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Research article

The genus *Luticola* (Bacillariophyta) on Ile Amsterdam and Ile Saint-Paul (Southern Indian Ocean) with the description of two new species

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Abstract. Five species of the terrestrial diatom genus *Luticola* D.G.Mann were found during a taxonomic survey of two small volcanic islands, Ile Amsterdam and Ile Saint-Paul (Southern Indian Ocean). Apart from the two already known *Luticola* species *L. beyensii* Van de Vijver *et al.* and *L. subcrozetensis* Van de Vijver *et al.*, two new species are described: *L. ivetana* Chattová & Van de Vijver sp. nov. and *L. vancampiana* Chattová & Van de Vijver sp. nov. Finally, one, up to now unknown, *Luticola* species is briefly discussed and illustrated. Detailed morphological descriptions of these taxa are provided based on both light and scanning electron microscopy observations. Morphological features of the new species are compared to morphologically similar taxa, and notes on their ecology and biogeography are added.

Keywords. Bacillariophyta, diatoms, *Luticola*, new species, morphology.

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Introduction

The genus *Luticola* D.G.Mann is one of the dominant genera in the Antarctic terrestrial diatom flora. *Luticola* taxa can be distinguished in having uniseriate striae, composed of rounded to transapically elongated areolae covered internally by perforated hymenes, a usually distinct isolated pore in the central area, a longitudinal canal positioned within the valve wall and by a simple, filiform raphe with variable raphe endings (Round *et al.* 1990; Levkov *et al.* 2013). However, the correct taxonomy and biogeography of this genus in the sub-Antarctic region was hampered due to species drift and force fitting the Antarctic species into European and North American names (Tyler 1996). Due to the lack of appropriate literature, the first studies mainly reported typical cosmopolitan taxa such as *L. cohnii* (Hilse) D.G.Mann (Round *et al.* 1990) or *L. nivalis* (Ehrenb.) D.G.Mann (Round *et al.* 1990) and taxa described in the early 20th century such as *L. gaussii* (Heiden) D.G.Mann (Round *et al.* 1990) and *L. suecorum* (G.W.F.Carlson) Van de Vijver (Van de Vijver & Mataloni 2008). Moreover, *L. muticopsis* (Van Heurck) D.G.Mann (Round *et al.* 1990) was used as a catch-all taxon for all capitate *Luticola* specimens, while the non-capitate forms were usually force-fitted into *L. mutica* (Kütz.) D.G.Mann (Round *et al.* 1990). This resulted in stretched biogeographical distributions of those species, making them the most widespread in the entire Antarctic Region.

Recently, all sub-Antarctic *Luticola* species have been the subject of a thorough taxonomic and morphologic revision, in order to unravel the correct diversity of this genus. This resulted in the description of more than 25 new Antarctic *Luticola* taxa, mainly from the Maritime Antarctic Region and the Antarctic Continent (Van de Vijver *et al.* 2006, 2011; Kopalová *et al.* 2011; Levkov *et al.* 2013; Zidarova *et al.* 2014; Kohler *et al.* 2015). Several new taxa were also found in the sub-Antarctic region. In 2002, *L. beyensii* Van de Vijver *et al.* (Van de Vijver *et al.* 2002b) was described from Ile Saint-Paul, whereas *L. ledeganckii* Van de Vijver (Van de Vijver *et al.* 2002a), *L. robusta* Van de Vijver *et al.* (Van de Vijver *et al.* 2002a), *L. crozetensis* Van de Vijver *et al.* (Levkov *et al.* 2013), *L. ipevii* Van de Vijver & Levkov (Levkov *et al.* 2013), and *L. subcrozetensis* Van de Vijver *et al.* (Levkov *et al.* 2013), were described from Ile de la Possession, the main island of the Crozet Archipelago.

The present paper continues this revision of the genus *Luticola* with an analysis of five taxa observed on Ile Amsterdam and Ile Saint-Paul, two islands in the southern Indian Ocean. Two *Luticola* taxa are described as new based on detailed light and scanning electron microscopy whereas a fifth unidentified taxon could only be found in light micrograph and is illustrated and discussed but due to the lack of sufficient observations, it is still unclear whether it also represents a new species.

Material and methods

During two short visits (1998 and 1999) and two fieldwork seasons on the volcanic islands Ile Amsterdam (77°30′ E, 37°50′ S) and Ile Saint-Paul (77°31′ E, 38°43′ S) in 2007 and 2016, more than 300 samples were collected from various habitats including waterbodies, soils and moss vegetations. Both islands are among the most remote islands in the world, situated in the southern Indian Ocean, north of the sub-Antarctic islands, halfway between South Africa and Australia, and form a separate district within the Terres Australes et Antarctiques Françaises (TAAF). In geological terms, these islands are very young, with the main part of Ile Amsterdam formed during the period 400–200 kyr BP and Ile Saint-Paul being even younger (< 50 kyr). More information regarding climate, vegetation and geology can be found in Lebouvier & Frenot (2007).

Sampling sites were chosen in order to represent a maximum diversity of habitat types. The samples were collected in PVC bottles and fixed with 3% formalin. In order to determine the moisture content of the sample, the F-value, referring to the F-classification of Jung (1936) was selected as representative for moisture and used for each sample. It is a humidity scale based on water content as follow: FI =

submerged mosses, FII = free floating mosses, FIII = very wet (water drips from the samples without pressure), FIV = wet (water drips with a slight pressure), FV = quasi-wet (water drips after moderate pressure), FVI = moist (little water produced after high pressure), FVII = quasi-dry (only a few drops of water can be squeezed out), FVIII = dry (contains no water).

