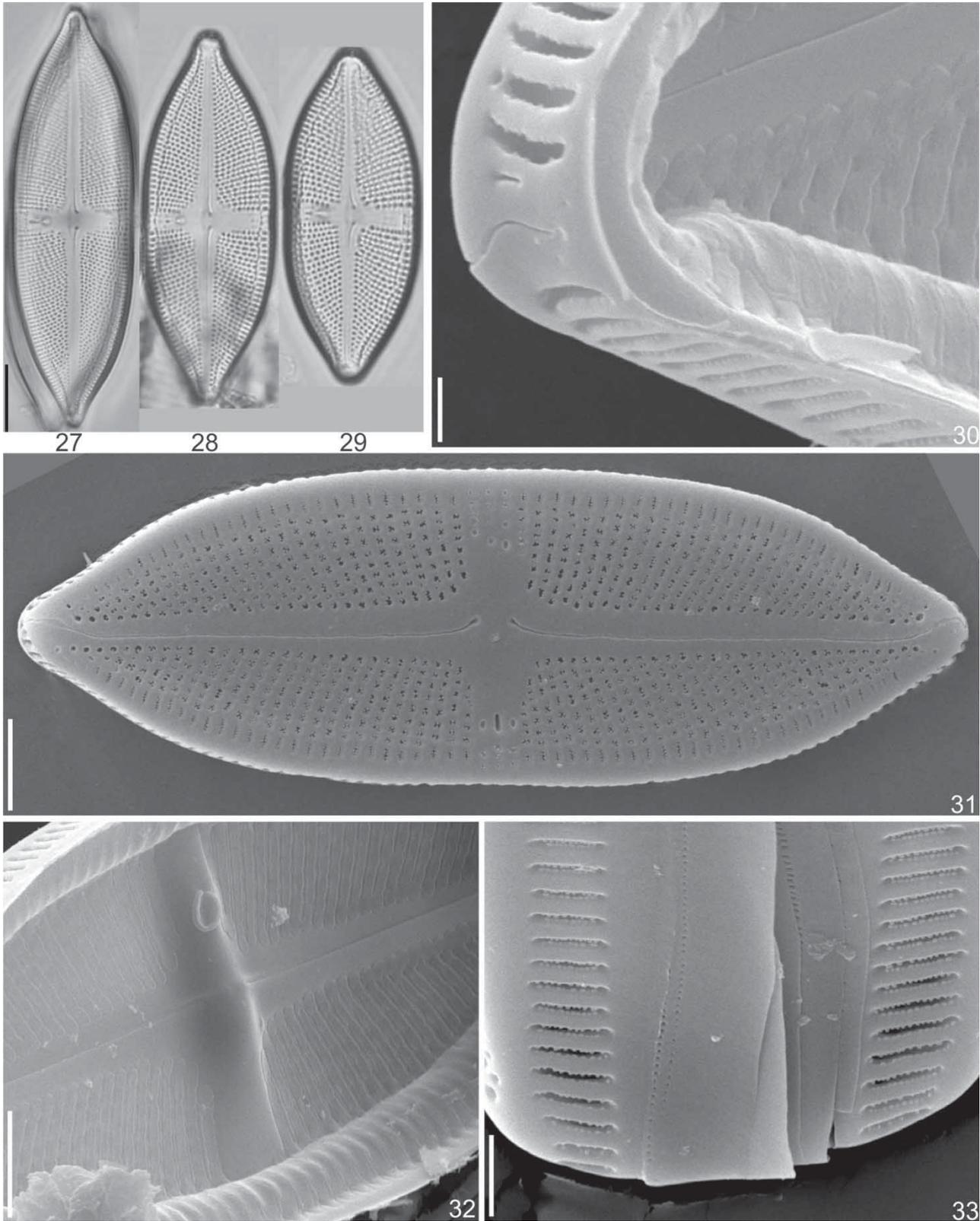
Remarks: The analysed specimens agree with Frenguelli’s (1953) description of *L. dapaoides*. *Luticola hilgenbergii* Metzeltin, Lange-Bertalot *et al.* (Garcia-Rodriguez and



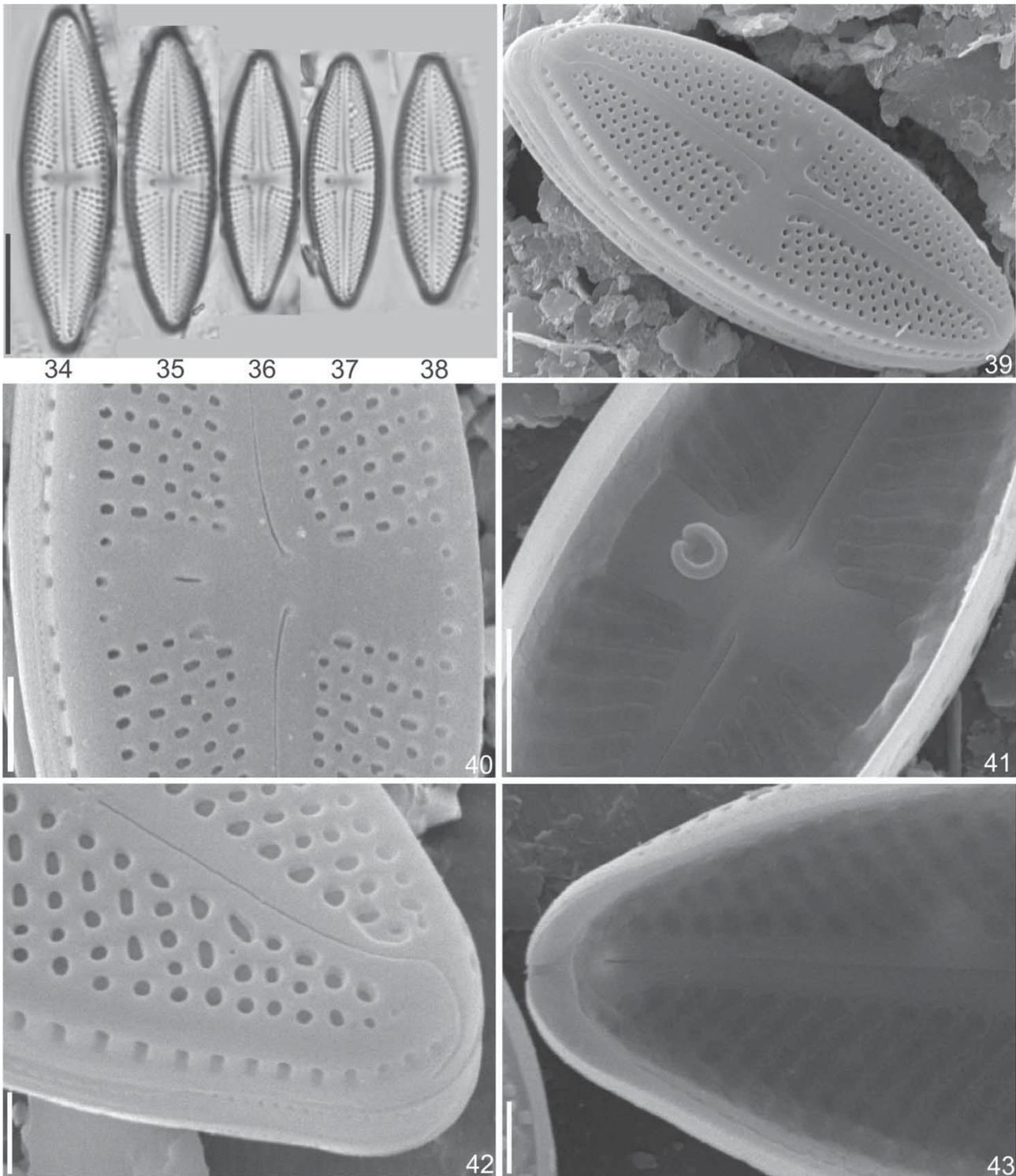
Figs. 17–26. *Luticola cristinae*. Figs 17–21. Valves in LM. Fig. 22. External view of valve apex showing the distal raphe ending and mantle, SEM. Fig. 23. Central area with linear stigma and proximal raphe endings, SEM. Fig. 24. Internal overview of the valve, SEM. Fig. 25. Internal view of central area with stigma, SEM. Fig. 26. Internal view showing distal raphe ending, SEM. Scale bars = 10 μ m (Figs 17–21), 2 μ m (Fig. 24), 1 μ m (Figs 22, 23, 25, 26).

