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New and interesting small-celled naviculoid diatoms (Bacillariophyceae) from a lava tube cave on Île Amsterdam (TAAF, Southern Indian Ocean)

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Abstract – The analysis of a sample taken in a lava tube cave on Île Amsterdam (southern Indian Ocean) revealed the presence of three interesting small-celled naviculoid diatom taxa. Based on light and detailed scanning electron microscopy, two of these taxa are described as new: *Mayamaea cavernicola* sp. nov. and *Sellaphora barae* sp. nov.
A third taxon, *Chamaepinnularia aerophila* Van de Vijver *et* Beyens, was previously only found in the type locality on the nearby Crozet Archipelago. The three taxa are compared to other morphologically similar species from Europe, South America and the (sub-)Antarctic Region.

Bacillariophyceae / *Chamaepinnularia* / Île Amsterdam / new species / *Mayamaea* / *Sellaphora* / sub-Antarctica

Résumé – Durant l'analyse d'un échantillon récolté dans une caverne de lave sur l'Île Amsterdam (Océan Indien austral), trois taxons naviculoïdes intéressants de petite taille ont été observés. Sur la base d'observations en microscopie optique et électronique à balayage, *Mayamaea cavernicola* sp. nov. and *Sellaphora barae* sp. nov. ont été décrits comme nouveaux taxons. Un troisième taxon, *Chamaepinnularia aerophila* Van de Vijver & Beyens avait auparavant seulement été trouvé dans la localité type sur l'Archipel de Crozet situé à proximité. Les nouveaux taxons sont comparés avec des taxons morphologiquement similaires de l'Europe, de l'Amérique du Sud et de la Région sub-antarctique.

Bacillariophyceae / *Chamaepinnularia* / Île Amsterdam / Nouvelles espèces / *Mayamaea* / *Sellaphora* / sub-Antarctique

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INTRODUCTION

Diatoms are able to survive in the most diverse microhabitats, ranging from submerged substrata in typically aquatic habitats such as lakes and rivers (Lange-Bertalot & Metzeltin, 1996), to epiphytic on terrestrial mosses (Hickman & Vitt, 1973; Van de Vijver & Beyens, 1999), in soils (Van de Vijver *et al.*, 2002a; Moravcová *et al.*, 2010), or on wet walls (Denys & De Smet, 1996; Johansen, 2010). Several genera are even found living epizoically on whales (Denys, 1997) and turtles (Wetzel *et al.*, 2012).

An interesting microhabitat occurs in lava tubes, formed during recent eruptions of shield volcanoes, when massive flows of lava are released (Bunnell, 2008). These tubes are created when flowing lava, often several meters thick, cools at its surface forming a crust over the still flowing lava stream below. As the lava flow subsides, a channel remains below the crust resulting in a hollow cave-like tube. Subsequent erosion causes these tubes to collapse, resulting in a series of small caves and caverns where light and water (often rain or humidity) provide the conditions for algal colonization. On several islands, such as the Hawaiian islands and Île Amsterdam, lava tubes seem to present unique microhabitats that apparently harbour many unique endemic species and are perhaps some of the least anthropogenically impacted habitats (Lowe & Sherwood, 2010). Rushforth et al. (1984) investigated the subaerial diatom flora collected from wet mucilage and bryophytes on walls in the Thurston Lava Tube, Hawaii.

In a sample taken from a collapsed lava tube on Île Amsterdam, a small island in the southern Indian Ocean, several interesting small-celled naviculoid diatoms were found.

Previously all placed within the catch-all genus *Navicula* s.l., most small-celled naviculoid diatoms are now classified in a large number of (sometimes recently erected) genera such as *Eolimna* Lange-Bertalot *et* Schiller in Schiller & Lange-Bertalot (1997), *Mayamaea* Lange-Bertalot and *Fistulifera* Lange-Bertalot (Lange-Bertalot, 1997), *Sellaphora* Mereschkowsky (Mereschkowsky, 1902), *Chamaepinnularia* Lange-Bertalot *et* Krammer in Lange-Bertalot *et* Metzeltin (1996), *Geissleria* Lange-Bertalot *et* Metzeltin (Lange-Bertalot *et* Metzeltin, 1996) or *Navigolum* Lange-Bertalot, Cavacini, Tagliavento & Alfinito (Lange-Bertalot *et al.*, 2003).