Samples were prepared for microscopy analysis following the method described in van der Werff (1955): small parts of the samples were cleaned by adding 37% H_2O_2 and heating to 80°C for about 1 h. The reaction was completed by addition of an excessive amount of $KMnO_4$. Following digestion and centrifugation (three times 10 min at 3700×g), cleaned material was diluted with distilled water to avoid excessive concentrations of diatom valves on the slides. Cleaned diatom valves were mounted in Naphrax®. Light microscopy (LM) observations were done at Olympus BX53 microscopes, equipped with Differential Interference Contrast (Nomarski) optics. LM micrographs were taken using Olympus UC30 camera connected to the Cell Sense Standard program. Samples and slides are stored at the BR-collection (Botanic Garden Meise, Belgium). For scanning electron microscopy (SEM), parts of the oxidized suspensions were filtered through a 1 µm Isopore™ polycarbonate membrane filter (Merck Millipore). The stubs were sputter-coated with a platinum layer of 2 nm and studied in a JEOL JSM-7100F SEM microscope at 1 kV (Botanic Garden Meise, Belgium).

Morphological terminology follows Round *et al.* (1990), Van de Vijver & Mataloni (2008) and Levkov *et al.* (2013). The morphology of the new species is discussed based on detailed light and scanning electron microscopy observations and has been compared with known *Luticola* species using the most current literature: Rumrich *et al.* (2000), Van de Vijver & Mataloni (2008), Kopalová *et al.* (2011), Van de Vijver *et al.* (2011), Levkov *et al.* (2013), Zidarova *et al.* (2014) and Kohler *et al.* (2015).

Results

Five *Luticola* taxa were found in the samples during the survey. Two taxa, *L. beyensii* and *L. subcrozetensis*, could be identified using the currently available literature. Based on a morphological analysis, two taxa are described as new species: *L. ivetana* Chattová & Van de Vijver sp. nov. and *L. vancampiana* Chattová & Van de Vijver sp. nov. Observation of the material in LM revealed the presence of a fifth unknown *Luticola* taxon with a highly asymmetrical central area. As the taxon could not be found during SEM analysis, we have insufficient data regarding its morphological ultrastructure and therefore the decision was taken not to describe it as new to science.

Class Bacillariophyceae Haeckel emend. Medlin & Kaczmarska (Medlin & Kaczmarska 2004)
Subclass Bacillariophycidae D.G.Mann (Round *et al.* 1990)
Order Naviculales Bessey (Bessey 1907)
Family Diadesmidaceae D.G.Mann (Round *et al.* 1990)
Genus *Luticola* D.G.Mann (Round *et al.* 1990)

Luticola beyensii Van de Vijver, Ledeganck & Lebouvier
Figs 1–12

Diatom Research 17: 235–241 (Van de Vijver *et al.* 2002b).

Type

ILE SAINT PAUL: TAAF, sub-Antarctica, 16 Dec. 1999, *B. Van de Vijver* sample *A9* (holo-: CAS 220051, California Academy of Science; iso-: slide no. BR–4045, University of Antwerp, Belgium).

Description

Light microscopy (Figs 1–10)

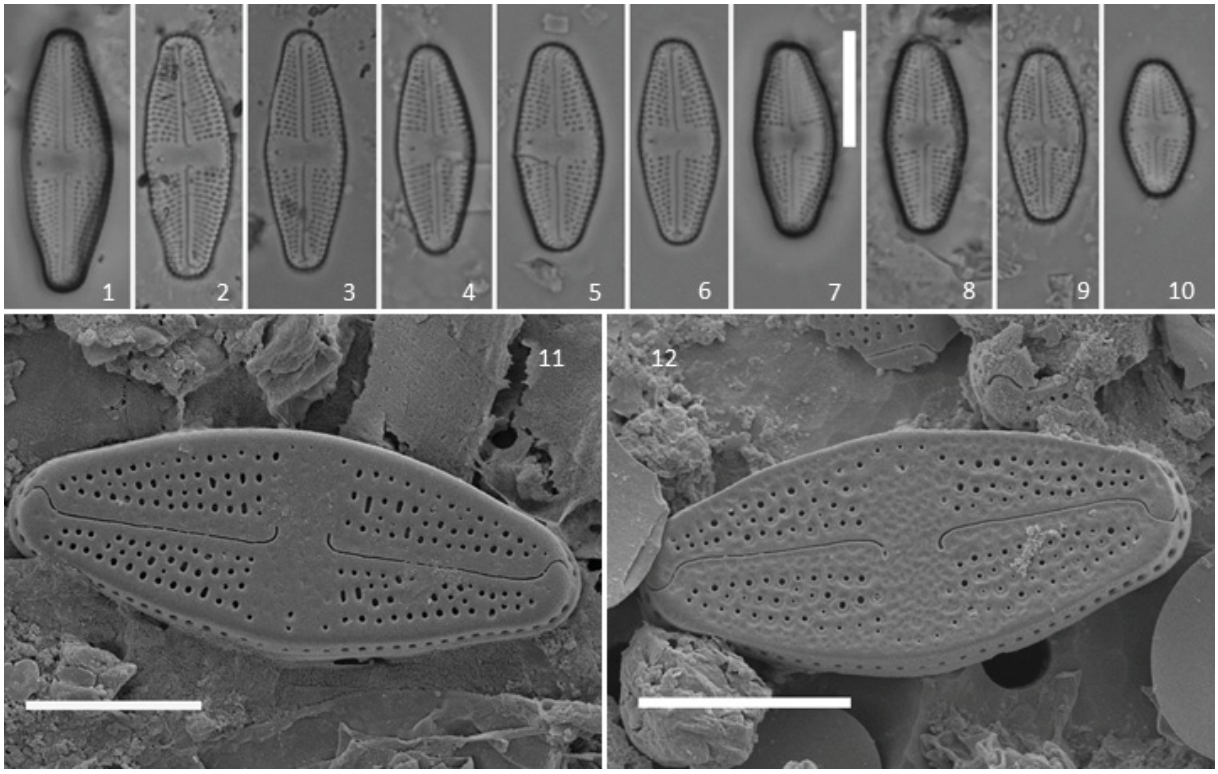
Valves rhombic-lanceolate with clearly convex margins. Larger individuals with more or less rostrate apices, in smaller specimens apices more broadly rounded. Valve dimensions (n = 25): length 14.5–22.0 µm, width 6.0–8.5 µm. Axial area relatively narrow, linear. Central area with a large fascia, rarely reaching the valve margins, due to a series of small areolae bordering the central area near the margins. Isolated pore solitary, round, located close to the valve margin, never connected to a stria. Raphe filiform, straight, with simple, bent proximal raphe endings, away from the isolated pore. Terminal raphe fissures clearly hooked. Striae weakly radiate near the central area, becoming more radiate towards the apices, 22–24 in 10 µm. Areolae well visible in LM.