L. uruguayensis Metzeltin, Lange-Bertalot et García-Rodríguez resemble *L. dapaoides* in the structure and position of the stigma and the undulate outline

of the valves, but are distinguished by having more lanceolate valves, protracted apices (abruptly protracted in *L. hilgenbergii*, cuneate to slightly protracted in



Figs. 27–33. *Luticola dapaoides*. Figs 27–29. Valves in LM. Fig. 30. Detail of valve apex showing the distal raphe ending extending onto the mantle, SEM. Fig. 31. External view of valve face, SEM. Fig. 32. Internal view of median valve region showing the stigma and the longitudinal channel, SEM. Fig. 33. Apex of frustule in girdle view showing the valve mantle and girdle bands, SEM. Scale bars = 10 μm (Figs 27–29), 5 μm (Figs 31, 32), 2 μm (Fig. 33), 1 μm (Fig. 30).



Figs. 34–43. *Luticola goeppertiana*. Figs 34–38. Valves in LM. Fig. 39. External valve view, SEM. Figs 40–41. External and internal views of median region of valve showing the stigma and proximal raphe endings, respectively, SEM. Fig. 42. Detail of valve apex showing the distal raphe ending extending onto the mantle, SEM. Fig. 43. Internal view of distal raphe ending, SEM. Scale bars = 10 μm (Figs 34–38), 2 μm (Figs 39–41), 1 μm (Figs 42, 43).

L. uruguayensis) and evident marginal channel (Frenguelli 1953, Metzeltin et al. 2005, Levkov et al. 2013). *Luticola dapalis* (Frenguelli) D.G. Mann differs from

L. dapaloides by having punctiform stigma, lanceolate valves and apiculate apices (Frenguelli 1941, 1953). *Luticola frenguelli* Metzeltin et Lange-Bertalot

and *L. plausibiloides* Metzeltin, Lange-Bertalot et García-Rodríguez are similar in shape and valve length to *L. dapaoides*, but they have punctiform stigma, obtuse apices and narrower valves (Metzeltin & Lange-Bertalot 1998, Metzeltin *et al.* 2005).

Luticola dapaoides was only found in South America (Guiry & Guiry 2017). In Brazilian samples, *L. dapaoides* occurred in slightly acidic to neutral waters (pH 6.2–6.9) in fast-flowing rivers.

***Luticola goeppertiana* (Bleisch) D.G. Mann in Round *et al.* (1990: 670)**

(Figs 34–43)

Description: Valves elliptic-lanceolate to elliptic, 20.3–28.1 µm long and 6.4–7.8 µm wide, with rostrate to subrostrate apices. Raphe sternum linear. Central area expanded towards valve margin, delimited by 3–4 areolae. Stigma in central area, close to valve margin, externally linear and internally covered by ‘C’-like structure. Marginal channel not evident in LM. Raphe straight with external proximal ends dilated, deflected to side opposite the stigma; distal raphe ends slightly hooked over the mantle, and internally ending in a small helictoglossa. Striae radiate, 16–22 in 10 µm, composed of rounded to elliptic areolae, 16–24 in 10 µm. Valve mantle with single row of elliptic areolae.

Material examined: UPCB 72981, UPCB 72982, UPCB 72989, UPCB 72993.

Remarks: The specimens studied agree with the type material of *L. goeppertiana* reviewed by Pavlov *et al.* (2009). *Luticola goeppertiana* is similar to *L. stigma* (Patrick Johansen, with a sharply demarcated, linear stigma in the central area and similar valve dimensions, but differs in valve outline and apical shape (Pavlov *et al.* 2009). *Luticola goeppertiana* has elliptic to elliptic-lanceolate valves and rounded apices, while *L. stigma* has lanceolate valves and rostrate apices (Patrick & Reimer 1966, Johansen *et al.* 2004).

Luticola goeppertiana is tolerant to pollution and occur in eutrophic environments (Pavlov *et al.* 2009, Levkov *et al.* 2013). In Brazilian samples, this species was recorded in fast-flowing clean waters with neutral pH (6.9–7.2).

***Luticola hustedtii* Levkov *et al.* (2013: 131, pl. 24, fig. 49, pl. 166, figs 24–37, pl. 168, figs 7–26, pl. 170, figs 1–7)**

(Figs 44–48)

Description: Valves rhombic to rhombic-lanceolate, slightly undulate in the larger valves, 8.2–23.0 µm long and 5.4–8.1 µm wide, with rounded apices. Raphe sternum linear. Central area slightly expanded towards valve margin,

delimited by 3–5 areolae. Stigma in central area, rounded, submarginal. Marginal channel not evident in LM. Raphe straight, with dilated proximal ends, deflected to side opposite the stigma. Striae radiate, 18–24 in 10 µm, composed of rounded areolae, 16–17 in 10 µm.

Material examined: UPCB 72985.

Remarks: *Luticola hustedtii* was mistakenly identified as *L. lagerheimii* (Cleve) D.G. Mann in some Brazilian studies (Tremarin *et al.* 2009) because of the rhombic valve outline. In this study, we observed valves smaller than those recorded by Levkov *et al.* (2013) for *L. hustedtii* (length 12–32 µm, width 6.5–9.5 µm), but the population still shows the diagnostic features of the species. The taxon occurred in the epiphyton of slightly acidic waters (pH 6.2) of the do Nunes river.

***Luticola intermedia* (Hustedt) Levkov *et al.* (2013: 138, pl. 20, figs 1–16, pl. 21, figs 28–40)**

(Figs 49–51, 56–57)

Description: Valves lanceolate to elliptic-lanceolate, 17.0–26.8 µm long and 6.2–6.2 µm wide, with rounded apices. Raphe sternum linear. Central area expanded towards the valve margin, bounded by 4–5 areolae. Stigma in central area, rounded, submarginal. Marginal channel not evident in LM. Raphe straight with proximal ends strongly deflected to side opposite the stigma; distal raphe ends slightly hooked over the mantle. Striae radiate, 22–24 in 10 µm, composed of rounded to elliptic areolae, 22–24 in 10 µm. Valve mantle with single row of rounded areolae.