Two of the observed taxa in the lava tube sample could not be identified using the currently available literature and are described as new species: *Sellaphora barae* sp. nov. and *Mayamaea cavernicola* sp. nov. A third small-celled diatom was previously described from the nearby Crozet archipelago as *Chamaepinnularia aerophila* Van de Vijver *et* Beyens (Van de Vijver *et al.*, 2002b). Based on light and scanning electron microscopy, the morphological features of the three species are illustrated, comparing them to similar small-celled naviculoid species elsewhere.

STUDY SITE

Île Amsterdam (77°34′E, 37°47′S) is a small, volcanic island situated in the southern part of the Indian Ocean, halfway between the African continent and Australia. With a total surface area of only 55 km^2, this small island is one of

the most remote places in the world. Together with the nearby Île Saint-Paul, the island forms a separate district within the Terres Australes Antarctiques Françaises (TAAF). Geologically spoking, this entirely volcanic island is very young, probably formed within the last 700,000 years (Doucet *et al.*, 2003) and having the shape of a small cone rising to 881 m a.s.l. (Mont de la Dives). The climate is temperate oceanic (Frenot & Valleix, 1990) with a mean annual temperature of 13.8°C with minimum and maximum temperatures of 11.2°C (August) and 17.0°C (February) respectively (Lebouvier & Frenot, 2007). Relative humidity is generally high due to the frequency of low cloud cover, varying between 80% and 82.9% throughout the year. Precipitation is usually high with an annual average of 1,114 mm distributed over 239 days, falling primarily as rain. Permanent waterbodies are scarce and restricted to the higher plateau in the centre of the island (Plateau des Tourbières) and the W-SW part of the island (Aptroot et al. 2011). Almost all other areas do not have (semi-)permanent waterbodies due to the steepness of the slopes and the permeability of the lava tunnels, holes and fissures. The largest lava tunnel on the island probably originated from the eruption of the Cratère de Vénus Inférieur (Lower Venus Crater) (ca. 400 m alt.), extending almost to the Indian Ocean, 2 km away. In several places, the lava tunnel collapsed resulting in a series of large open depressions and small caves in which luxuriant vegetation developed, composed of ferns, grasses, mosses and the endemic tree *Phylica nitida* Lam. More information on Île Amsterdam can be found in Aptroot *et al.* (2011) and Van de Vijver *et al.* (2012).

MATERIAL & METHODS

During the austral summer of 2007-2008, an extensive sampling campaign was undertaken on the island, aiming to better document the diatom biodiversity of Île Amsterdam. Several samples were taken in accessible caverns of the collapsed Grand Tunnel. One sample proved to have a quite diverse, species-rich diatom flora and was used for the study of the small-celled naviculoid taxa in the present paper: AMS-W033 (37°48′47.1″ S, 077°33′42.6″ E).

A small sub-sample of AMS-W033 was prepared for LM observation 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 $KMnO_4$. Following digestion and centrifugation (three times 10 minutes at 3700 × g), cleaned material was diluted with distilled water to avoid excessive concentrations of diatom valves on the slides. Cleaned diatom material was mounted in Naphrax®. For scanning electron microscopy (SEM), part of the cleaned suspension was pipetted onto small coverglasses glued to aluminium stubs, and sputter coated with a 20 nm thick layer of gold-palladium. Observations and photomicrography were performed at the Natural History Museum in London (UK) using a Zeiss® Ultra plus scanning electron microscope at 3 kV. Sample, slide and stub are stored at BR (National Botanic Garden of Belgium, Meise, Belgium), abbreviations following the Index Herbariorum (http://sciweb.nybg.org/science2/IndexHerbariorum.asp).

