

New and interesting *Luticola* species (Bacillariophyta) from the mangroves of Nosy Be Island, NW Madagascar

by

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Abstract

Madagascar is an isolated island characterized by a high degree of endemism at all taxonomic levels. Diatom assemblages of the region are still poorly known and sporadic sampling events in various habitats (e.g. lagoons, mangroves) have revealed a large number of taxa that could not be identified. This study presents detailed descriptions of two new species of *Luticola*: *L. nosybeana* and *L. madagascarensis*, collected from mangrove roots on Nosy Be Island. Comparisons with the described congeners showed that the density of striae in *Luticola nosybeana* is higher than that in *L. belawanensis* and proximal raphe endings terminate as irregular, shallow grooves. *Luticola madagascarensis* differs from *L. similis* in the shape of proximal raphe endings, which are short and expanded in the latter, while continue with irregular, shallow, elongated L-shaped grooves in *L. madagascarensis*. *Luticola nosybeana* and *L. madagascarensis* can be distinguished under a light microscope by the shape of the central area (bow-tie shaped in *L. madagascarensis* and deltoid in *L. nosybeana*) and isolated pores (robust and well visible in *L. madagascarensis*, poorly discernible in *L. nosybeana*). The two new species are unique in their habitat preferences: while all known congeners are freshwater, the new species inhabit estuarine mangroves.

Key words: Bacillariophyta, diatoms, Madagascar, *Luticola*, new species

Introduction

Nosy Be Island is the largest (ca. 320 km²) coastal island off Madagascar, located off its NW coast. Along with a number of smaller islands, including Nosy Fanihy, Nosy Sakatia, Nosy Faly, Nosy Ambariobe, Nosy Tanikely, Nosy Komba, Nosy Mamoko and Nosy Tonga, it forms an archipelago, the islands of which originated as volcanoes (Melluso & Morra 2000; Collins & Windley 2002), probably during the Tertiary (Besairie 1968–69–71).

The diatoms of Madagascar are still rather poorly studied. The first studies, containing analyses of materials collected in 1904–2000, were published in 2002. Those surveys concerned only freshwater diatoms and at that time the authors identified 177 new freshwater diatom species (Metzeltin & Lange-Bertalot 2002). The knowledge about marine benthic diatoms from both Madagascar and Nosy Be Island is much more scant. However, there are publications on diatoms from areas close to the Madagascar region, including the analysis of 13 samples collected from Tanzania (Midwest Africa) near the city of Dar-es-Salaam and of one sample from Malindi in Kenya (Foged 1975), as well as a comprehensive study on marine diatoms of the Mascarenhas Archipelago (Mascarene Islands), concerning mainly La Réunion and Rodrigues Islands, where diatoms have been explored in various freshwater environments for many years (Coste & Ricard 1984; Klee et al. 2000), marine diatoms having been addressed since 2005 within the framework of the COSADIM (Coral Sand Diatoms off Mascarenes) project (Riaux-Gobin & Compère 2008; Riaux-Gobin et al. 2010a,b; 2011a,b).

The genus *Luticola* D.G. Mann, established in 1990 (Round et al. 1990), groups widespread species, from both fresh and brackish water. Levkov et al. (2013) revised the genus and described 91 *Luticola* species as new to science. In total, the monograph of Levkov et al. (2013) contains descriptions of about 200 species.

Since then, new species have been described and new combinations in this genus have been developed (e.g. Zidarova et al. 2014; Glushchenko & Kulikovskiy 2015; Kohler et al. 2015; Bąk et al. 2017; Chattová et al. 2017; Glushchenko et al. 2017; Straube et al. 2017). Taking into account the *Luticola* species listed in AlgaeBase (Guiry 2017) and those recently proposed as new to science, it is estimated that the genus currently contains about 220 species. Ecological, taxonomic, molecular and biogeographical studies of the genus are in progress (e.g. Kociolek et al. 2017; Wu & Bergey 2017).

Luticola species have rarely been recorded in our study area. A recent study on marine diatom assemblages of Nosy Be Island (Kryk 2016) revealed the presence of only two *Luticola* species, which are described herein. Previous studies from freshwater habitats of the Madagascar region (Metzeltin & Lange-Bertalot 2002) also identified only two *Luticola* species: *L. mutica* (Kützing) D.G.Mann in Round, R.M.Crawford & D.G.Mann (1990: 670) and *L. muticoides* (Hustedt) D.G.Mann in Round, R.M.Crawford & D.G.Mann (1990: 671) from Ivato. In addition, Metzeltin & Lange-Bertalot (2002) reported the third, unidentified *Luticola* species from Lac Mantasoa. However, more *Luticola* species have been recorded in the West Indian Ocean in the vicinity of Madagascar. A summary of the *Luticola* species reported from the region is presented in Table 1. The relatively small number of *Luticola* species in the region is likely due to the paucity of studies and suggests the need for further taxonomic revisions and research on *Luticola* species from Madagascar as well as from the entire Indian Ocean.

The present report describes LM and SEM observations on two *Luticola* species from a single sample collected from mangrove roots on Nosy Be Island. The sample contained numerous other taxa, both aerophytes, e.g. *Humidophila* (Lange-Bertalot & Werum) R.L.Lowe et al. (2014) and those tolerant of a high osmotic pressure, e.g. *Tryblionella debilis* Arnott

Table 1

Luticola species reported from the region in the vicinity of Madagascar

Species	Source	Region	Comments
<i>L. rhombica</i>	(S.J.C.Zimmermann) Levkov, Metzeltin & A.Pavlov 2013: 208	Tanzania	Coll. F. Fricke
<i>L. frickei</i>	Levkov, Metzeltin & A.Pavlov 2013: 114	Tanzania	Coll. F. Fricke
<i>L. gesierichiae</i>	Levkov, Metzeltin & A.Pavlov 2013: 119	Tanzania	Coll. F. Fricke
<i>L. hustedtii</i>	Levkov, Metzeltin & A.Pavlov 2013: 131	Tanzania	Coll. Leg. B. Schröder
<i>L. kraeuselii</i>	(Cholnoky) Metzeltin & Lange-Bertalot 1998: 139	South Africa	Acc. No. MKNDC 6283
<i>L. distinguenda</i>	(Hustedt) Levkov, Metzeltin & A.Pavlov 2013: 106	South Africa	Acc. No. MKNDC 6396
<i>L. tropica</i>	Levkov, Metzeltin & A.Pavlov 2013: 241	South Africa, Indonesia	–
<i>L. novaeguineensis</i>	(Tempère) Levkov, Metzeltin & A.Pavlov 2013: 177	New Guinea, Sumatra	Coll. Adams

ex O'Meara (1873: 310). Ecology of the two *Luticola* new species can be inferred from measurements of environmental parameters taken during sampling.