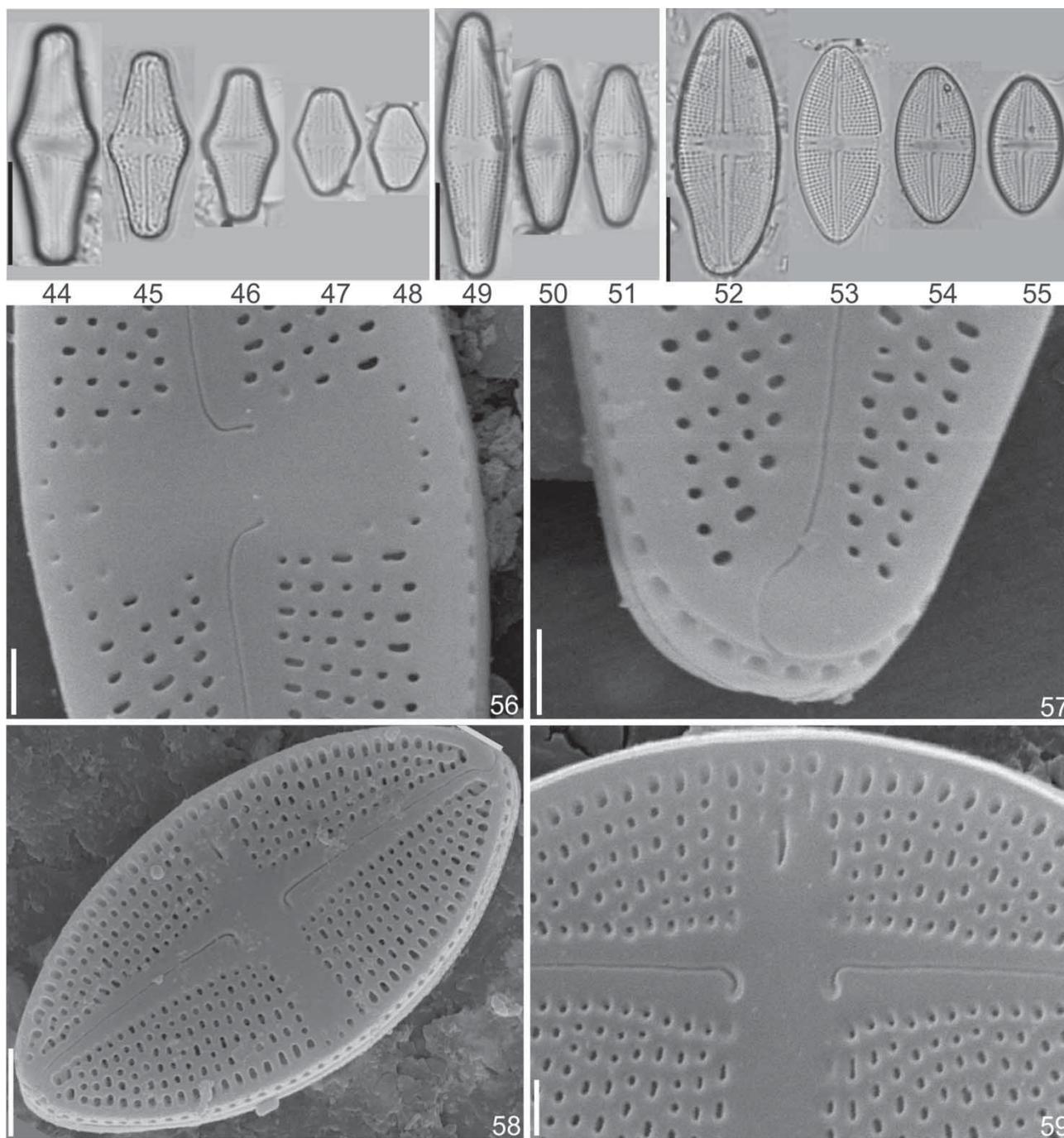
Material examined: UPCB 72982.

Remarks: Few valves of *L. intermedia* were found in the sample ($n = 5$). The species occurred only in the epiphyton of the Cachoeira river that has neutral waters (pH 6.98) and low conductivity (39.4 µS cm⁻¹).

***Luticola isabelae* Metzeltin et Levkov in Levkov *et al.* (2013: 140, pl. 106, fig. 6, pl. 108, figs 1–21, pl. 109, figs 1–20)**

(Figs 52–55, 58–59)

Description: Valves elliptic, 16.5–31.1 µm long and 8.4–12.3 µm wide, with broadly rounded apices. Raphe sternum narrowly lanceolate. Central area linear, delimited by three areolae. Stigma in central area, linear, close to valve margin. Marginal channel not evident in LM. Raphe straight with external proximal ends deflected to the side opposite the stigma; distal raphe ends hooked towards the stigma and extending towards valve mantle. Striae radiate, 19–23 in 10 µm, composed of rounded to elliptic areolae, 16–21



Figs. 44–48. *Luticola hustedtii*, LM. Figs 49–51, 56–57. *Luticola intermedia*. Figs 49–51. Valves in LM. Fig. 56. Median region of valve showing the stigma and proximal raphe endings, SEM. Fig. 57. Apex of valve showing the distal raphe ending extending onto the mantle, SEM. Figs 52–55, 58–59. *Luticola isabelae*. Figs 52–55. Valves in LM. Fig. 58. External valve view, SEM. Fig. 59. External view showing detail of stigma and proximal raphe endings, SEM. Scale bars = 10 μm (Figs 44–55), 2 μm (Fig. 58), 1 μm (Figs 56, 57, 59).

in 10 μm . Valve mantle ornamented with a row of rounded areolae.

Material examined: UPCB 47493, UPCB 47494, UPCB 47495, UPCB 47496, UPCB 47497, UPCB 47498, UPCB 47499, UPCB 47500, UPCB 47501, UPCB 47502, UPCB

47509, UPCB 47510, UPCB 47511, UPCB 47511, UPCB 47512, UPCB 47513, UPCB 47514, UPCB 47515, UPCB 47516, UPCB 47517, UPCB 47518, UPCB 47519, UPCB 47520, UPCB 47521, UPCB 47523, UPCB 47524, UPCB 47525, UPCB 47526.

Remarks: *Luticola isabelae* was recently recorded from Brazil by Levkov *et al.* (2013). The species was very common in several samples obtained from the Guaraguaçu river and was previously recorded for this locality as *L. saxophila* (Tremarin *et al.* 2009). The Guaraguaçu river is influenced by the tidal regime since part of its course is in a coastal plain, thus, salinity at the sampling points varied from 0 to 23 psu (Tremarin *et al.* 2008). The Guaraguaçu river has humic waters and low flow rates.

***Luticola lancettula* Levkov *et al.* (2013: 151, pl. 73, figs 1–30, pl. 75, figs 6–8)**

(Figs 60–67)

Description: Valves lanceolate to rhombic-lanceolate, 17.4–30.1 µm long and 6.3–8.1 µm wide, with rounded apices. Raphe sternum linear. Central area straight to slightly expanded towards the valve margin, bounded by 3–4 areolae. Stigma in central area, linear, located close to proximal raphe ends. Marginal channel evident in LM. Raphe straight with external proximal ends deflected away from the stigma; distal raphe ends hooked towards the stigma and extending towards valve mantle. Striae radiate, 20–24 in 10 µm, composed of rounded to elliptic areolae, 18–22 in 10 µm. Valve mantle with two rows of areolae.

Material examined: UPCB 73001, UPCB 72965, UPCB 47499, UPCB 47519, UPCB 47520, UPCB 47514, UPCB 47515, UPCB 47500, UPCB 47506, UPCB 47509, UPCB 47510, UPCB 47511, UPCB 47501, UPCB 475251, UPCB 47493, UPCB 47494, UPCB 47523, UPCB 47514, UPCB 47515, UPCB 47524, UPCB 47516, UPCB 47517, UPCB 47518.

Remarks: *Luticola lancettula* is a common taxon in the Brazilian flora, mistakenly identified as *L. goeppertiana* in some studies (see Tremarin *et al.* 2009). The species was recently described and recorded from several localities in the country (Levkov *et al.* 2013). *Luticola amazonica* Wetzel, Ector & Levkov is similar to *L. lancettula*, but has more linear, narrower valves (width: 5.5–7.5 µm), and higher stria density (25–27 in 10 µm) (Levkov *et al.* 2013).

Our specimens are very similar to the type material, except in having two rows of areolae on the mantle. The species was found in slightly acidic waters (pH 6.1–7.2) of the das Pombas and Cambará rivers, but was more commonly found in the Guaraguaçu river.

***Luticola moreirae* Straube, Tremarin *et T. Ludwig* sp. nov.**

(Figs 68–77)

Description: Valves rhombic-elliptic to elliptic, slightly expanded in valve middle, 8.3–20.5 µm long and 5.2–6.3 µm wide, with broadly rounded apices. Raphe sternum linear. Central area bow-tie-shaped, expanded towards valve margin, delimited by 3–4 areolae. Stigma in central area, slightly elongated, located close to valve margin. Marginal channel not evident in LM. Raphe straight with external proximal ends deflected away from the stigma and internally straight; distal raphe ends slightly hooked towards the stigma, terminating on valve face, not extending onto mantle, and internally ending in a small helictoglossa. Striae radiate, 22–26 in 10 µm, composed of rounded to elliptic areolae, 18–24 in 10 µm. Valve mantle with single row of elongated areolae. Valvocopula perforated by two rows of rounded pores.