Scanning electron microscopy (Figs 11–12)

Striae composed of 2–4 rounded areolae (Figs 11–12). Occasionally areolae fused within one stria forming transapically enlarged areolae (Fig. 11). Terminal raphe fissures clearly hooked, first deflected towards the side opposite the isolated pore, then hooked into the other side, weakly continuing onto the valve mantle (Fig. 12).

Ecology and associated diatom flora

Luticola beyensii was found in relatively dry, bare soils and on dry mosses (F-value VII-VIII) on both islands. The samples with *L. beyensii* were dominated by several taxa of the genus *Humidophila* R.L.Lowe *et al.* [*Humidophila contenta* (Grunow) R.L.Lowe *et al.* (Lowe *et al.* 2014), *Humidophila brekkaensis*



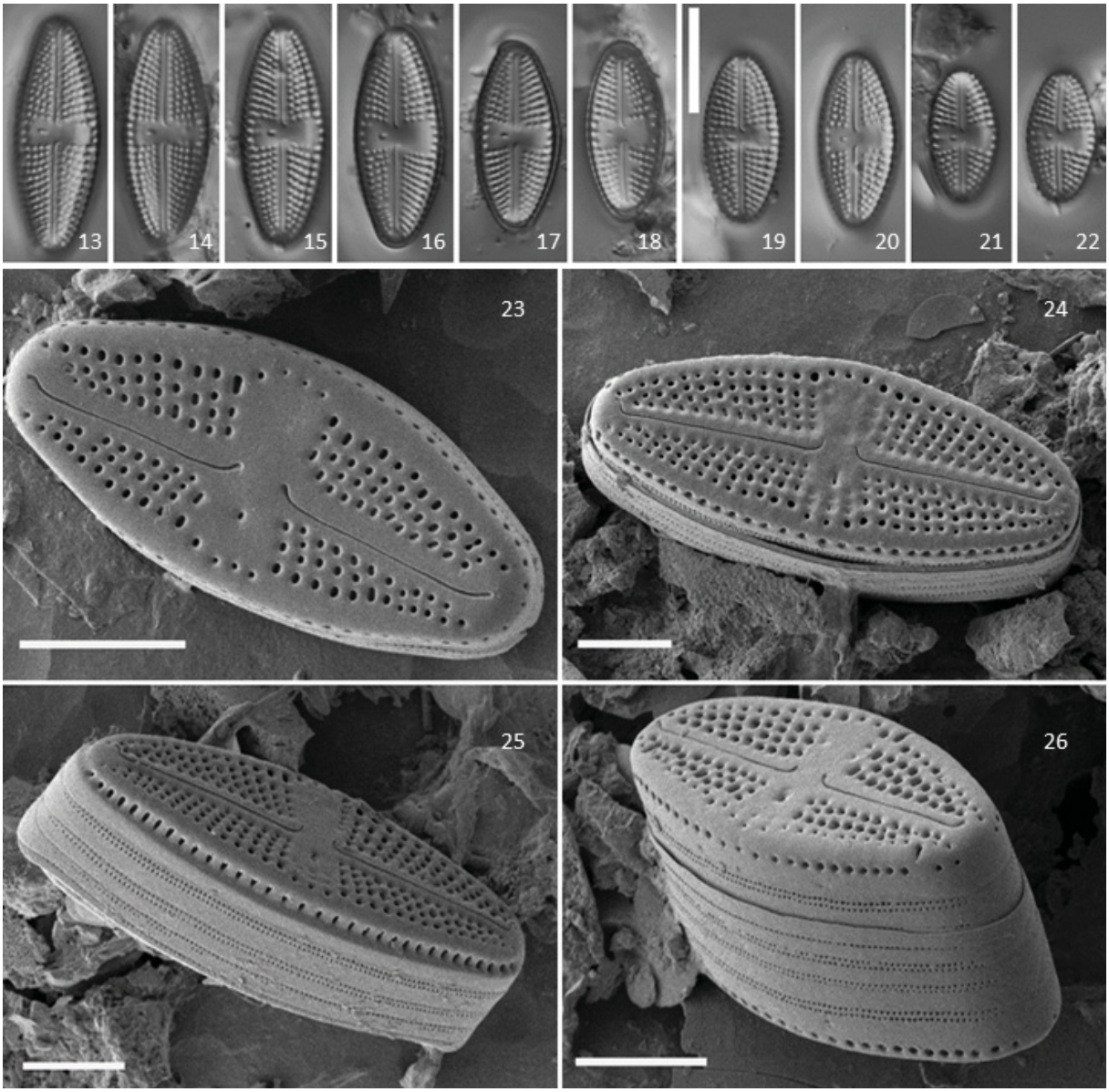
Figs 1–12. *Luticola beyensii* Van de Vijver *et al.* Light (LM) and scanning electron micrographs (SEM) of a population from Ile Amsterdam. **1–10**. LM of valve face views. **11–12**. SEM of external view of entire valve, showing raphe structure, position of the isolated pore and striae structure. Scale bars: 1–10 = 10 µm; 11–12 = 5 µm.

(J.B.Petersen) R.L.Lowe *et al.* (Lowe *et al.* 2014)], and *Pinnularia borealis* Ehrenb. (Ehrenberg 1843) and *Hantzschia amphioxys* (Ehrenb.) Grunow (Cleve & Grunow 1880).

Luticola subcrozetensis Van de Vijver, Kopalová, Zidarova & Levkov

Figs 13–26

Diatoms of Europe: Diatoms of the European Inland Waters and Comparable Habitats 7: 228, pl. 46 figs 15–31, pl. 47 figs 4–6 (Levkov *et al.* 2013).



Figs 13–26. *Luticola subcrozetensis* Van de Vijver *et al.* Light (LM) and scanning electron micrographs (SEM) of a population from Ile Saint-Paul. **13–22**. LM of valve face views. **23–24**. SEM of external view showing composition of striae and typical raphe structure. **25–26**. SEM girdle view. Scale bars: 13–22 = 10 µm; 23–26 = 5 µm.