Terminology follows Hendey (1964), Cox & Ross (1981), Mann (1981) and Round *et al.* (1990). Comparisons are mostly based on Lange-Bertalot & Metzeltin (1996), Wydrzycka & Lange-Bertalot (2001), Van de Vijver *et al.* (2002b), Werum & Lange-Bertalot (2004) and Kulikovskiy *et al.* (2010).

RESULTS

Species descriptions

***Chamaepinnularia aerophila* Van de Vijver *et* Beyens** **Figs 1-20**

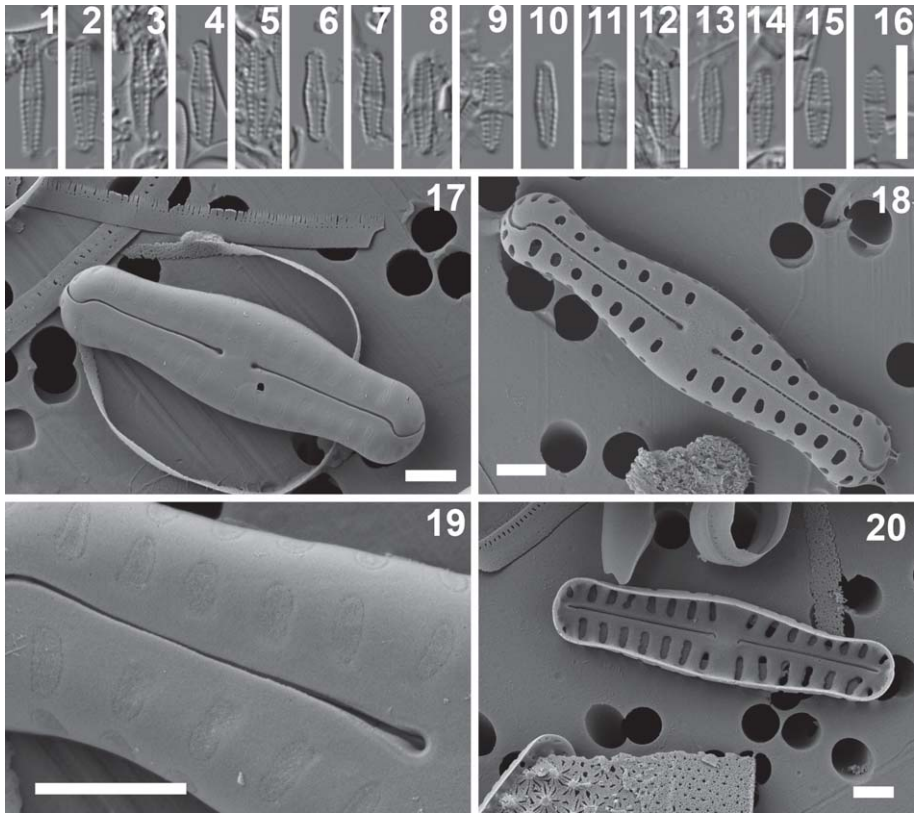
Morphological observations: Valves lanceolate to linear-lanceolate with a usually inflated central part and capitate to subcapitate, broadly rounded apices (Figs 2-16). Valves with less protracted apices rarely observed (Fig. 1). Valve length 7-12 µm, width 1.5-2.1 µm (n = 25). Axial area moderately broad ($^1/_3$ to almost $^1/_2$ of the valve width), linear to linear-lanceolate. Central area forming a rectangular, rather broad fascia lacking any shortened striae near the valve margin (Figs 17, 18). Raphe filiform with droplike expanded straight proximal raphe endings and sickle-shaped distal raphe endings, continuing onto the valve mantle (Figs 17, 18). Internally, proximal raphe endings deflected (Fig. 20), and distal endings terminating in small helictoglossae (Fig. 20). Transapical striae parallel to very weakly radiate throughout the entire valve, becoming slightly convergent towards the apices, 15-20 in 10 µm. Virgae wider than the striae (Fig. 19). Striae interrupted near the valve face/mantle junction (Figs 17, 18), composed of a single large (relative to valve size) areola (Figs 18, 20), covered on the outside by a porous hymen (Figs 17, 19).