Type: – BRAZIL. Paraná: Antonina, Cachoeira river, 25°19'9.9"S, 48°42'26.8"W, December/2011, UPCB 72982 – diatom collection of the Botany Department, Universidade Federal do Paraná; holotype slide UPCB 72982, holotype designated here in Fig. 69.

Isotype: BM 101848 (Natural History Museum, London).

Etymology: The name “moreirae” is given in honour of Dr. Hermes Moreira-Filho, Universidade Federal do Paraná.

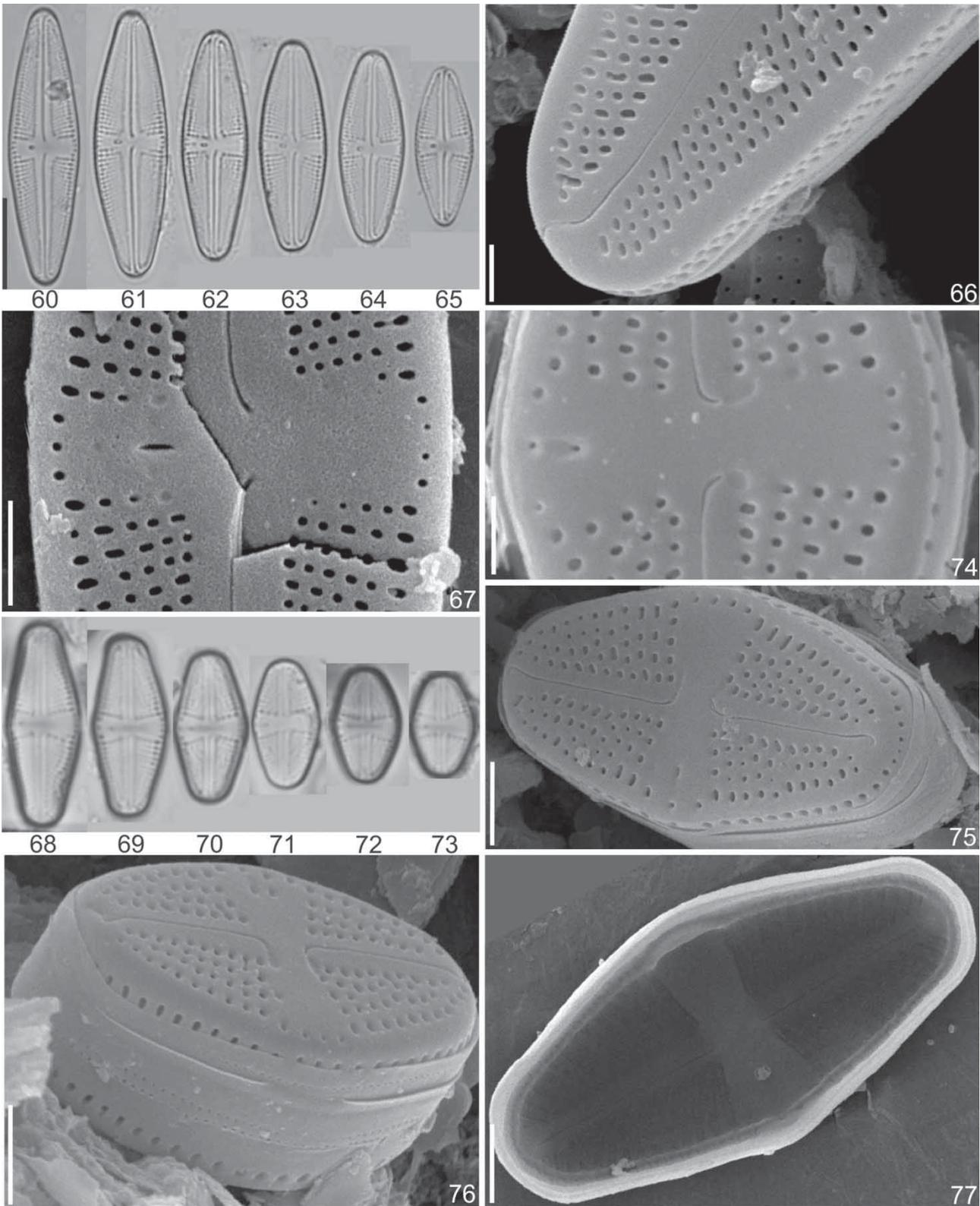
Distribution: This species was also found in the Guaraguaçu river and Cacatu river, in addition to the type locality.

Material examined: UPCB 47513, 72982, 76000.

Remarks: *Luticola moreirae* resembles *L. fuhrmannii* Metzeltin *et* Levkov, *L. beyensii*, *L. acidoclinata* Lange-Bertalot and *L. intermedia* (Hustedt) Levkov, Metzeltin *et* Pavlov in valve outline and shape of the central area, however these other four species have distal raphe ends that extending onto the mantle, proximal raphe ends that are clearly deflected away from the stigma, and a rounded stigma. Moreover, *L. fuhrmannii* has larger valves (length 18–34 µm, width 7.5–8.5 µm), *L. beyensii* has bluntly rounded apices and *L. intermedia* has 4–5 areolae surrounding the central area (Van de Vijver *et al.* 2002, Levkov *et al.* 2013).

Luticola pseudoimbricata Levkov, Metzeltin & Pavlov also has a slit-like stigma and short distal raphe ends, not extending onto the valve mantle, but differs from *L. moreirae* by its more lanceolate valve outline, shorter proximal raphe endings that are slightly expanded into central pores, and a smaller number of areolae surrounding the central area (2–3 vs. 3–4) (Levkov *et al.* 2013).

Luticola moreirae occurred in slightly acidic to neutral waters (pH 6.3–6.9) with low conductivity (11.3–39.4 µS cm⁻¹). The species was more common in the epiphyton of the Cachoeira river along with *L. papilioformis*.



Figs. 60–67. *Luticola lancettula*. Figs 60–65. Valves in LM. Fig. 66. Apex of valve showing the distal raphe ending and mantle, SEM. Fig. 67. Detail of central area with linear stigma and proximal raphe endings, SEM. **Figs 68–77.** *Luticola moreirae* sp. nov. Figs 68–73. Valves in LM. Fig. 69. Holotype. Fig. 74. Detail of central area with submarginal stigma and proximal raphe endings, SEM. Figs 75–76. Apex of frustule showing the raphe endings, valve mantle and girdle bands, SEM. Fig. 77. Internal valve view showing the staura and stigma. Scale bars = 10 μ m (Figs 60–65, 68–73), 2 μ m (Figs 67, 75–77), 1 μ m (Figs 66, 74).

***Luticola papilioformis* Straube, Tremarin et T. Ludwig
sp. nov.**

(Figs 78–88)

Description: Valves broadly lanceolate, 9.5–18.2 µm long and 5.8–7.1 µm wide, with capitate to broadly rounded ends. Raphe sternum linear. Central area broad, bow-tie-shaped, expanded towards the valve margin, delimited by 3–4 areolae. Stigma in central area, rounded, close to valve margin. Marginal channel not evident in LM. Raphe straight with external proximal ends deflected away from stigma and internally straight; distal raphe ends slightly hooked towards the stigma, terminating on valve face, not extending onto valve mantle, and internally ending in small helictoglossa. Striae radiate, 22–24 in 10 µm, composed of irregular to rounded areolae, 16 in 10 µm. Valve mantle ornamented with single row of elongated areolae. Valvocopula perforated by two rows of rounded pores.

Type: BRAZIL. Paraná: Antonina, Cachoeira river, 25°19'9.9"S, 48°42'26.8"W, December/2011, UPCB 72982 – diatom collection of the Botany Department, Universidade Federal do Paraná; holotype slide UPCB 72982, holotype designated here in Fig. 79.