Material and methods

The analyzed material was collected on 30 June 2014 as an epiphytic sample from mangrove roots at a site designated as NB4a, located near the mouth of a small river on the southern coast of Nosy Be Island (GPS coordinates: 13°24'0.06"S, 48°17'8.58"E; Fig. 1). The authors obtained a permission for sampling from the Ministry of Higher Education and Scientific Research, Antananarivo, Madagascar.

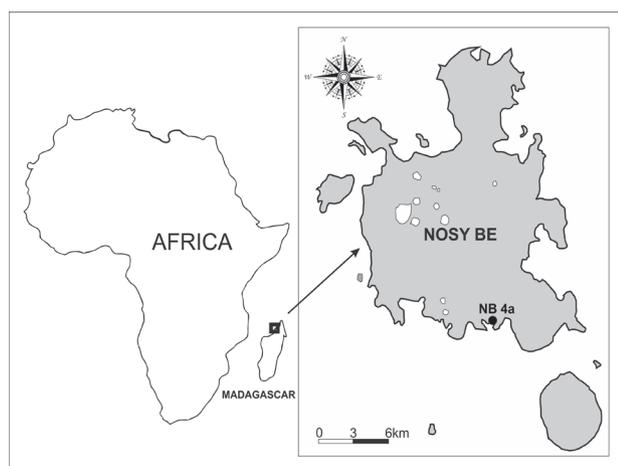


Figure 1
Nosy Be Island with the diatom sampling site (NB 4a)

In the laboratory, the sample was treated with 10% hydrochloric acid (HCl) to remove calcium carbonate and, following thorough washing, boiled in 37% hydrogen peroxide (H₂O₂) to eliminate organic matter. After washing four times with distilled water, the final suspension was pipetted onto coverslips, left for evaporation, and mounted onto glass slides using Naphrax® diatom mountant. The slides were examined under a Zeiss Axio Scope A1 light microscope. Measurements and photographic documentation were performed with the Canon EOS 500D and Canon EOS Utility software. A total of 400 valves were identified to the level of species or variety (or numbered in the case of new species) and counted (Battarbee 1986; Bodén 1991) to assess the relative abundance of all species (including those new to science). Biodiversity indices (i.e. species richness, the Shannon H' index and the evenness index) were calculated (Shannon 1948; Tuomisto 2012). For scanning electron microscope (SEM) observations, the cleaned material was pipetted

onto 25 mm diameter Whatman® Nuclepore 2 µm mesh polycarbonate membrane filters attached to aluminum stubs and sputtered with 20 nm of gold using a Turbo-Pumped Sputter Coater Quorum Q 1500T ES. Diatoms were examined under a Hitachi SU 8010 SEM at the Podkarpackie Innovative Research Center of the Environment (PIRCE), University of Rzeszów.

During sampling, relevant environmental parameters (water pH, temperature, conductivity, salinity, redox potential and dissolved oxygen content) were recorded using the Multiparameter HANNA HI98194 device.

The new species are compared with similar taxa from around the world described in the relevant literature (Metzeltin & Lange-Bertalot 1998, 2002; Moser et al. 1998; Metzeltin et al. 2005; Levkov et al. 2013; Zidarova et al. 2014; Glushchenko & Kulikovskiy 2015; Kohler et al. 2015; Chattová et al. 2017; Glushchenko et al. 2017; Bąk et al. 2017; Kociolek et al. 2017; Straube et al. 2017; Wu & Bergey 2017). The adopted terminology follows Round et al. (1990) and Levkov et al. (2013).

Results

Descriptions of new *Luticola* species

Luticola nosybeana sp. nov. Kryk, Bąk & Peszek. Figures 2–4

Description

Light microscopy (Fig. 2): Valves elliptic-lanceolate in larger specimens to elliptic in smaller specimens, with narrowly rounded apices. Valve length 9–27 µm, width 6.0–10.5 µm. Axial area linear, slightly narrower at the apices and weakly expanded toward the central area. Central area wide, asymmetrical, deltoid or rectangular. Raphe filiform, straight to slightly curved. Proximal raphe endings hooked, finishing T- or L-shaped fissures, barely visible in LM (e.g. Fig. 2d, k, m, q, v, aa, ab). Transapical striae in LM punctate, weakly radiate close to the valve center, becoming strongly radiate toward apices, 20–24 in 10 µm.

Scanning electron microscopy: External view (Fig. 3) – valve mantle with a single row of large elliptic areolae. Few slit-like or elliptic surface depressions ("ghost areolae") present within the central area (Fig. 3e, arrow). Single isolated pore present in the central area, external, round opening located close to the valve margin (Fig. 3b, arrow). Central area on both valve margins bordered by shortened striae composed