***Mayamaea cavernicola* sp. nov.** **Figs 21-40**

Descriptions: *Valvae late lanceolatae ad stricte lanceolatae marginibus convexis apicibusque protractis, rostratis. Valvae minors plusminusve ellipticae apicibus late rotundatis, non-protractis. Longitudo 6.5-12 µm, latitudo 2.8-3.2 µm. Area axialis angusta, linearis. Area centralis rectangularis, marginita 2-3 striis abbreviatis. Raphe filiformis terminationibus proximalibus leviter deflexis, fissurisque distalibus uncinatis. Striae leviter radiatae omnino, non convergentes ad apices, 26-28 in 10 µm.*
Type: Grand Tunnel, Île Amsterdam, TAAF sample AMS-W033, leg. B. Van de Vijver, coll. date 04/12/2007, slide no. BR-4268 (holotype BR), slide PLP-212 (isotype University of Antwerp, Belgium), slide ZU8/58 (isotype BRM).
Etymology: The specific epithet refers to the habitat of the new species (Latin *caverna* = cave, *-cola* = living in).
Morphological observations: Valves broadly lanceolate to strictly lanceolate with clearly convex margins and gradually tapering, slightly protracted broadly rostrate apices (Figs 21-35). Smaller valves have a more elliptical outline with broadly rounded, unprotracted apices (Fig. 36). Valve length 6.5-12.0 µm, width 2.8-3.2 µm (n = 25). Axial area narrow, linear. Central area rectangular to wedge-shaped, bordered by 2-3 shorter striae (Figs 37, 38). Raphe filiform with short, weakly deflected, hardly expanded external proximal raphe endings and hooked external distal raphe fissures (Figs 37, 38). Internally, proximal raphe endings clearly deflected (Fig. 40). Distal raphe endings terminating in small helictoglossae (Fig. 40). Transapical striae weakly radiate throughout the entire valve, not becoming convergent towards the apices, 26-28 in 10 µm. Striae composed of rounded areolae, covered externally by porous hymenes. Striae interrupted by a hyaline line (Figs 37, 39) at the valve face/mantle junction. Areolae sometimes lacking near the central area, giving the impression of the presence of hyaline areas on the valve face (Figs 39, 40).

***Sellaphora barae* sp. nov.** **Figs 41-57**

Descriptions: Valvae lineares-lanceolatae ad late lanceolatae marginibus clare convexis apicibusque protractis, rostratis, late rotundatis. Longitudo 7.0-16.5 µm,