Isotype: BM 101848 (Natural History Museum, London).

Etymology: The name “papilioformis” refers to the central region in the shape of butterfly wings.

Distribution: This species was also found in the Guaraguaçu river, in addition to the type locality.

Material examined: UPCB 72981, 72982, 47515.

Remarks: A specimen identical to *L. papilioformis* was found by Metzeltin *et al.* (2005) from Laguna Rocha in Uruguay, and recorded as “*Luticola* (? nov.) spec.” *Luticola papilioformis* is characterized mainly by its valve outline, apices and central area. *Luticola gaussiiformis* Levkov, Metzeltin et Pavlov and *L. muticopsis* (Van Heurck) Mann resemble *L. papilioformis*, but the former has larger, elliptic-lanceolate valves (16–22 µm long, 7.5–8.5 µm wide), narrower apices and wedge-shaped central area (Levkov *et al.* 2013). *Luticola muticopsis* has linear-elliptical valves with a lower stria density (15–19 in 10 µm) and rectangular to bow tie-shaped central area (Kohler *et al.* 2015).

Other similar taxa include *L. murrayi* (West & G.S. West) D.G. Mann and *L. bilyi* Levkov, Metzeltin & Pavlov. However, the valves of *L. murrayi* are larger (length 28.1–40.4 µm, width 6.8–10.2 µm) and narrowly lanceolate with rounded apices, have short proximal and distal raphe ends weakly deflected away from the stigma, and a lower stria density (12–17 in 10 µm) (Hustedt 1966, Kohler *et al.* 2015). *Luticola bilyi* can be differentiated from *L. moreirae* by the linear valves, shape of the central area (rectangular

to wedge-shaped) and stria density (18–20 in 10 µm). In addition, the stigma in *L. bilyi* is located near the valve centre, associated with a long median stria (Levkov *et al.* 2013).

In the type material, *L. papilioformis* co-occurred with *Melosira varians* Agardh, *Aulacoseira pusilla* (Meister) Tuji et Houki, *L. goeppertiana*, *L. moreirae* and *Gomphonema parvulum* (Kützing) Kützing.

***Luticola permuticoides* Metzeltin and Lange-Bertalot
(2007: 158, pl. 146, figs 10–19)**

(Figs 89–93)

Description: Valves elliptic to linear-elliptic, 13.8–19.7 µm long and 6.4–7.3 µm wide, with narrowly rounded apices. Raphe sternum linear. Central area linear delimited by 2–3 areolae. Stigma in central area, linear, located quite near valve margin. Marginal channel not evident in LM. Raphe straight with external proximal ends dilated in pores and strongly deflected away from the stigma; distal external raphe ends hooked towards the stigma, extending onto valve mantle. Striae radiate, 24–26 in 10 µm, composed of rounded areolae, 24 in 10 µm. Valve mantle with single row of elliptic areolae.

Material examined: UPCB 47493, UPCB 72975, UPCB 73005.

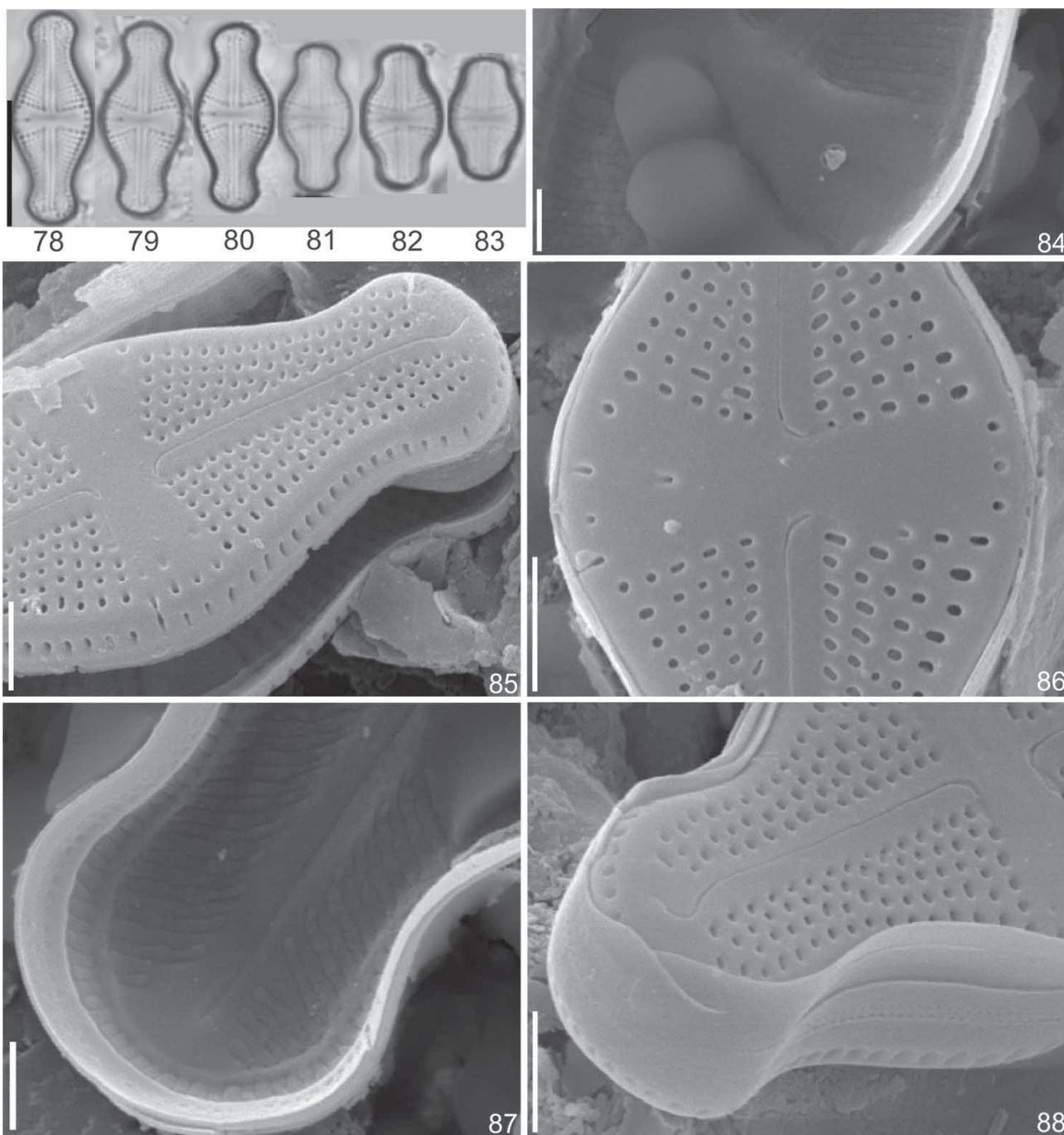
Remarks: *Luticola muticoides* (Hustedt) D.G. Mann and *L. pseudokotschyi* (Lange-Bertalot) Lange-Bertalot are similar to *L. permuticoides* in valve outline and shape of the stigma. However, *L. muticoides* differs in having a lanceolate axial area and submarginal stigma; and *L. pseudokotschyi* in having subrostrate apices, wedge-shaped central area, stigma associated with striae, and lower stria density (Krammer & Lange-Bertalot 1986, Metzeltin & Lange-Bertalot 2007, Levkov *et al.* 2013).

Luticola permuticoides was found in the epiphyton of slightly acidic waters (pH 6.1–6.6).