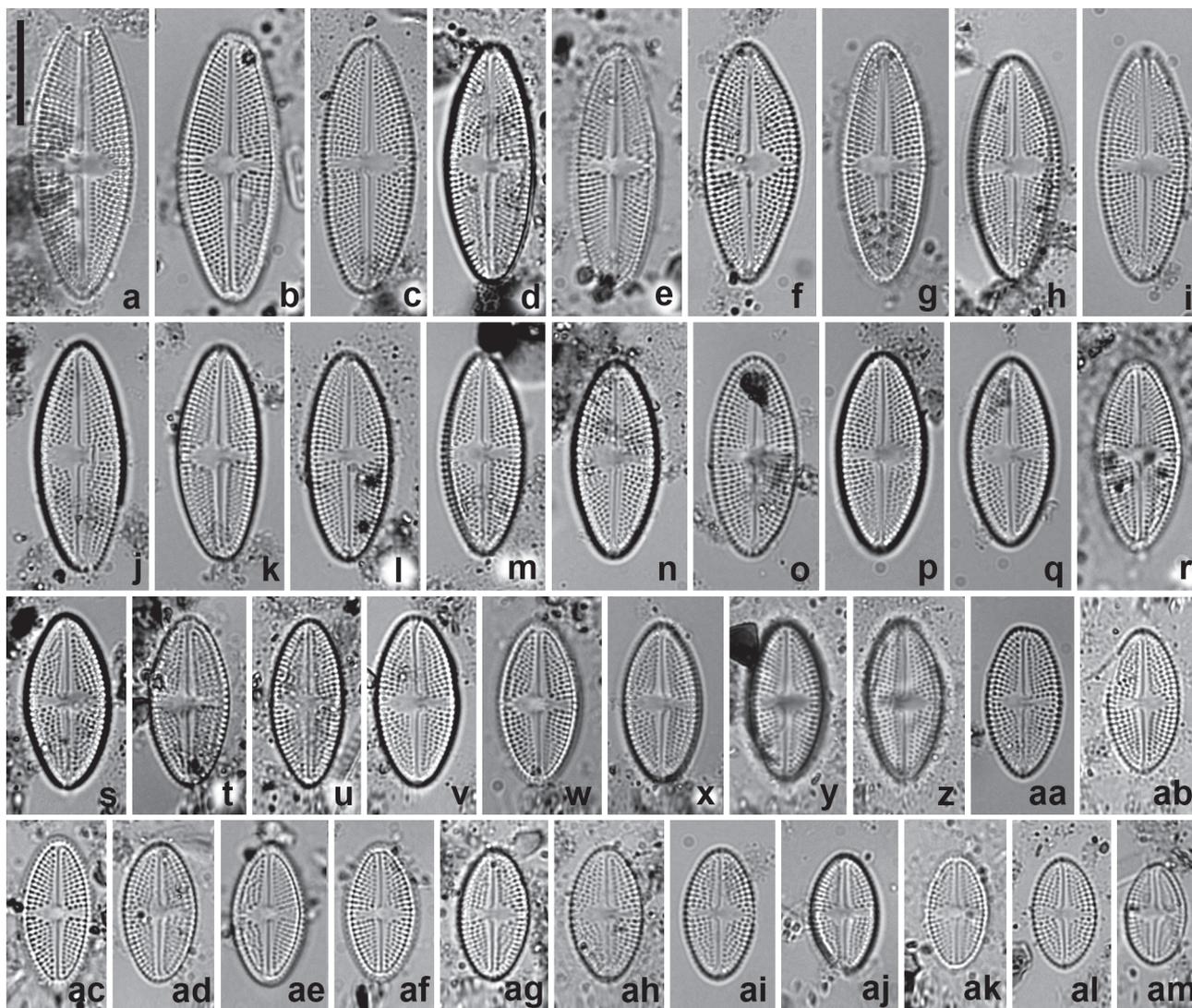


Figure 2a–am

Luticola nosybeana sp. nov. LM images. Valve views, showing variation in size and outline. Fig. 2p presents the holotype. Scale bar = 10 μ m

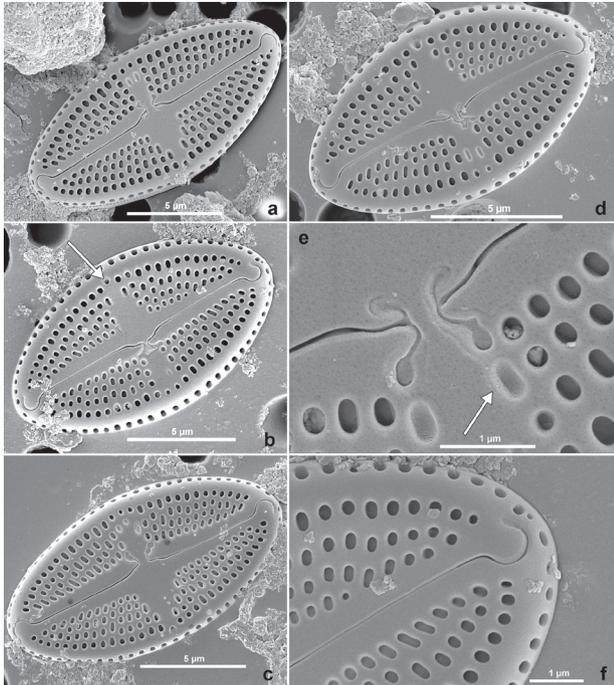
of 1–2(3) round or elongated areolae. Proximal raphe ends close to each other, hooked to the side opposite the isolated pore, continuing with irregular, shallow grooves, insect-antennae-like (L-shaped, Fig. 3c) or butterfly-like (T-shaped, Fig. 3e). Transapical striae composed of 4–5 round to elliptic areolae. Distal raphe fissures hooked (question mark form) to the same side (but opposite the proximal raphe endings), not extending onto the valve mantle (Fig. 3f).

Internal view (Fig. 4) – the inner valve surface flat, the central area and the central nodule thickened, forming a stauros. The isolated pore with small, round opening covered by a large, triangular structure, located halfway between valve center and margin (Fig. 4f, arrow). Proximal raphe branches slightly

deflected toward the isolated pore (Fig. 4f). Distal raphe branches straight, each terminated as a small helictoglossa (Fig. 4c, arrow). Areolae occluded by hymenes, forming a continuous strip across the striae (Fig. 4e, arrow). Marginal channel narrow, located on the valve face/mantle junction (Fig. 4e, arrowhead).