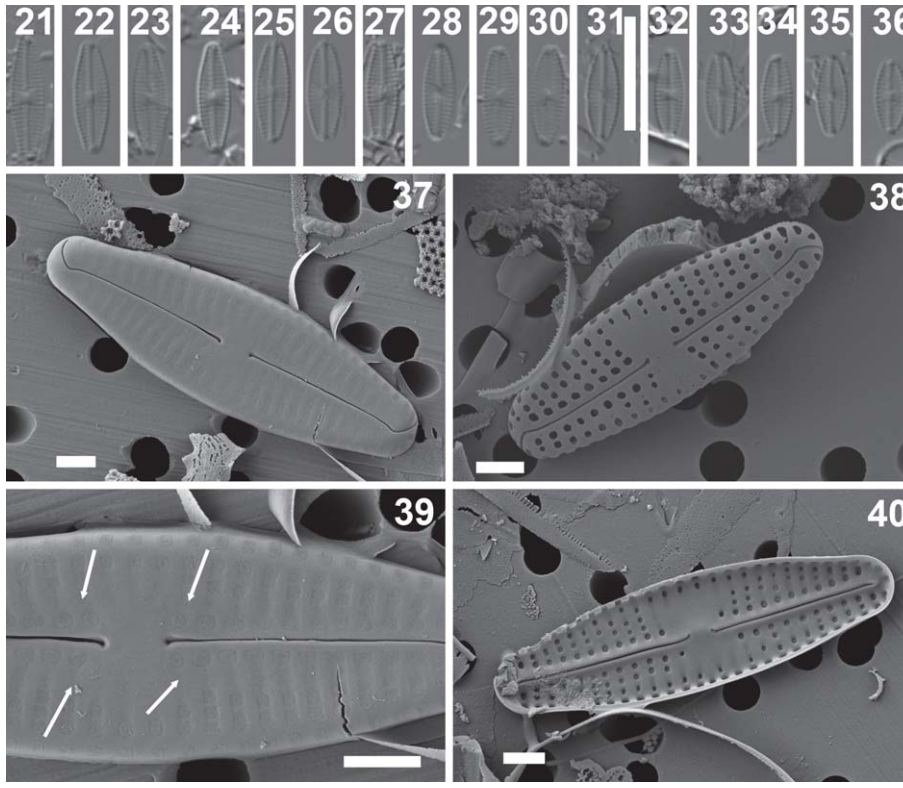


Figs 1-20. *Chamaepinnularia aerophila* Van de Vijver & Beyens. **1-16.** LM observations showing the morphological variability of the species in the lava tube cave sample of Île Amsterdam. **17.** SEM external observation of a non-eroded valve showing the raphe structure and the striae with hymenate occlusions. **18.** SEM external observation of an eroded valve with a clear view of the large, elongated areolae. Note the interruption near the valve face/mantle junction. **19.** SEM external observation of a detail of the stria structure with the hymenate occlusions. **20.** SEM internal observation of an entire valve. Scale bar represents 10 µm except for Figs 17-20 where scale bar = 1 µm.

latitudo 3.6-4.4 µm. Area axialis moderate lata. Raphesternum angusta, marginata fissuris angustis longitudinalibus. Area centralis rectangularis marginata pluribus striis abbreviatis. Raphe filiformis, leviter undulate, terminationibus proximalibus leviter deflexis expansibusque. Fissurae distales flexae, terminatae in faciei valvae. Striae leviter radiatae ad parallelae, non-convergentes in apices, 22-24 in 10 µm. Striae biseriatae in limbo propeque margines, uniseriatae in aream axialem. Areolae aliqando vacant in striis.

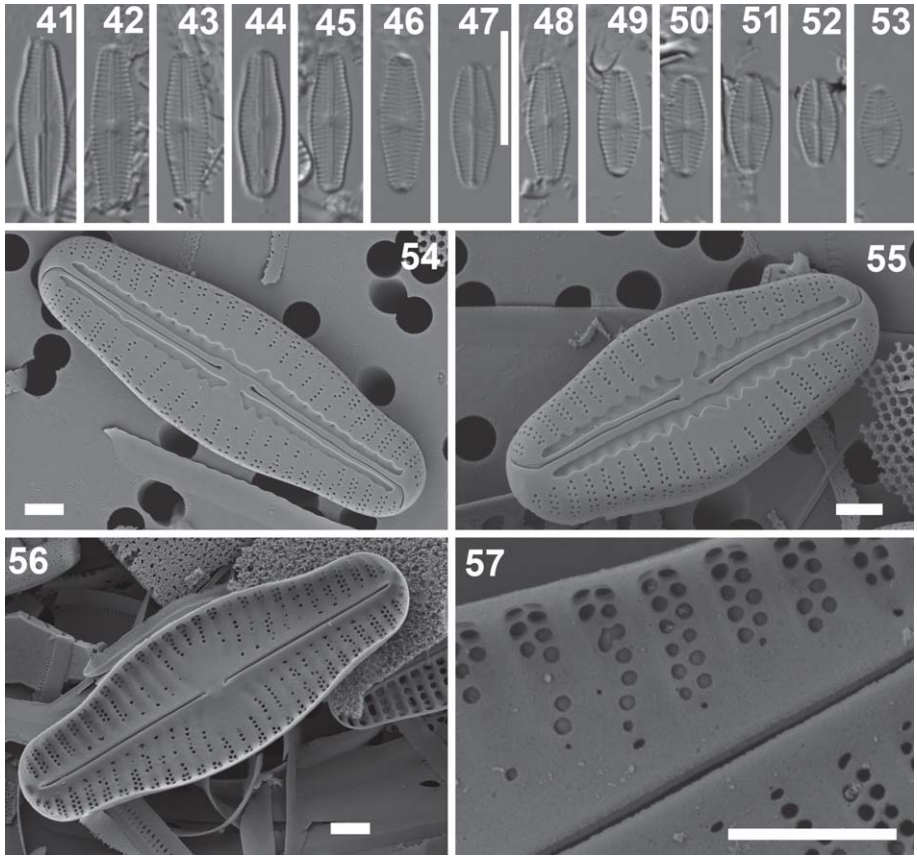
Type: Grand Tunnel, Île Amsterdam, TAAF sample AMS-W033, leg. B. Van de Vijver, coll. date 04/12/2007, slide no. BR-4269 (holotype BR), slide PLP-213 (isotype University of Antwerp, Belgium), slide ZU8/59 (isotype BRM).