Type

ILE DE LA POSSESSION: Crozet Archipelago, sub-Antarctica, 5 Dec. 1999, *B. Van de Vijver* (holo-: slide no. BR–4290; iso-: slides BRMZU9/25, MKNDC 006278/B).

Description

Light microscopy (Figs 13–22)

Valves rhombic-lanceolate to elliptic-lanceolate and even elliptic in smaller specimens with clearly convex margins and broadly rounded, non-protracted apices. Valve dimensions (n = 25): length 12–29 µm, width 7.0–8.5 µm. Axial area linear, slightly widening towards apices and central area. Central area bow-tie shaped, wider opposite the isolated pore, bordered by shortened striae on both sides. An isolated pore present in the central area, located halfway between the valve centre and the valve margin. Raphe branches straight, bent away from the isolated pore at both proximal and distal ends. Striae radiate throughout the entire valve, 15–17 in 10 µm.

Scanning electron microscopy (Figs 23–26)

Striae composed of 3–5 small, rounded to slightly elongated areolae at the apices, only 1–2 rounded areolae per stria, extending past the terminal raphe fissures on the valve face (Fig. 23). A single row of rounded areolae present along entire valve mantle, interrupted at apices (Fig. 26). Isolated pore rounded, slightly elongated, not associated with a stria. Central area usually bordered by one, rarely two, series of small, rounded areolae. Raphe branches straight to slightly curved. Proximal raphe endings bent to the side opposite the isolated pore, terminating into weakly developed pores. Terminal raphe fissures bent to the same side as the proximal endings terminating on the valve face, not extending onto the mantle (Fig. 24).

Ecology and distribution

Luticola subcrozetensis is a typical sub-Antarctic and Maritime Antarctic species. Originally described from Ile de la Possession (Crozet archipelago), the species was also reported from Livingston Island (Zidarova *et al.* 2016), one of the major South Shetland Islands, located in the southern Atlantic Ocean. The species was recently found in moss samples from Gough Island (Vinšová, unpubl. res.). It was present in samples from both Ile Saint-Paul and Ile Amsterdam.

The largest population was observed in a soil sample collected near the rockhopper penguin rookery of Ile Saint-Paul, at an altitude of 110 m, hidden in cracks in the rocks that border the penguin rookery.

Luticola ivetana Chattová & Van de Vijver sp. nov.
Figs 27–43

Etymology

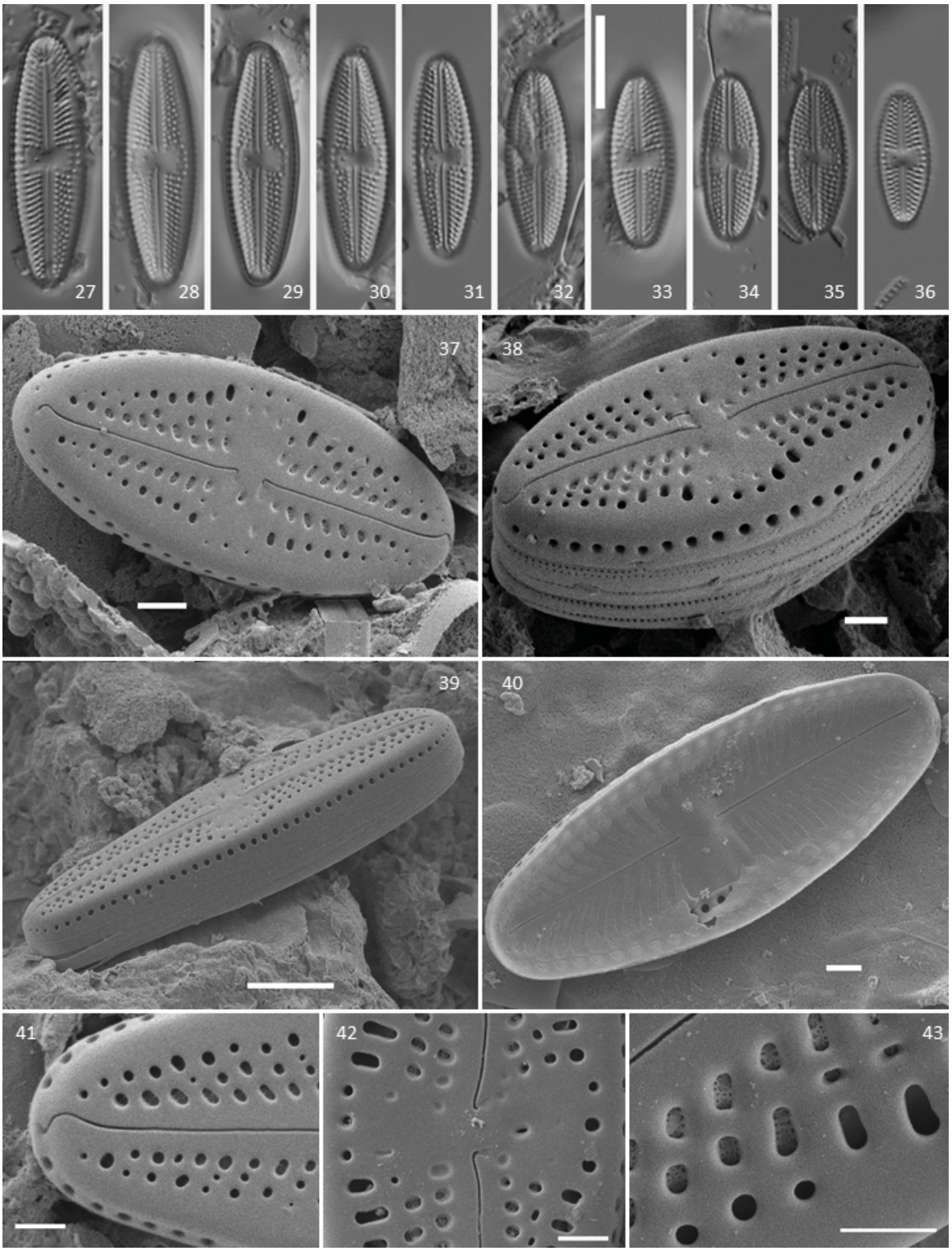
The new species was named after Mrs. Iveta Chattová, mother of the first author, on the occasion of her 50th birthday.