Type: MADAGASCAR. Nosy Be Island, near Andoany Bay, 13°24'0.06"S, 48°17'8.58"E, July 2014, holotype (assigned here): Slide no. 22010 in Coll. of Andrzej Witkowski at the University of Szczecin (SZCZ), represented by Fig. 2p.

Type locality: Andoany Bay, southern coast, Nosy Be Island, Madagascar

**Figure 3a–f**

Luticola nosybeana sp. nov. SEM images. External valve views. Figs 3a–d: whole valve with straight axial area, expanded at the center to form a wide, asymmetrical, deltoid or rectangular fascia and isolated pore opening (arrow in Fig. 3b). Fig. 3e: proximal raphe endings, hooked to the side opposite the isolated pore, continuing with irregular, shallow, T-shaped or L-shaped grooves. Note the presence of a few slit-like or elliptic irregular surface depressions (“ghost areolae”) within the central area (arrow). Fig. 3f: distal raphe end curved and not extending onto the mantle

Type habitat: Mangrove roots.

Etymology: The specific epithet refers to the type location, Nosy Be.

Distribution: Known only from the type locality.

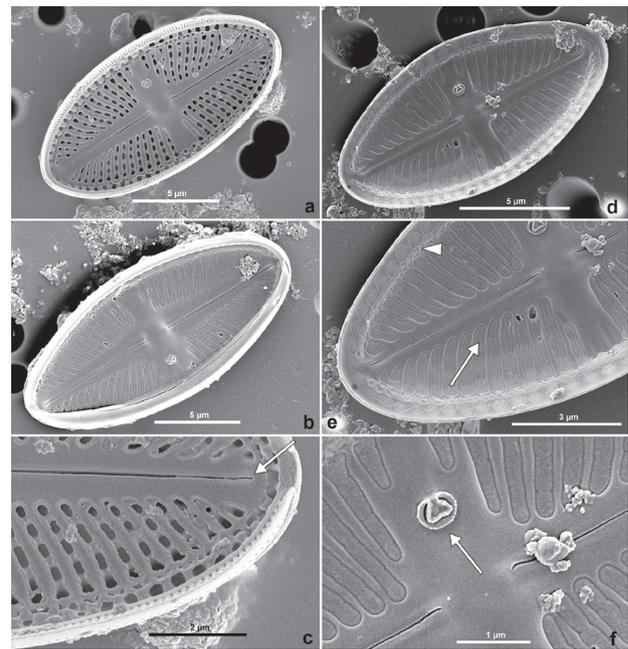
***Luticola madagascarensis* sp. nov.** Bąk, Kryk & Peszek Figures 5–6

Description

Light microscopy (Fig. 5): Valves elliptic-lanceolate in larger specimens to elliptic in smaller specimens, with narrowly rounded apices. Valve length 13.0–22.5 μm , width 6.0–7.5 μm . Axial area linear, slightly

narrower at the apices and weakly expanding toward the central area. Central area wide, symmetrical, bow-tie-shaped on both valve margins bordered by shortened striae composed of one round or elliptical areola. Raphe filiform, straight to slightly curved. Single isolated pore present in the central area, located halfway between the valve center and margin. Proximal raphe endings close to each other, hooked to the opposite side of the isolated pore, continuing with irregular, shallow, elongated, L-shaped grooves, barely visible in smaller valves, but visible in larger valves in LM (e.g. Fig. 5b, d, e). Transapical striae in LM punctate, weakly radiate close to the valve center, becoming strongly radiate toward the apices, 20–24 in 10 μm .

Scanning electron microscopy: External view (Fig. 6) – Valve mantle with a single row of large elliptic areolae. Single isolated pore distinct, present in the central area, with external, slit-like opening located in a surface depression, halfway between the valve

**Figure 4a–f**

Luticola nosybeana sp. nov. SEM images. Internal valve views. Figs 4a, 4b, 4d: whole valve views with the marginal canal and isolated pore. Fig. 4c: distal raphe branch terminating in small helictoglossa (arrow). Fig. 4e: close-up of the valve interior showing the hyemate occlusions of areolae (arrow) and the marginal narrow channel, located at the valve face/mantle junction (arrowhead). Fig. 4f: central area with a small, round isolated pore opening covered by large, triangular structure (arrow)

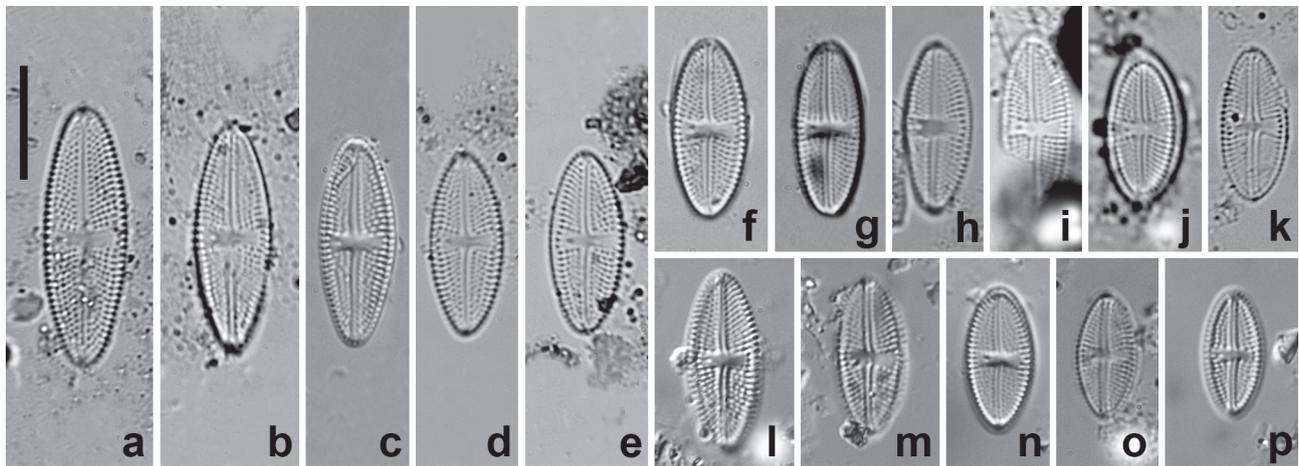


Figure 5a–p

Luticola madagascarensis sp. nov. LM images. Valve views, showing size diminution series. Fig. 5f presents the holotype.