***Luticola rionegrensis* Wetzel, Ector et Levkov in
Levkov *et al.* (2013: 209, pl. 29, figs 1–29, pl. 31, figs–7)**

(Figs 94–100)

Description: Valves lanceolate to elliptic-lanceolate, 21.3–47.4 µm long and 7.1–11.9 µm wide, with rounded apices. Raphe sternum linear. Central area transversely expanded towards valve margins, interrupted by ‘ghost areolae’ and delimited by 1–4 rounded areolae. Stigma in central area, linear, located close to proximal raphe ends. Marginal channel not evident in LM. Raphe straight with external proximal ends deflected away from stigma; distal external raphe ends hooked onto valve mantle. Striae radiate, 12–14 in 10 µm, composed of irregular to rounded areolae,



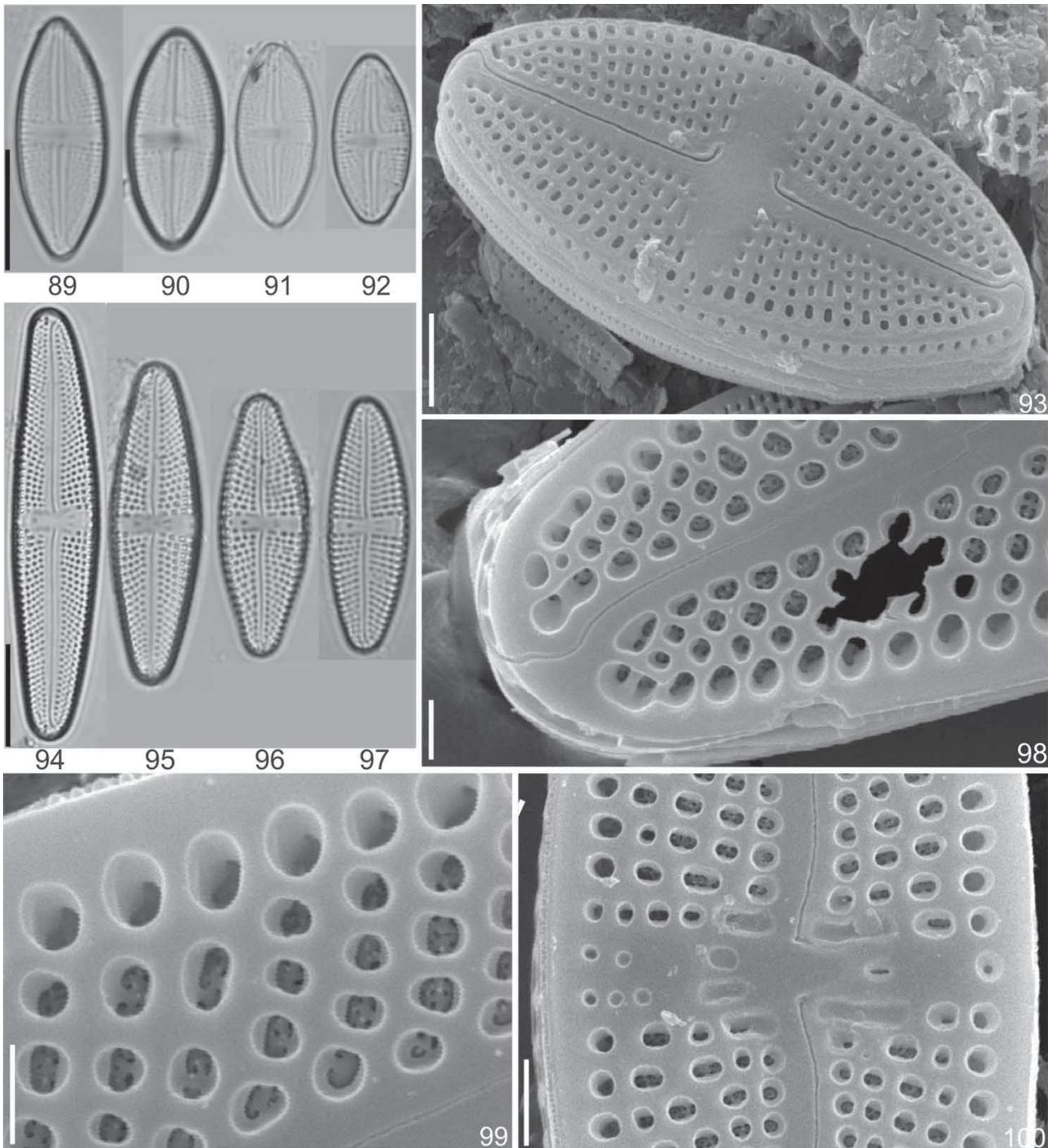
Figs. 78–88. *Luticola papilioformis* sp. nov. Figs 78–83. Valves in LM. Fig. 79. Holotype. Fig. 84. Detail of central area with stigma, SEM. Fig. 85. External valve view showing the raphe endings, stigma and mantle, SEM. Fig. 86. External valve view showing central area with stigma and proximal raphe endings, SEM. Fig. 87. Internal view showing distal raphe ending, SEM. Fig. 88. Apex of frustule showing the distal raphe ending and girdle bands. Scale bars = 10 μm (Figs 78–83), 2 μm (Figs 85, 86, 88), 1 μm (Figs 84, 87).

10–16 in 10 μm , coarser near the valve margin and internally occluded by hymenes. Valve mantle with single row of elongated areolae.

Material examined: UPCB 72985, UPCB 72978, UPCB 47493, UPCB 47494, UPCB 47495, UPCB 47499, UPCB 47500, UPCB 47503, UPCB 47506, UPCB 47509, UPCB

47510, UPCB 47511, UPCB 47512, UPCB 47513, UPCB 47523, UPCB 47516, UPCB 47518, UPCB 47525, UPCB 47520.

Remarks: All analysed individuals of *L. rionegrensis* were characterized by the presence of depressions ('ghost areolae') in the central part of the valve. Specimens with a



Figs. 89–93. *Luticola permuticoides*. Figs 89–92. Valves in LM. Fig. 93. External valve view, SEM. Figs 94–100. *Luticola rionegrensis*. Figs 94–97. Valves in LM. Fig. 98. External view showing distal raphe ending, SEM. Fig. 99. External view of areolae, SEM. Fig. 100. External valve view showing the stigma, ghost areolae and proximal raphe endings, SEM. Scale bars = 10 μm (Figs 89–92, 94–97), 2 μm (Figs 93, 99, 100), 1 μm (Fig. 98).

similar valve outline to *L. rionegrensis* were described as *L. falknerorum* Metzeltin et Lange-Bertalot from Colombia, but the latter has its stigma close to the valve margin, strongly curved proximal raphe ends and higher stria density (18–23 in 10 μm) (Metzeltin & Lange-Bertalot 2007).

Luticola rionegrensis is a tropical species described from the Brazilian Amazon (Levkov *et al.* 2013) and previously recorded from Brazil and Guyana as *Luticola dismutica* (Hustedt) D.G. Mann by Metzeltin & Lange-Bertalot (1998). However, *L. dismutica* is characterized

by having undulate valves with produced apices and delicate striae (16–20 in 10 µm) (Hustedt 1966). This is the first recorded of *L. rionegrensis* in subtropical region. The species was rare in the samples, occurring in the plankton and epiphyton of slightly acidic environments (pH 6.1–6.25).

***Luticola saprophila* Levkov et al. (2013: 213, pl. 58, figs 20–36, pl. 59, figs 1–7, pl. 77, figs 23–26)**

(Figs 101–105, 113)

Description: Valves rhombic-lanceolate to elliptic, 20.1–33.9 µm long and 7.6–9.5 µm wide, with subrostrate to rounded apices. Raphe sternum linear. Central area bow-tie-shaped, delimited by 3–4 areolae. Stigma in central area, linear, close to proximal raphes ends. Marginal channel not evident in LM. Raphe straight with external proximal ends deflected away from the stigma, distal raphe ends externally hooked towards the stigma, extending onto valve mantle. Striae radiate, 21–23 in 10 µm, composed of rounded to elliptic areolae, 16–19 in 10 µm. Valve mantle with single row of elliptic areolae.

Material examined: UPCB 72982.

Remarks: *Luticola saprophila* was recorded from Macedonia and Netherlands (Guiry & Guiry 2017). This is the first record of the taxon for Brazil, from neutral waters of the Cachoeira river.