Type

ILE AMSTERDAM: Entrecasteaux, TAAF, sub-Antarctica, 37°51′18.6″ S, 77°31′23.5″ W, 21 Dec. 2016, *B. Van de Vijver* sample *W030* (holo-: slide no. BR–4495, Fig. 27; iso-: slide PLP–330; University of Antwerp, Belgium).

Description

Light microscopy (Figs 27–36)



Figs 27–43. *Luticola ivetana* Chattová & Van de Vijver sp. nov. Light (LM) and scanning electron micrographs (SEM) from the type population from Entrecasteaux on Ile Amsterdam, *B. Van de Vijver* sample *W030*. **27–36**. LM of valve face views. **37–38**. SEM of valve exterior. **39**. SEM girdle view. **40**. SEM of valve interior. **41**. SEM of external detail of hooked terminal raphe fissures. **42**. SEM of external detail view of central area showing the typical deflection of proximal raphe endings. **43**. SEM of external detail view of areolae structure. Scale bars: 27–36 = 10 µm; 37–38, 40–43 = 1 µm; 39 = 5 µm.

Valves elliptic-lanceolate with convex margins and broadly rounded, non-protracted apices. Valve dimensions (n = 50): length 11.0–25.5 µm, valve width 6.0–7.5 µm. Axial area narrow, linear, almost not widening towards the apices and central area. Central area forming a bow-tie shaped stauros. One isolated pore present in the central area, positioned close to the valve centre. Raphe filiform, straight with weakly deflected simple proximal raphe endings and elongated terminal raphe fissures. Striae radiate throughout the entire valve, 16–18 in 10 µm.

Scanning electron microscopy (Figs 37–43)

Striae composed of 2–4 round to elongated areolae, clearly enlarged near the central area and the valve margins (Figs 37, 43). Mantle areolae very large, rounded, never slitlike (Fig. 39). Central area bordered by 1–2 rounded to weakly transapically elongated areolae. Isolated pore elliptic, clearly isolated from the central striae (Fig. 38). Raphe branches straight with short proximal raphe endings bent towards the side with the isolated pore (Fig. 42). Terminal raphe fissures hooked, continuing onto the valve mantle (Fig. 41). Internally, poroids of valve face occluded by hymens forming a continuous strip on each stria. Distinct stauros visible. Internal proximal raphe endings straight, terminating on the edge of the stauros. Distal raphe endings terminating onto small helictoglossae (Fig. 40).

Ecology and distribution

So far, *L. ivetana* sp. nov. was observed on Ile Amsterdam only. The type locality where a large population of this new species was observed, was a small crack in a rock face at Entrecasteaux, clearly under the permanent influence of seaspray. A very thin film of water was present in the crack together with wet mud. The sample was taken by scraping off the mud and the water from the crack. Another large population where *L. ivetana* sp. nov. was found is a lava cavern in the partly collapsed Grand Tunnel, running from the Cratères Vénus to the northern coast. The sample was taken from wet mosses (F-value IV-V), growing on the wall of the cavern, close to the entrance, in a population of *Blechnum australe* L. The sample was dominated by *Ferocia setosa* (Greville) Van de Vijver & Houk (Van de Vijver *et al.* 2017), *Orthoseira verleyenii* Van de Vijver (Lowe *et al.* 2013), *Sellaphora barae* Van de Vijver & E.J.Cox (Van de Vijver & Cox 2013) and various *Humidophila* species.

Luticola vancampiana Chattová & Van de Vijver sp. nov.
Figs 44–71

Etymology

The species is named after Prof. Dr. Karel Van Camp (University of Antwerp, Belgium), to thank him for his efforts in conserving the Van Heurck Collection and his broad interest in diatom research.