Scale bar = 10 μm

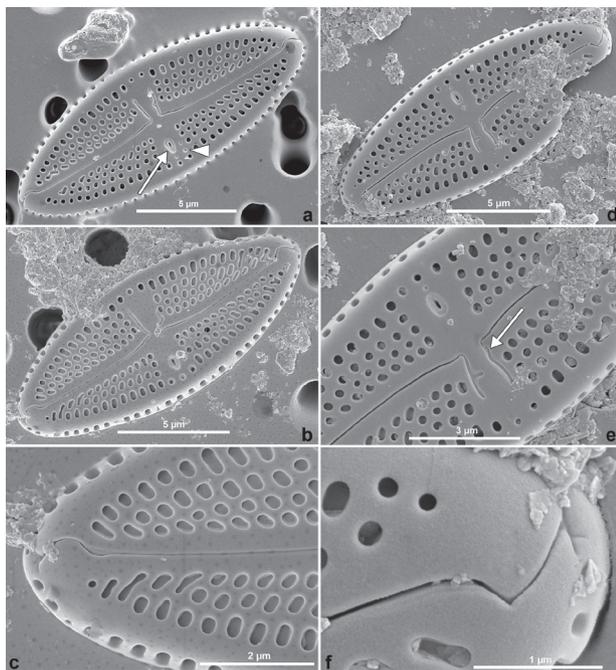


Figure 6a–f

Luticola madagascarensis sp. nov. SEM external valve views. Figs 6a, 6b, 6d: entire valve showing a narrow axial area expanded at the center to form a wide symmetrical, bow-tie shaped fascia on both valve margins. A single isolated pore (arrow in Fig. 6a) is present. Figs 6c, 6f: distal raphe fissures hooked on the same side, extending to the valve mantle. Fig. 6e: proximal raphe endings hooked to the opposite side of the isolated pore, continuing with irregular, shallow, elongated, L-shaped grooves (arrow)

center and valve margin (Fig. 6a, arrow). Few small, round surface depressions (“ghost areolae”) present around the isolated pore (Fig. 6a, arrowhead). Proximal raphe ends elongated, deflected at 90° (Fig. 6e, arrow). Transapical striae composed of 3–4 round to elliptic or slit-like areolae. Distal raphe fissures hooked on the same side (but opposite the proximal raphe endings), extending to the valve mantle.

An internal valve view is not available due to the limited number of specimens.

Type: MADAGASCAR. Nosy Be Island, near Andoany Bay, $13^\circ 24' 0.06''\text{S}$, $48^\circ 17' 8.58''\text{E}$, July 2014, holotype (assigned here): Slide no. 22010 in Coll. of Andrzej Witkowski at the University of Szczecin (SZCZ), represented by Fig. 5f.

Type locality: Andoany Bay, southern coast, Nosy Be Island, Madagascar.

Type habitat: Mangrove roots.

Etymology: The specific epithet refers to the type location, Madagascar.

Distribution: The species has been found so far only in the type locality.

Ecology and associated diatom flora

During sampling (at low tide), the water temperature and salinity were 32.4°C and slightly above 15 PSU, respectively. Based on the salinity value, the environment is considered brackish.

The oxygen saturation and dissolved oxygen content were 76% and 6.6 mg l⁻¹, respectively. The remaining physicochemical measurements are summarized in Table 2.

The sample examined was found to contain a total of 48 diatom taxa. The genera identified included *Nitzschia* Hassall (1845), *Luticola*, *Denticula* Kützing (1844), *Fallacia* Stickle & D.G.Mann (1990), *Giffenia* F.E.Round & Basson (1997), *Diademsis* Kützing (1844), *Humidophila*, *Tryblionela* W.Smith (1853), *Achnanthes* Bory (1822) and *Rhopalodia* Otto Müller (1895). The slide analyzed for the community composition showed that the newly described *Luticola madagascarensis* and *L. nosybeana* account for almost 30% of the diatom valves counted. As the mangrove roots sampled were close to the mouth of a small river, a small proportion of taxa regarded as freshwater-brackish and subaerial were present, including *Humidophila* sp. (7.3%), *Tryblionella debilis* (0.7%) and the newly described *Luticola nosybeana* (27.9%). All the taxa listed above accounted for almost 50% of the diatom assemblage. Taxa representing *Nitzschia* were the second largest group in terms of relative abundance (25%) and included *Nitzschia* sp. 15 (12.3%), *Nitzschia obtusa* W.Smith (1853: 39; 6%), *Nitzschia* sp. 11 (3%), *Nitzschia* sp. 12 (2.7%), and *Nitzschia sigma* (Kützing) W.Smith (1853: 39; 1.3%). The remaining taxa with relative abundance exceeding 1% included: *Luticola madagascarensis* (1.3%), *Denticula* sp. (4%), *Giffenia cocconeiformis* (Grunow) F.E.Round & Basson (1997: 348; 2.7%), *Diademsis* sp. (1.7%), *Giffenia* sp. (1.7%), *Achnanthes* sp. (1.3%), *Fallacia florinae* (M. Møller) Witkowski (1993: 215; 1.3%), and *Rhopalodia brebissonii* Krammer in Lange-Bertalot & Krammer (1987: 76; 1.3%). The Shannon index (H') and the evenness index were 2.67 and 0.6, respectively.

Discussion

Luticola nosybeana and *L. madagascarensis* are similar in the valve outline, but differ in width (up to 7.5 µm in *L. madagascarensis* and up to 10.5 µm in *L. nosybeana*). Under LM, they can be distinguished by the shape of the central area (bow-tie shaped in *L. madagascarensis* and deltoid in *L. nosybeana*) and the isolated pores (while the isolated pore is robust and well visible in *L. madagascarensis*, it is not easily

discernible in *L. nosybeana*). Under SEM, the two species are easily distinguishable due to different shapes and positions of the isolated pores (the external opening in *L. madagascarensis* slit-like, located in a surface depression, positioned halfway between the center and the valve margin; a round opening located close to the valve margin in *L. nosybeana*).