***Luticola saxophila* (Bock) D.G. Mann in Round et al. (1990: 671)**

(Figs 107–111)

Description: Valves elliptic to elliptic-lanceolate, 9.5–22.1 µm long and 5.8–9.7 µm wide, with broadly rounded apices. Raphe sternum linear to slightly lanceolate. Central area rectangular, transversely expanded, delimited by 3–4 areolae. Stigma in central area, linear, submarginal. Marginal channel slightly evident in LM. Raphe straight with proximal ends deflected away from stigma. Striae radiate, 22–24 in 10 µm, composed of rounded areolae, 16–20 in 10 µm.

Material examined: UPCB 47493, UPCB 47494, UPCB 47495, UPCB 47499, UPCB 47500, UPCB 47503, UPCB 47506, UPCB 47509, UPCB 47510, UPCB 47511, UPCB 47512, UPCB 47513, UPCB 47516, UPCB 47518, UPCB 47520, UPCB 47523, UPCB 47525, UPCB 72994, UPCB 76001.

Remarks: *Luticola muticoides* Hustedt resembles *L. saxophila* in overall valve morphology, but differs by having a marginal stigma and 26–30 striae in 10 µm (Hustedt 1966, Levkov et al. 2013). *Luticola saxophila* was very common in the Guaraguaçu river and occurred in slightly acidic to neutral waters (pH 6.6–6.98).

***Luticola tropica* Levkov et al. (2013: 7: 241, pl. 196, figs. 1–35)**

(Figs 106, 114, 115)

Description: Valves elliptic-lanceolate with strongly undulate margins, 8.8–19.8 µm long and 6.3–10.3 µm wide, with rostrate apices. Raphe sternum linear. Central area transversely expanded, delimited by 2–3 areolae. Stigma rounded or weakly elongated in central area, located close to valve margin. Marginal channel not evident in LM. Raphe straight with external proximal ends deflected away from the stigma; distal raphe ends hooked to the same side, extending onto valve mantle. Striae radiate, 16–18 in 10 µm, composed of rounded to elongated areolae, 12–14 in 10 µm. Valve mantle ornamented with single row of rounded areolae. Girdle bands perforated by two rows of small poroids.

Material examined: UPCB 47502, UPCB 47506, UPCB 47517, UPCB 47518, UPCB 47519, UPCB 47503, UPCB 47521, UPCB 47526.

Remarks: *Luticola tropica* is commonly found in brackish waters of tropical environments (Levkov et al. 2013). In this study, the species occurred only in the Guaraguaçu river, a subtropical environment influenced by the tidal cycle.

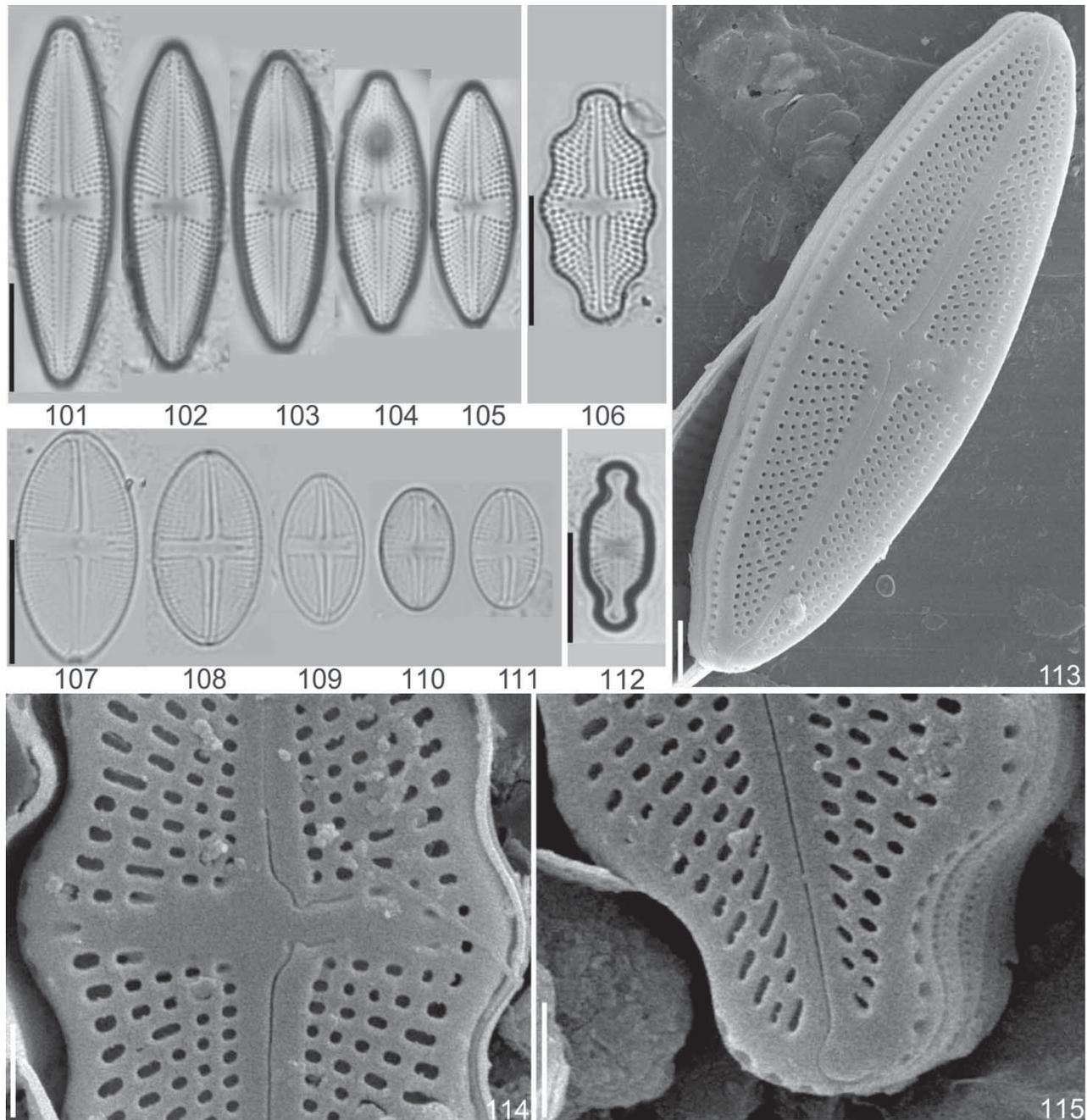
***Luticola uruguayensis* Metzeltin et al. (2005: 111, figs. 83, 84, 232)**

(Figs 116–117, 119–121)

Description: Valves lanceolate, slightly undulate, 62.7–79.0 µm long and 16.7–23.7 µm wide, with a rostrate to subrostrate apices. Raphe sternum linear and wide. Central area linear delimited by 3–4 striae. Stigma submarginal in central area, externally linear and internally covered by “C”-shaped structure. Marginal channel evident in LM. Raphe straight with external proximal ends dilated in pores, deflected away from the stigma and internally straight; distal external raphe ends hooked towards the stigma, extending onto valve mantle, and internally ending in small helictoglossa. Striae radiate, 12 in 10 µm, composed of rounded to elliptic areolae, 14–16 in 10 µm, with fimbriate edges. Areolae next to valve margin transversely elongated. Valve mantle with single row of elongated areolae.

Material examined: UPCB 72982.

Remarks: *Luticola uruguayensis* resembles *L. dapalis* and *L. frenguelli* Metzeltin et Lange-Bertalot in valve shape and apices, but is smaller than *L. dapalis* and larger than *L. frenguelli* (Metzeltin & Lange-Bertalot 1998). According to Metzeltin et al. (2005), *L. uruguayensis* has one stigma and 1–5 “stigmoids”, which cannot be observed due



Figs. 101–105, 113. *Luticola saprophila*. Figs 101–105. Valves in LM. Fig. 113. External view of a tilted valve depicting also the valve mantle, SEM. Fig. 106, 114, 115. *Luticola tropica*. Fig. 106. Valve in LM. Fig. 114. Central area with stigma and proximal raphe endings, SEM. Fig. 115. Apex of frustule showing the distal raphe ending, mantle and girdle bands, SEM. Figs 107–111. *Luticola saxophila*, LM. Fig. 112. *Luticola ventricosa*, LM. Scale bars = 10 μm (Figs 101–112), 2 μm (Figs 113–115).