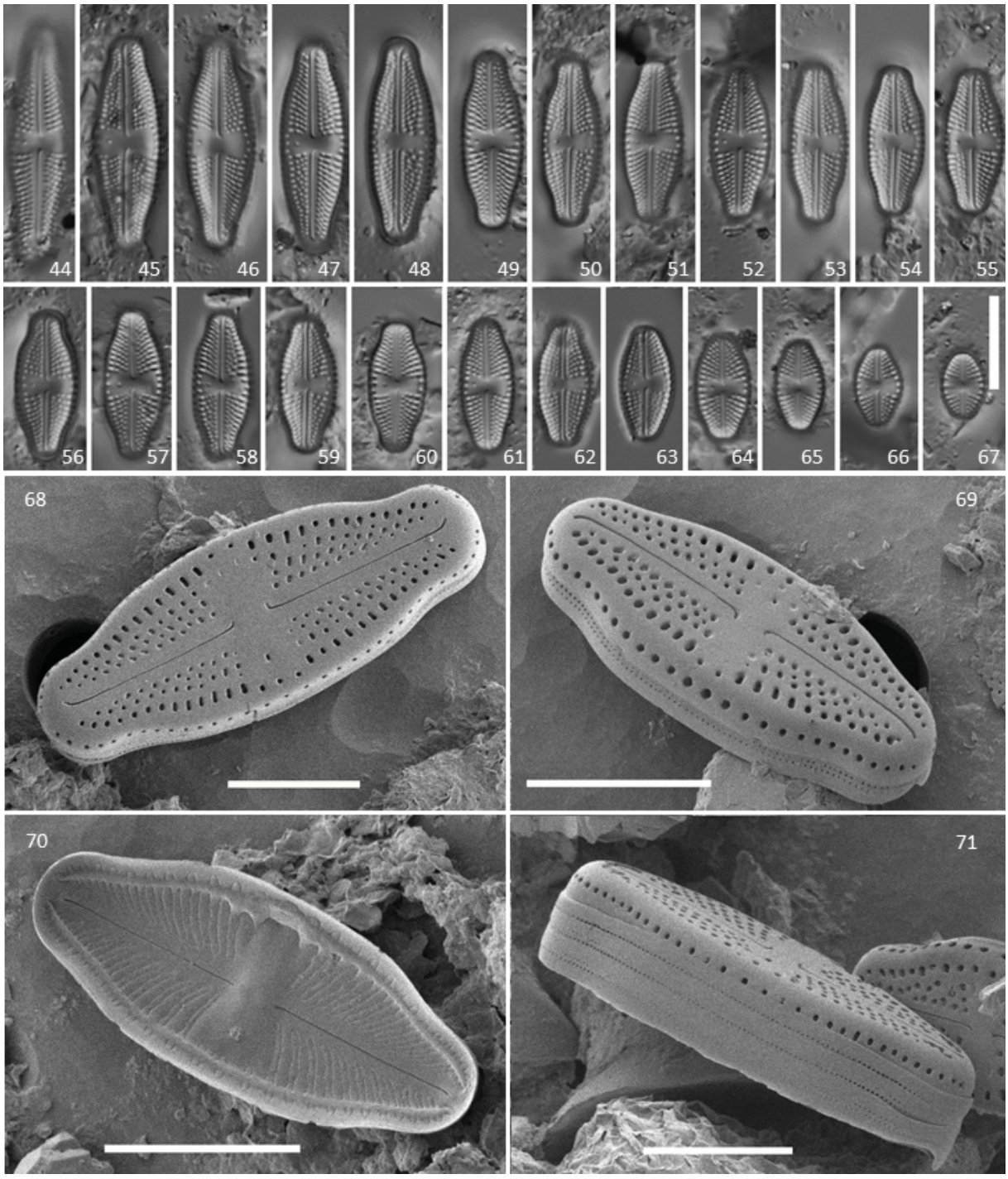
Type

ILE SAINT-PAUL: Conserverie, TAAF, sub-Antarctica, 38°42′52.0″ S, 77°31′55.5″ W, 24 Nov. 2016, *B. Van de Vijver* sample *S029* (holo-: slide no. BR–4496, Fig. 47; iso-: slide PLP–331; University of Antwerp, Belgium).

Description

Light microscopy (Figs 44–67)

Valves linear-lanceolate to elliptic-lanceolate, elliptic in the smallest specimens, with protracted, subcapitate to rostrate apices. In smaller specimens, valve ends not as protracted, only subrostrate or obtusely rounded. Initial cells rhombic-lanceolate. Valve dimensions (n = 35): length 10.0–26.0 µm, width 5.0–8.5 µm. Axial area linear, narrow. Single, rounded isolated pore present in the central area, located halfway between the valve centre and margin, sometimes attached to a stria. Central area wide, bow–tie shaped, bordered on both sides with a series of 3–5 round areolae. Raphe branches straight,



Figs 44–71. *Luticola vancampiana* Chattová & Van de Vijver sp. nov. Light (LM) and scanning electron micrographs (SEM) from the type population from Conserverie on Ile Saint-Paul, *B. Van de Vijver* sample *S029*. **44–67**. LM showing the variation in size and shape of the valve apices. **68–69**. SEM of valve exterior. **70**. SEM of valve interior. **71**. SEM girdle view. Scale bars: 44–67 10 µm; 68–71 = 5 µm.

deflected away from the isolated pore at both proximal and distal ends. Transapical striae radiate throughout, 16–19 in 10 µm.

Scanning electron microscopy (Figs 68–71)

Valve mantle with a single row of round areolae (Fig. 71), interrupted at the apices. Striae composed of 3–4 areolae, 1–2 areolae at the apices. Areolae round to elongated, clearly enlarged and prolonged close to the valve margins (Fig. 68). Internally, areolae occluded by hymens, forming a continuous strip across the valve (Fig. 70). Isolated pore showing an elliptic external opening. Internally, central nodule thickened, expanding into stauros. Isolated pore with semi-lunar opening formed by tongue-like structure. Raphe branches straight. Proximal raphe endings short, deflected to side opposite to the isolated pore. Terminal raphe fissures deflected to the same side as the proximal endings, not extending onto the mantle (Fig. 69). Internally, proximal raphe endings straight, while distally, raphe branches terminating on small helictoglossae.

Ecology and distribution

So far *L. vancampiana* sp. nov. was found on both Ile Amsterdam and Ile Saint-Paul. The largest population was found in a wet soil covered by green algae close to the ocean on Ile Saint-Paul. The sampling site is frequently visited by fur seals and penguins, as was visible in the macroremains (feathers, excrements). The sample was almost entirely dominated by the new *Luticola* species. Other (smaller) populations were found in soil samples collected near penguin rookeries where similar conditions (considerable biotic influence, considerable salinity input) prevailed.

Luticola sp.
Figs 72–82

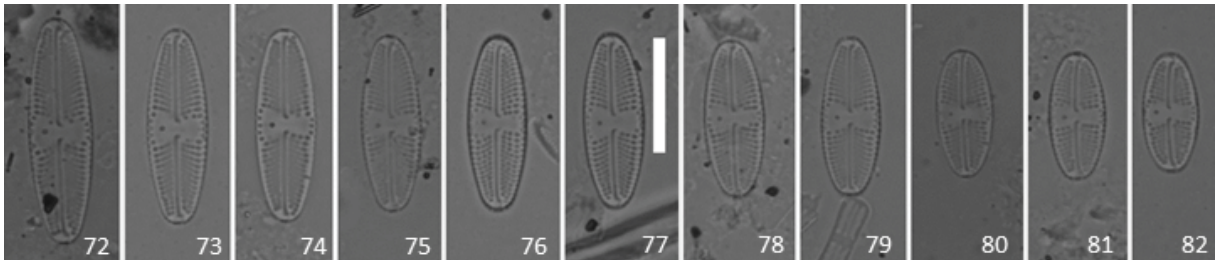
Description

Light microscopy (Figs 72–82)

Valves linear-lanceolate to elliptic-lanceolate in smaller specimens, with rounded, non-protracted apices. Valve dimensions (n = 12): length 10.7–20.5 µm, width 4.5–6.5 µm. Axial area narrow, linear. Central area wide, bow-tie shaped, clearly asymmetrical with the side bearing the isolated pore markedly wider. Isolated pore present in the central area, located halfway between the valve centre and margin. Raphe branches straight, deflected away from the isolated pore at both proximal and distal ends. Transapical striae punctate, radiate throughout the entire valve, 20–24 in 10 µm.