The valve outlines and the shape of the central area in specimens of *L. nosybeana* are remarkably similar to those in *L. belawanensis* Levkov & Metzeltin in Levkov, Metzeltin & A.Pavlov (2013: 74), also described from an island in the Indian Ocean (Sumatra). The two species differ primarily in the stria density, which is higher in *L. nosybeana* (20–24 vs. 18–20 in 10 µm), and the lack of continuation of proximal raphe endings to irregular, shallow grooves, butterfly-like (T-shaped) or insect-antennae-like (L-shaped) in *L. belawanensis*. *Luticola kochiae* Metzeltin in Levkov, Metzeltin & A.Pavlov (2013: 143) and *L. similis* Levkov, Metzeltin & A.Pavlov (2013: 219) differ from both our new species in the valve outline (more elliptic than lanceolate in *L. nosybeana* and *L. madagascarensis*) and, in the case of *L. kochiae*, also in the shape of the central area, larger and wider in *L. kochiae*. The shape of the proximal raphe ends in *L. kochiae* is typically hooked, whereas in *L. nosybeana* they are irregular or butterfly-shaped. The valves of *L. nosybeana* are smaller (length 9–27 µm, width 6.0–10.5 µm) than those of *L. kochiae* (14.5–33.0 and 8.0–14.5 µm). The shape of the central area in *L. similis* is different, more rectangular vs. deltoid, and the valves are more lanceolate, compared to those of *L. nosybeana* (elliptic). Moreover, *L. kochiae* and *L. similis* are known only from their type localities in Columbia and New Caledonia, respectively. In terms of the valve outline, *L. nosybeana* is also similar to a taxon shown in Levkov et al. (2013: 499) as "*Luticola* sp. aff. *permuticoides* Metzeltin & Lange-Bertalot" from Brazil, but differs in the shape of the central area (more rectangular in Levkov's taxon) and in the proximal raphe ends (typically hooked and distant from each other in *Luticola* sp. aff. *permuticoides*).

The valve shape and striae arrangement in *L. nosybeana* are similar to those in many other *Luticola* species, e.g. *L. hlubikovae* Levkov, Metzeltin & A.Pavlov (2013: 130); smaller valves are in *L. saprophila* Levkov, Metzeltin & A.Pavlov (2013: 212), *L. wetzellii* Levkov, Metzeltin & A.Pavlov (2013: 257) and *L. isabellae*

Table 2

Physicochemical parameters of water recorded at the study site on Nosy Be Island during sampling

Temp. °C	pH	ORP mV	DO mg l ⁻¹	O %	TDS mg l ⁻¹	Salinity PSU	Atm. pressure mbar
32.4	6.9	-104	6.6	76	44	15.3	1016.5

Metzeltin & Levkov in Levkov, Metzeltin & A.Pavlov (2013: 140); however, these can be distinguished from *L. nosybeana* under both LM and SEM. Differences between these other *Luticola* taxa and *L. nosybeana* involve mostly shapes of the central area (which can be asymmetrical, deltoid or rectangular) and the external, round opening of the isolated pore located close to the valve margin in *L. nosybeana*, which is indiscernible under LM, but is robust and well visible in all similar taxa listed above. None of the similar taxa shows L- or T-shaped central raphe endings like those in *L. nosybeana*.

The valve outlines in the specimens of *L. madagascarensis* examined in this study are similar to those in *L. similis* described from New Caledonia. Both species have similar dimensions and densities of striae. The two species differ in their proximal raphe ends, which are short and expanded into small central pores in *L. similis*, while continue with irregular, shallow, elongated, L-shaped grooves in *L. madagascarensis*; the latter species is also characterized by a clearly visible elongated isolated pore. The proximal raphe fissures are bent in the opposite direction relative to the distal endings in *L. madagascarensis*. The two species differ also in their ecological preferences: *L. similis* was found in freshwater, a highly eutrophic and polluted environment (a tributary of the Hienghène River), while *L. madagascarensis* occurred in mangrove-associated water with salinity of 15 PSU. *Luticola frequentissima* Levkov, Metzeltin & A.Pavlov (2013: 112) shows similar proximal raphe endings, but they are shorter, more variable in shape, widened at the end, and pointing to the same side as distal endings (Noga et al. 2017). The distal fissures terminate on the valve face (not on the valve mantle as in *L. madagascarensis*), and the isolated pore of *L. frequentissima* is rounded and located near the valve margin, as opposed to the slit-like isolated pore located halfway between the valve center and valve margin in *L. madagascarensis*.

With regard to the valve outline, the shape of the valve apices and striation, *L. madagascarensis* resembles most closely several other *Luticola* species, such as *L. tomesii* Moser, Lange-Bertalot & Metzeltin (1998: 198), *L. pseudoimbricata* Levkov, Metzeltin & A.Pavlov (2013: 193) and *L. wetzelii*. The new species can be distinguished by narrowly rounded apices and proximal raphe endings located close to each other, which in *L. madagascarensis* continue as irregular, shallow, elongated grooves. Also, the species mentioned above differ in their ecology, particularly their salinity preference: *L. madagascarensis* was found on mangrove roots in water with salinity of 15 PSU, while other species were reported from freshwater environments.

In *L. nosybeana*, the isolated pore openings from the exterior to the interior are displaced; externally, the isolated pore opening is located near the margin, while internally, the isolated pore opening is located halfway between the valve margin and valve center. This is a relatively distinctive feature of the species. The only other *Luticola* taxa showing this arrangement include *L. voigtii* (Meister) D.G.Mann in Round et al. (1990: 671) and *L. galapagoensis* Witkowski, Bąk, Kociolek, Lange-Bertalot & Seddon in Bąk et al. (2017: 203) – both tropical brackish-water species.