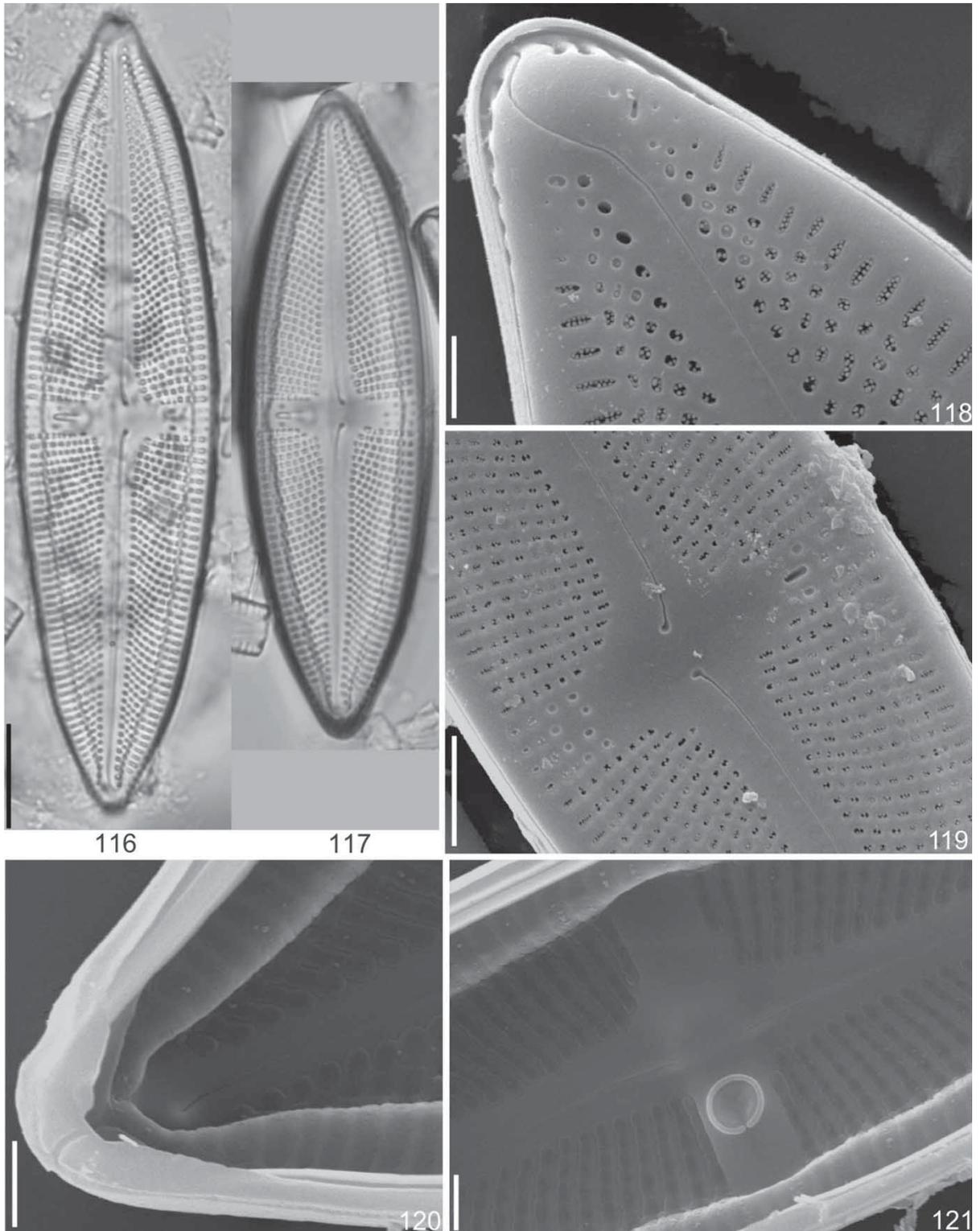
to the internal overlap of the longitudinal channel. However, no internal perforations were observed in the central area beyond the stigma (see Fig. 121). Thus, we believe that ‘stigmoids’ correspond to occluded areolae (‘ghost areolae’).

Few valves of *L. uruguayensis* were found in the sample of the Cachoeira river. This species is commonly found in tropical and subtropical regions of South America.

***Luticola ventricosa* (Kützing) D.G. Mann in Round et al. (1990: 671)**

(Fig. 112)

Description: Valves linear-lanceolate, 15 μm long and 6.4 μm wide, with capitate apices, 3.6 μm in width. Raphe sternum linear and narrow. Central area bow-tie-shaped, delimited by 3–4 areolae. Stigma in central area, rounded,



Figs. 116–121. *Luticola uruguayensis*. Figs 116, 117. Valves in LM. Fig. 118. Distal raphe ending extending to the mantle, SEM. Fig. 119. Median valve region showing the linear stigma and proximal raphe endings, SEM. Fig. 120. Internal view showing the distal raphe ending and the longitudinal channel, SEM. Fig. 121. Internal valve view showing the stigma, SEM. Scale bars = 10 μ m (Figs 116–117), 5 μ m (Fig. 119), 2 μ m (Figs 118, 120, 121).

located close to proximal raphe ends. Marginal channel not evident in LM. Raphe straight with external proximal ends slightly deflected to away from the stigma. Striae radiate, 18 in 10 μm , composed of rounded areolae, 20 in 10 μm .

Material examined: UPCB 47524.

Remarks: *Luticola muticopsis* (Van Heurck) D.G. Mann is most similar to *L. ventricosa*. However, *L. muticopsis* has larger valves (width: 7.0–9.0 μm), with broadly capitate apices and lower stria density (15–18 in 10 μm) (Levkov *et al.* 2013). *Luticola dolia* Spaulding et Esposito, recently described from the Antarctic region, is also similar to *L. ventricosa*, distinguished by its lanceolate raphe sternum, central area bordered by 2–3 short striae, and lower stria density (14–18 in 10 μm) (Esposito *et al.* 2008, Levkov *et al.* 2013).

Luticola ventricosa is an aerophilic diatom with worldwide distribution. Only one valve was found in the Guaraguaçu river sample, and this was very similar to the specimens recorded by Levkov *et al.* (2013).

General remarks

Luticola species were found in rivers at Serra do Mar, but we have not detected them in 4 (da Onça, Sertãozinho, Colônia Pereira and Iporanga) of the 15 analysed rivers. The Guaraguaçu and Cachoeira rivers had the highest richness for this genus, nine taxa each. In general, *Luticola* species occur in mildly acidic to neutral waters with low conductivity, absent from the more alkaline environments (Onça and Iporanga rivers). Generally, fast-flowing rivers with clean waters seem to facilitate the development of these species.

We believe that these *Luticola* species may have wider geographical distributions, since some taxa recorded by us have already been found in Brazilian samples, but were identified under other names or the records were in unpublished studies. We therefore emphasize the importance of taxonomic revisions, particularly accompanied by analysis of type material to clarify the diagnostic features of the species. In addition, it is important to disseminate the results of taxonomic surveys to improve knowledge of local diatom diversity.

Acknowledgements

We thank the Centro de Microscopia Eletrônica (CME) of Universidade Federal do Paraná for technical assistance. We thank the editor and reviewers for their careful reading of, and comments on, the paper.

Disclosure statement

No potential conflict of interest was reported by the authors.

Funding

We would like to thank the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) for the postdoctoral scholarship grant to Dr P. Tremarin, the Conselho Nacional de

Desenvolvimento Científico e Tecnológico (CNPq) for the scientific productivity grant to Dr T. Ludwig (308332/2013-0) and for the master's scholarship grant to A. Straube.

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