Etymology: The species is named after our colleague Mgr. Barbora ('Bara') Chattová (Masaryk University Brno, Czech Republic) who has conducted research on freshwater diatom communities of Île Amsterdam.



Figs 21-40. *Mayamaea cavernicola* sp. nov. **21-36.** LM observations of the type population showing the morphological variability of the species in the lava tube cave sample of Île Amsterdam. **37.** SEM external observation of a non-eroded valve showing the raphe structure and areolae with hymenate occlusions. **38.** SEM external observation of an eroded valve in which the hymenate occlusions of the areolae have been lost. **39.** SEM external observation of a detail of the areolae with the hymenate occlusions. Note the absence of some areolae in the striae (see arrows). **40.** SEM internal observation of an entire valve. Scale bar represents 10 µm except for Figs 37-40 where scale bar = 1 µm.

Morphological observations: Valves linear-lanceolate to broadly lanceolate with clearly convex margins and protracted, broadly rounded, slightly rostrate ends (Figs 41-53). Valve length 7.0-16.5 µm, width 3.6-4.4 µm (n = 25). Axial area rather broad (relative to the valve width), formed by a narrow raphe sternum bordered by narrow, longitudinal grooves with indented distal margins (Figs 54, 55). Central area rectangular to wedge-shaped bordered by several shortened striae at the valve margin (Figs 54, 55). Raphe filiform, slightly undulating with weakly deflected, slightly drop-like expanded external proximal raphe endings (Figs 54, 55). External distal raphe fissures bent, rather long but terminating on the valve face. Internally, proximal raphe endings short, hardly deflected (Fig. 56). Distal raphe endings terminating in small helictoglossae (Fig. 56). Transapical striae weakly radiate becoming parallel, not convergent near the valve apices, 22-24 in 10 µm (Figs 41-53). Striae showing an irregular areola pattern: biseriate on the mantle and near the valve margin, becoming gradually uniseriate towards the axial area



Figs 41-57. *Sellaphora barae* sp. nov. **41-53.** LM observations of the type population showing the morphological variability of the species in the lava tube cave sample of Île Amsterdam. **54.** SEM external observation of a non-eroded valve showing the raphe structure, the longitudinal grooves and the areolae. Note the irregular areola pattern in some striae. **55.** SEM external observation of a non-eroded valve. The striae appear more regular, uniseriate near the axial area becoming biseriate towards the margin. **56.** SEM internal observation of an entire valve. **57.** SEM internal observation of a detail of the striae. Scale bar represents 10 μm except for Figs 53-57 where scale bar = 1 μm.

(Figs 54-56). Striae often interrupted by missing areolae (Figs 54, 56), internally flanked by raised virgae (Fig. 56). Areolae appearing externally as large, rounded openings (Fig. 57), no internal pore occlusions observed (Fig. 57). No internal expression of the longitudinal external groove visible (Fig. 56).