The genus *Luticola* is usually regarded as freshwater and has been frequently reported from inland waters and associated habitats (mostly aerophilous environments). Hustedt (1964) and Levkov et al. (2013) refer to (and describe) several species from brackish-water habitats, mostly in the tropics. It would be interesting to find out whether the ecological preferences of the species, and thus the distribution, are related to its phylogeny.

Finally, the species of *Luticola* described in this paper, for which we were able to observe the valve interior, i.e. *L. nosybeana*, is characterized by canals developed around the internal margins (see Fig. 4a–e), a feature common to most *Luticola* species described to date (e.g. Metzeltin et al. 2005; Levkov et al. 2013; Bąk et al. 2017; Glushchenko et al. 2017; Straube et al. 2017). In the species from Madagascar, however, these canals are not well developed, and – as opposed to other *Luticola* taxa (e.g. *L. uruguayensis* Metzeltin, Lange-Bertalot & García-Rodríguez, 2005: 118) – not conspicuous on one side of the central area. Further research on this interesting genus is necessary to understand whether the difference in the size of the marginal canals, as well as the distinctive external proximal raphe endings present in the two new species described from Madagascar have ecological, biogeographic and/or phylogenetic significance.

Conclusions

The study involved materials collected from mangrove roots at the coast of Nosy Be, a virtually unexplored tropical island off NW Madagascar. The materials contained numerous unidentified taxa from exposed habitats, including *Humidophila* and *Luticola*. Two taxa of *Luticola* described here, *L. nosybeana* and *L. madagascarensis*, are new to science, which was confirmed by LM and SEM examination and comparisons with already known taxa. The comparisons show that the newly described species are different in terms of their morphology (valve shape, raphe structure, isolated pore location

and structure) and dimensions. Importantly, they also differ in terms of habitat, with *L. nosybeana* and *L. madagascarensis* inhabiting the mangrove roots of brackish waters, whereas all similar taxa live in freshwaters. Research on the mangrove root materials is ongoing and aims to explore the whole diversity of diatoms of this important habitat.

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References

- Bąk, M., Kociolek, J.P., Lange-Bertalot, H., Łopato, D., Witkowski, A. et al. (2017). Novel diatom species (Bacillariophyta) from the freshwater discharge site of Laguna Diablas (Island Isabela = Albemarle) from the Galapagos. *Phytotaxa* 311(3): 201–224. DOI: 10.11646/phytotaxa.311.3.1.
- Battarbee, R.W. (1986). Diatom analysis. In B.E. Berglund (Ed.), *Handbook of Holocene Palaeoecology and Palaeohydrology* (pp. 527–570). Chichester, UK: Wiley & Sons.
- Besairie, H. (1968–69–71). *Description géologique du massif ancien de Madagascar*. Tananarive, Madagascar: Doc. Bureau Géologique de Tananarive.
- Bodén, P. (1991). Reproducibility in the random setting method for quantitative diatom analysis. *Micropalontology*. 37(3): 313–319. DOI:10.2307/1485893.
- Chattová, B., Lebouvier, M., de Haan, M. & Van de Vijver, B. (2017). The genus *Luticola* (Bacillariophyta) on Ile Amsterdam and Ile Saint-Paul (Southern Indian Ocean) with the description of two new species. *Eur. J. Taxon.* 387: 1–17. DOI: 10.5852/ejt.2017.387.
- Collins, A.S. & Windley, B.F. (2002). The tectonic evolution of central and northern Madagascar and its place in the final assembly of Gondwana. *J. Geol.* 110: 325–339. DOI: 10.1080/09670260903560076.
- Coste, M. & Ricard, M. (1984). A systematic approach to the Freshwater Diatoms of Seychelles and Mauritius Islands. In V. Cassie (Ed.), *Proceedings of the Seventh International Diatom Symposium*. *Phycologia* 24(2): 307–326. DOI: 10.2216/i0031-8884-24-2-254.1.
- Foged, N. (1975). *Some Littoral Diatoms from the Coast of Tanzania*. Bibliotheca Phycologica. Band 16.
- Glushchenko, A.M. & Kulikovskiy, M.S. (2015). Species of the genus *Luticola* in waterbodies of Laos and Vietnam. *Bot. Z.* 100(8): 799–804. (In Russian).
- Glushchenko, A.M., Kulikovskiy, M.S. & Kociolek, J.P. (2017). New and interesting species from the genus *Luticola* (Bacillariophyceae) in waterbodies of Southeastern Asia. *Nova Hedwigia*. 146: 157–173. DOI: 10.1127/1438-9134/2017/157.
- Guiry, M.D. in Guiry, M.D. & Guiry, G.M. (2017). *AlgaeBase. World-wide electronic publication*. Retrieved November 28, 2017, from <http://www.algaebase.org>.
- Hustedt, F. (1964). Die Kieselalgen Deutschlands, Österreichs und der Schweiz unter Berücksichtigung der übrigen Länder Europas sowie der angrenzenden Meeresgebiete. In L. Rabenhorst (Ed.), *Kryptogamen Flora von Deutschland, Österreich und der Schweiz* (pp. 557–816). Leipzig, Germany: Akademische Verlagsgesellschaft m.b.h.
- Klee, R., Houk, V. & Bielsa, S. (2000). *Cyclotella mascarenica* nov. spec., a new stelligeroid *Cyclotella* (Bacillariophyceae) from a pond of the Réunion Island (France). *Arch. Hydrobiol. Suppl. Algol. Stud.* 98: 7–25.
- Kociolek, J.P., Kopalová, K., Hamsher, S.E., Kohler, T.J., Van de Vijver, B. et al. (2017). Freshwater diatom biogeography and the genus *Luticola*: an extreme case of endemism in Antarctica. *Polar Biol.* 40(6): 1185–1196. DOI:10.1007/s00300-017-2090-7.
- Kohler, T.J., Kopalová, K., Van de Vijver, B. & Kociolek, J.P. (2015). The genus *Luticola* D.G.Mann (Bacillariophyta) from the McMurdo Sound Region, Antarctica, with the description of four new species. *Phytotaxa* 208: 103–134. DOI:10.11646/phytotaxa.208.2.1.
- Kryk, A. (2016). *Taxonomy and biodiversity of diatom assemblages of coral reefs of Nosy Be island and NW Madagascar*. Unpublished master's thesis. Szczecin, Poland: Faculty of Geosciences, University of Szczecin. (In Polish).
- Levkov, Z., Metzeltin, D. & Pavlov, A. (2013). *Luticola* and *Luticolopsis*. In H. Lange-Bertalot (Ed.), *Diatoms of Europe 7*. Koenigstein, Germany: Koeltz Scientific Books.
- Melluso, L. & Morra, V. (2000). Petrogenesis of Late Cenozoic mafic alkaline rocks of the Nosy Be archipelago northern Madagascar: relationships with the Comorean magmatism. *J. Volcanol. Geoth. Res.* 96: 129–142. DOI: 10.1016/S0377-0273(99)00139-0.
- Metzeltin, D. & Lange-Bertalot, H. (1998). Tropical diatoms of