Remarks

So far, this species has only been observed with light microscopy. Further studies and SEM observations will be necessary to determine its correct taxonomic position. The species was so far found in only two soil samples (A6 and A7) taken from Ile Saint-Paul. Both samples are dominated by *L. beyensii*,



Figs 72–82. *Luticola* sp. Light micrographs of a population from Ile Saint-Paul. Scale bar: 10 µm.

Humidophila brekkaensis, *Pinnularia acidicola* Van de Vijver & Le Cohu (Van de Vijver *et al.* 2002a) and *Hantzschia amphioxys*.

Discussion

The genus *Luticola* is one of the dominant components of the diatom flora in terrestrial habitats on sub-Antarctic Islands. These habitats show a diverse and very characteristic terrestrial flora with high degree of regional endemism in the entire Antarctic region, as is demonstrated by the large number of endemic taxa in typical terrestrial genera such as *Microfissurata* Lange-Bertalot *et al.* (Cantonati *et al.* 2009), *Orthoseira* Thwaites (Van de Vijver & Kopalová 2008, Lowe *et al.* 2013), *Humidophila* (Kopalová *et al.* 2015; Chattová *et al.*, 2017), *Hantzschia* Grunow (Zidarova *et al.* 2010) and *Muelleria* Frenguelli (Frenguelli) (Van de Vijver *et al.* 2010, 2014).

The morphological and taxonomical analysis of the genus *Luticola* on Ile Amsterdam and Ile Saint-Paul revealed the presence of two new species. A wide combination of morphological features such as valve outline, shape of the valve apices, shape of the central and axial area, position and shape of the isolated pore, stria pattern and density and raphe and areola structure were used for comparison with all similar taxa known worldwide so far. Sufficient morphological differences were found to justify the separation of both taxa as new to science. The main discriminative features between the new species and their morphologically similar taxa are summarized in Table 1 (*Luticola ivetana* sp. nov.) and Table 2 (*Luticola vancampiana* sp. nov.).

Luticola ivetana sp. nov. resembles several *Luticola* species with elliptic lanceolate valves, however the new species can be easily distinguished by the proximal raphe endings typically bent towards the isolated pore. There are only a few species showing a similar deflection such as *L. ledeganckii*, *L. frequentissima* Levkov *et al.* (Levkov *et al.* 2013) and *L. raynae* Zidarova & Van de Vijver (Van de Vijver *et al.* 2011). *Luticola raynae* and *L. ledeganckii* have typical capitate apices, always lacking in *L. ivetana* sp. nov. The most similar is *L. frequentissima*, but the latter species can be differentiated by the shape of the central area, much smaller in *L. ivetana* sp. nov. and by its stria structure. *Luticola frequentissima* has transapical striae composed of 4–6 areolae per stria contrary to *L. ivetana* sp. nov. that has only 2–4 areolae per stria. The two species also differ ecologically, *L. ivetana* sp. nov. seems to be an aerophilic and most likely even slightly brackish taxon given the habitat in Entrecasteaux where it was found, while *L. frequentissima* always occurs in freshwater habitats. *Luticola mutica* and *L. imbricata* (Bock) Levkov *et al.* (Levkov *et al.* 2013) have longer proximal raphe endings curved doubly, a feature lacking in *L. ivetana* sp. nov. *Luticola imbricata* additionally differs from the new taxon by the shape of its isolated pore (rounded vs elliptical) and by the apices that are narrowly rounded vs broadly rounded. *Luticola mutica* does not only differ by the shape and deflection of the raphe endings but also by the different shape of central area and the structure of the striae. *Luticola australomutica* Van de Vijver (Van de Vijver & Mataloni 2008) is an Antarctic species described from Deception Island, with a similar valve outline as *L. ivetana* sp. nov. Nonetheless, both species can be distinguished without any difficulties based on the morphology of the distal and proximal raphe endings. *Luticola australomutica* has short, almost straight distal raphe fissures, terminating before the last row of areolae, while in *L. ivetana* sp. nov. the distal raphe fissures are hooked, continuing onto the valve mantle. Additionally, *L. australomutica* has striae composed of 4–5 areolae contrary to 2–4 areolae per stria in *L. ivetana* sp. nov.

Smaller specimens of *L. ivetana* sp. nov. also resemble *L. pseudoimbricata* Levkov *et al.* (Levkov *et al.* 2013) based on their valve shape, but can however be separated by the different shape and deflection of both raphe proximal and distal fissures. *Luticola similis* Levkov *et al.* can be differentiated from *L. ivetana* sp. nov. by the wide and asymmetrical central area, by its lanceolate valve outline and its narrowly rounded valve apices.

Table 1. Morphological comparison between *L. ivetana* sp. nov. and morphologically similar taxa.

Taxon	*Luticola ivetana* sp. nov.	*Luticola ledeganckii*	*Luticola frequentissima*	*Luticola raynae*	*Luticola mutica*	*Luticola imbricata*	*Luticola australomutica*	*Luticola pseudoimbricata*	*Luticola similis*
Length (µm)	11–25	14–28	12–27	15–27	11–28	10–23	17–35	9–22	8–33
Width (µm)	6.0–7.5	7.0–9.0	6.4–9.0	7.0–10.0	6.0–9.5	5.0–7.0	5.5–8.5	5.0–7.0	5.5–7.5
Striae (in 10 µm)	16–18	15–18	12–24	14–15	16–18	18–22	16–21	20–24	21–24
Areolae (per stria)	2–4	3–4	4–6	3–5	3–4	3–4	4–5	3–4	3–5
Valve shape	elliptic-lanceolate	elliptic-lanceolate	elliptic-lanceolate to elliptic	linear-elliptic to rectangular	elliptic-lanceolate to linear-elliptic	linear-lanceolate to elliptic-lanceolate	lanceolate to elliptic-lanceolate	linear-elliptic	elliptic-lanceolate to elliptic
Valve apices	broadly rounded	capitate to subcapitate	rounded	broadly rostrate	rounded	narrowly rounded	slightly rostrate	rounded	narrowly rounded
Central area	bow-tie-shaped	rectangular to elliptic	wide, bow-tie-shaped	transversally elongated	narrow, elliptical	bow-tie-shaped	wedge to bow-tie-shaped	rectangular to bow-tie-shaped	wedge-shaped, asymmetrical
Axial area	narrow, linear	narrow, linear	narrow, linear	narrow, linear	narrow, linear	narrow, linear	narrow, linear	narrow, linear	narrow, linear
Proximal raphe endings	hooked, deflected towards the isolated pore	deflected towards the isolated pore	hooked, deflected towards the isolated pore	hooked	doubly-curved	short, deflected	weakly deflected	weakly curved	bent
Distal raphe endings	hooked	weakly curved	curved	hooked	hooked	"?"-shaped	short, deflected	short, deflected	"?"-shaped