Habitat and Distribution

The lava cavern in which the three species were found is part of the partly collapsed Grand Tunnel, running from the Cratère de Vénus inférieur to the northern Indian Ocean coast. The sample was taken from the bottom of a small, shallow pool (diameter 30 cm, maximum depth 5 cm) at the end of a small cavern. The entire cavern is only sparsely illuminated and vegetated by mosses,

liverworts and small ferns. The pool, part of a series of small pools, is continuously fed by water dripping from the cavern's ceiling, and has a pH of 5.8, and specific conductance of 239 µS cm^{-1}.

The sample was dominated by several *Diadesmis* species (a.o. *D. vidalii* Van de Vijver & Ledeganck and *D. crozetikerguelensis* Le Cohu & Van de Vijver), *Planothidium lanceolatum* (Brébisson) Lange-Bertalot, *Karayevia oblongella* (Østrup) Aboal in Aboal *et al.*, *Melosira dickiei* (Thwaites) Kützing and several unidentified centric taxa belonging to different genera such as *Orthoseira* and an at present undescribed new genus (Van de Vijver *et al.*, unpubl. data).

Chamaepinnularia aerophila and *Mayamaea cavernicola* have already been observed in small caves on Île de la Possession, the main island of the nearby Crozet Archipelago (Van de Vijver *et al.*, 2002b, Van de Vijver pers. obs.). *Sellaphora barae* has so far not been observed in these samples. *Mayamaea cavernicola* could perhaps also be present in a lava tube cave on the Hawaiian Islands and has probably been illustrated in LM by Rushforth *et al.* (1984, Figs 97-99) under the incorrect name *Navicula seminulum* Grunow var. *hustedtii* Patrick.

DISCUSSION

The population of *Chamaepinnularia aerophila* from Île Amsterdam shows some minor differences compared to the type population from the Crozet Archipelago. Van de Vijver *et al.* (2002b) reported a valve width of 2-3 µm whereas narrower valves have been observed (up to 1.5 µm) on Île Amsterdam. The valves are also shorter on Île Amsterdam (7-12 µm *vs* 11-17 µm on Crozet). A higher stria density was observed on smaller valves but this is not an uncommon phenomenon. Van de Vijver *et al.* (2006) reported a similar finding for *Luticola higleri* Van de Vijver *et al.* The valves of *Chamaepinnularia aerophila* from Île de la Possession have somewhat less capitate apices than those from Île Amsterdam, although some more capitate forms occur there (Van de Vijver *et al.*, 2002b, plate 63, Figs 1-11). Since a large number of valves were found with intermediate morphological features between both populations and given the similar habitats, the populations are considered conspecific. *Chamaepinnularia aerophila* can be separated from similar small-celled *Chamaepinnularia* taxa, such *C. muscicola* (J.B. Petersen) Kulikovskiy *et al.*, *C. hassiaca* (Krasske) Cantonati *et* Lange-Bertalot and *C. soehrensis* (Krasske) Lange-Bertalot *et* Krammer by the presence of the large, rectangular fascia, which is absent in the latter three (Kulikovskiy *et al.*, 2010). *Chamaepinnularia krookiformis* (Krammer) Lange-Bertalot & Krammer, sometimes has a fascia but can be distinguished by its larger dimensions (length up to 40 µm *vs* 17 µm in *C. aerophila*) (Krammer, 1992). Also with a fascia, *C. reinventa* Lange-Bertalot *et* Wydrzycka *in* Wydrzycka *et* Lange-Bertalot has a more linear outline without capitate ends (Wydrzycka & Lange-Bertalot, 2001). Described by Krasske (1939) *Navicula submuscicola* was transferred to *Chamaepinnularia* by Werum *et* Lange-Bertalot (2004), whose illustrations (Werum & Lange-Bertalot, 2004, plate 83, Figs 9-14) indicate some affinities to *C. aerophila* but contrast with the original description of *Navicula submuscicola* in showing a fascia and a more slender outline. Whether they are conspecific with *C. aerophila* is at present not clear. *Chamaepinnularia australomediocris* (Lange-Bertalot *et* R. Schmidt) Van de Vijver, from the Antarctic Region, has a more

linear-elliptical valve outline lacking protracted apices (Van de Vijver *et al.*, 2002b). Taxa such as *C. mediocris* (Krasske) Lange-Bertalot and *C. begeri* (Krasske) Lange-Bertalot *in* Lange-Bertalot *et* Metzeltin have a strictly linear outline lacking capitate or protracted apices and the typical central inflation.