- South America I: About 700 predominantly rarely known or new taxa representative of the neotropical flora. In H. Lange-Bertalot (Ed.), *Iconographia Diatomologica* 5. Ruggell, Liechtenstein: A.R.G. Gantner Verlag Kommanditgesellschaft.
- Metzelin, D. & Lange-Bertalot, H. (2002). Diatoms from the "Island Continent" Madagascar. In H. Lange-Bertalot (Ed.), *Iconographia Diatomologica* 11. Ruggell, Liechtenstein: A.R.G. Gantner Verlag Kommanditgesellschaft.
- Metzeltin, D., Lange-Bertalot, H. & Garcia-Rodrigues, F. (2005). Diatoms of Uruguay. Compared with other taxa from South America and elsewhere. In H. Lange-Bertalot (Ed.), *Iconographia Diatomologica* 15. Ruggell, Liechtenstein: A.R.G. Gantner Verlag Kommanditgesellschaft.
- Moser, G., Lange-Bertalot, H. & Metzeltin, D. (1998). Insel der Endemiten Geobotanisches Phänomen Neukaledonien (Island of endemics New Caledonia – a geobotanical phenomenon). *Bibl. Diatomol.* 38: 1–464.
- Noga, T., Stanek-Tarkowska, J., Kochman-Kędziora, N., Rybak, M., Peszek, Ł. et al. (2017). *Luticola frequentissima* Levkov, Metzeltin & Pavlov – morphological and ecological characteristics of a population from Southern Poland. *Oceanol. Hydrobiol. St.* 46(2): 237–243. DOI: 10.1515/ohs-2017-0024.
- Riaux-Gobin, C. & Compère, P. (2008). New *Cocconeis* taxa (Bacillariophyceae) from coral sands of Réunion Island (Western Indian Ocean). *Diatom Research* 23: 129–146. DOI: 10.1080/0269249X.2008.9705742.
- Riaux-Gobin, C., Compère, P. & Al-Handal, A.Y. (2011a). The genus *Amphicocconeis* (Bacillariophyta) from coral sands off Mascarenes (Western Indian Ocean). *Diatom Res.* 26(2): 175–188. DOI: 10.1080/0269249X.2011.597958.
- Riaux-Gobin, C., Romero, O.E., Al-Handal, A.Y. & Compère, P. (2010a). Two new *Cocconeis* taxa (Bacillariophyceae) from coral sand off Mascarenes (Western Indian Ocean) and some related unknown taxa. *Eur. J. Phycol.* 45: 278–292. DOI: 10.1080/09670260903560076.
- Riaux-Gobin, C., Romero, O.E., Compère, P. & Al-Handal, A.Y. (2011b). Small-sized *Achnanthes* (Bacillariophyta) from coral sands off Mascarenes (Western Indian Ocean). *Bibl. Diatomol.* 57.
- Riaux-Gobin, C., Witkowski, A. & Compère, P. (2010b). SEM survey and taxonomic position of small-sized *Achnantidium* (Bacillariophyceae) from coral sands off Réunion Island (Western Indian Ocean). *Vie et Milieu.* 60: 157–172.
- Round, F.E., Crawford, R.M. & Mann, D.G. (1990). *The diatoms Biology and morphology of the genera*. Cambridge, UK: Cambridge University Press.
- Shannon, C.E. (1948). A Mathematical Theory of Communication. *Bell Syst. Tech. J.* 27(4): 623–666. DOI: 10.1002/j.1538-7305.1948.tb00917.x.
- Smith, W. (1853). *A synopsis of the British Diatomaceae; with remarks on their structure, function and distribution; and instructions for collecting and preserving specimens*. London, UK: John van Voorst. DOI: 10.5962/bhl.title.10706.
- Straube, A., Tremarin, P.I. & Ludwig, T.A.V. (2017). Species of *Luticola* D.G. Mann (Bacillariophyceae) in the Atlantic Forest rivers from southern Brazil. *Diatom Res.* 32(4): 417–437. DOI: 10.1080/0269249X.2017.1389771.
- Tuomisto, H. (2012). An updated consumer's guide to evenness and related indices. *Oikos.* 121: 1203–1218. DOI: 10.1111/j.1600-0706.2011.19897.x.
- Witkowski, A. (1993). *Fallacia florinae* (Møller) *comb. nov.*, a marine epipsammic diatom. *Diatom Res.* 8(1): 215–219. DOI: 10.1080/0269249X.1993.9705254.
- Wu, S.C. & Bergey, E.A. (2017). Diatoms on the carapace of common snapping turtles: *Luticola* spp. dominate despite spatial variation in assemblages. *PLoS One* 12(2): e0171910. DOI:10.1371/journal.pone.0171910.
- Zidarova, R., Levkov, Z. & Van de Vijver, B. (2014). Four new *Luticola* taxa (Bacillariophyta) from Maritime Antarctica. *Phytotaxa* 170: 155–168. DOI: 10.11646/phytotaxa.170.3.2.