Table 2. Morphological comparison between *L. vancampiana* sp. nov. and morphologically similar taxa.

Taxon	*Luticola vancampiana* sp. nov.	*Luticola robusta*	*Luticola ledeganckii*	*Luticola montana*	*Luticola suecorum*	*Luticola ipevii*	*Luticola truncata*	*Luticola muticopsis*	*Luticola permuticopsis*
Length (µm)	10–26	15–42	14–28	17–38	20–42	16–34	17–36	12–22	17–26
Width (µm)	5.0–8.5	7.5–11.5	7.0–9.0	7.0–10.0	7.5–13.0	6.0–9.0	8.3–10.7	7.0–9.0	7.0–9.2
Striae (in 10 µm)	16–19	13–14	15–18	19–22	13–14	14–18	16–19	15–18	18–22
Areolae (per stria)	3–5	3–4	3–4	5–8	3–5	4–5	3–5	3–4	4–6
Valve shape	linear-lanceolate to elliptic-lanceolate	linear-lanceolate to linear-elliptic	elliptic-lanceolate	lanceolate to elliptic-lanceolate	linear-lanceolate to elliptic-lanceolate	elliptic-lanceolate	lanceolate to linear-lanceolate	linear-elliptic	linear-lanceolate to linear-elliptic
Valve apices	subcapitate to rostrate	rostrate to capitate	capitate to subcapitate	broadly rostrate	broadly rounded, rostrate	broadly rounded	truncate	broadly capitate	broadly capitate
Central area	bow-tie-shaped	transversally elliptic	rectangular to elliptic	bow-tie-shaped	transversally elliptic	wedge-shaped	rectangular to elliptic	bow-tie-shaped	transversally elongated
Axial area	narrow, linear	wide, linear	narrow, linear	narrow, linear	narrow, linear	narrow, linear	narrow, linear	wide, linear	narrow, linear
Proximal raphe endings	short, deflected	distinctly deflected	deflected towards the isolated pore	slightly curved	doubly-curved	distinctly deflected	distinctly deflected	distinctly deflected	deflected
Distal raphe endings	deflected	short, deflected	weakly curved	hooked	weakly curved	weakly curved	weakly curved	weakly curved	weakly curved

The largest specimens of *L. vancampiana* sp. nov. bear some similarities to *L. robusta*. However, both taxa significantly differ in stria density (13–14 in 10 µm in *L. robusta* vs 16–19 in 10 µm in *L. vancampiana* sp. nov.). Additionally, *L. robusta* has a markedly wider axial area. *Luticola vancampiana* sp. nov. may also resemble *L. ledeganckii* based on valve shape and stria density. The main difference between these two species can be observed in the direction of proximal raphe endings, which are deflected towards the isolated pore in *L. ledeganckii*. *Luticola montana* Levkov *et al.* (Levkov *et al.* 2013) has a similar valve shape compared to *L. vancampiana* sp. nov., but can be easily differentiated from the latter species by its stria and areola density. *Luticola montana* has finer (19–22 in 10 µm) striae composed of 5–8 areolae, contrary to *L. vancampiana* sp. nov. that has only 3–5 areolae per stria. Additionally, the distal raphe fissures in *L. montana* continue onto the valve mantle, interrupting the row of areolae. *Luticola suecorum* has similar valve shape and protracted apices. Nevertheless, both species can be hardly confused and are easily distinguished by their valve dimensions and stria density. *Luticola suecorum* is much larger (20–42 µm, 7.5–13 µm) with coarser striae (13–14 in 10 µm). Additional differences can be observed in the SEM. *Luticola suecorum* has doubly hooked distal raphe endings that extend onto the valve mantle and an ornamented central area with surface depressions. *Luticola ipevii* can be differentiated from *L. vancampiana* sp. nov. by its slender, elongated valve outline and non-protracted, broadly rounded apices. Smaller valves of *L. vancampiana* sp. nov. are similar to *L. truncata* Kopalová & Van de Vijver (Kopalová *et al.* 2009). A clear distinction between the two taxa can be made due to the valve width. *Luticola vancampiana* sp. nov. (W = 5.0–8.5 µm) has narrower valves for any given valve width when compared to *L. truncata* (W = 8.5–10.5 µm). Finally, *L. muticopsis* and *L. permuticopsis* Kopalová & Van de Vijver (Kopalová *et al.* 2011) have both more capitate apices. Moreover, *L. permuticopsis* has a higher striae density (18–22 in 10 µm).

The last and unknown species of *Luticola*, presented here as *Luticola* sp., is characteristic by its asymmetrical central area, narrow valves and consistently linear-lanceolate outline, a combination of features that is almost never encountered within the genus *Luticola*. Based on the valve shape and striae density, the most similar species is *L. frequentissima*. Both species can be differentiated by their proximal raphe endings which are deflected towards the isolated pore in *L. frequentissima*. Moreover, *Luticola* sp. has slightly narrower valves for any given valve length when compared to *L. frequentissima*. The central area of *L. similis* Levkov *et al.* (Levkov *et al.* 2013) is slightly asymmetrical, but always wider on the side opposite to the isolated pore. *Luticola mutica* has a more variable valve outline, a narrower central area and coarser striae (16–18 in 10 µm).

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