Mayamaea cavernicola shows all the features of the genus *Mayamaea* except the valve outline. In the original genus description (Lange-Bertalot 1997), it is clearly stated that the valves are always elliptical with broadly rounded, non-protracted apices ("*Valvae semper ellipticae apicibus late rotundatis non protractis nec subcapitatis nec acuminatis*"). The raphe of *M. cavernicola* has deflected external proximal raphe endings and hooked distal fissures, and its areola structure also corresponds to that of *Mayamaea* with small, rounded areolae covered on the outside by hymenate occlusions. The latter feature distinguishes *Mayamaea* from *Eolimna*, which has areolae that are closed across the middle of the valve thickness (Schiller & Lange-Bertalot, 1997), so that the hymenes are visible from both the exterior and the interior.

At the ultrastructural level, *Mayamaea cavernicola* can hardly be confused with other members of the genus based on its valve outline. On the other hand, several *Eolimna* and *Sellaphora* taxa are similar under LM (although their ultrastructure clearly separates them from the new taxon). The cosmopolitan *Sellaphora seminulum* (Grunow) D.G. Mann has a similar valve outline but a higher stria density [18-22 in 10 µm (according to Krammer & Lange-Bertalot 1986) *vs* 26-28 in 10 µm in *M. cavernicola*]. *Eolimna minima* (Grunow) Lange-Bertalot has a clearly wedge-shaped central area with more distantly spaced shortened striae and a more elliptical valve outline lacking the protracted valve apices. *Eolimna tantula* (Hustedt) Lange-Bertalot has more linear valves with parallel margins and a larger central area. Two other *Sellaphora* taxa recently described from the nearby Crozet archipelago, *S. tumida* Van de Vijver *et* Beyens and *S. subantarctica* Van de Vijver *et* Beyens, have more radiate, almost geniculate striae and wider valves (up to 5 µm) (Van de Vijver *et al.*, 2002b).

The presence of the well-developed longitudinal grooves in *Sellaphora barae* somewhat resembles the structure of *Microcostatus* (Johansen & Sray, 1998; Taylor *et al.*, 2010; Van de Vijver *et al.*, 2010). The main difference with *Microcostatus* species is the absence of small costae in these grooves in *S. barae*, a key feature for *Microcostatus*. Similar grooves have also been observed in other *Sellaphora* species such as *S. stroemii* (Hustedt) H. Kobayashi (Falasco *et al.*, 2009). *Sellaphora barae* can be separated from all other *Sellaphora* spp. by the combination of the longitudinal grooves and the remarkable stria structure, uniseriate to biseriate, with randomly missing areolae. *Sellaphora seminulum* (Grunow) D.G. Mann has less protracted, but broadly rounded apices (in contrast to the more rostrate apices of *S. barae*). On the nearby Île de la Possession (Crozet archipelago), valves with a similar outline identified as *Naviculadicta seminulum* (Grunow) or *Naviculadicta elorantana* Lange-Bertalot, have been observed (Van de Vijver *et al.*, 2002b). These can be separated based on the lower stria density (18-20 in 10 µm *vs* 22-23 in 10 µm in *S. barae*). *Sellaphora vitabunda* (Hustedt) D.G. Mann can be distinguished by its less elongate valve outline, strictly uniseriate striae and the absence of longitudinal grooves. Finally, *Sellaphora radiosa* (Hustedt) H. Kobayasi in Mayama *et al.* (synonyme: *Navicula joubaudii* H. Germain) has a similar outline but a lower number of striae in 10 µm and a different central area with only one shortened stria.

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