On the identity of *Navicula gottlandica* (Bacillariophyta), with the description of two new species *Navicula eileencoxiana* and *Navicula bergstromiana* from the Australo-Pacific region

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Background and aims – During the past two decades, the subantarctic diatom flora has been the subject of several detailed taxonomic revisions, resulting in the description of a large number of new species. During a survey of the freshwater diatom flora of Macquarie Island (southern Pacific Ocean), an unknown *Navicula* species was observed showing resemblance to *Navicula gottlandica*. Populations of similar diatoms (previously reported as *N. gottlandica*) from Tasmania were also investigated. We here present a detailed morphological analysis of these diatoms, and compare it with the type material of *N. gottlandica*.
Methods – Materials were analysed using Light and Scanning Electron Microscopy.
Key results – The southern hemisphere populations represent two hitherto unknown taxa here described as *Navicula bergstromiana* and *N. eileencoxiana*. Important morphological differences include valve shape, stria density, shape of the central area, ultrastructure of the external central raphe endings, presence of a distinct internal accessory rib, and the relative width of the external longitudinal silica strips covering the valve face with respect to the longitudinal fissures separating these strips. While the new taxa show some affinity with the genus *Haslea*, the internal apical structure of the raphe, the external structure of the terminal raphe fissures and the central raphe endings (often with tooth-like protrusions, creating the impression of a satellite pore), and the apparent lack of the typical sandwich-type *Haslea* valve ultrastructure support the position of *N. gottlandica* and both new taxa within the genus *Navicula*.
Conclusions – The description of two additional species with close similarities to *N. gottlandica* (i.e. possessing the typical longitudinal striae/silica strips and tooth-like protrusions in hooked central raphe endings) suggests that the *N. gottlandica* species group is more diverse than previously thought. The existence of closely similar *Navicula* species recently described from rivers in tropical South America but also from marine littoral samples in South and North America and China, raises intriguing questions about their phylogenetic relationships, ecology and biogeography.

Key words – Tasmania, subantarctic, Bacillariophyta, diatoms, *Navicula*, *Haslea*, new taxa.

INTRODUCTION

For a long time, the genus *Navicula* Bory, based on a very broad generic concept, was one of the most taxon-rich diatom genera. A search for *Navicula* on DiatomBase (http://www.diatombase.org/, Kociolek et al. 2018) returns 9852 matching records (including species and intraspecific taxa). These records, however, also include invalid and illegitimate names and many synonyms. Since the late 1970s, a series of seminal papers on the taxonomy and morphology of the genus *Navicula* by Eileen J. Cox (e.g. Cox 1979, 1988) laid the basis for a drastic revision of the genus which is ongoing to date. Many sections defined by Hustedt (1961–1966) have been established as independent genera (e.g. Round et al. 1990) and only members of Hustedt's section 'Lineolatae' are currently recognized as belonging to *Navicula* s. str., based on the type of the genus, *Navicula tripunctata* (O.F.Müll.) Bory (Cox 1999).

The genus *Navicula* is only poorly represented in non-marine waters in the subantarctic region. Kellogg & Kellogg (2002) listed 238 species and infraspecific non-marine *Navicula* taxa but this list includes all *Navicula* (s. lat.) records. A revision (Van de Vijver et al. 2011) resulted in only 14 taxa belonging to *Navicula* s. str. for the region, including five new species, while Zidarova et al. (2016) described another new species. Most of these new species (*N. australoshetlandica* Van de Vijver, *N. dobrinatemniskovae* Zidarova & Van de Vijver, *N. cremeri* Van de Vijver & Zidarova, *N. bicephaloides* Van de Vijver & Zidarova and *N. romanedwardii* Zidarova, Kopalová & Van de Vijver) have so far been found only on islands in the Maritime Antarctic Region (South Shetland Islands, southern Atlantic Ocean) while *N. conveyi* Van de Vijver was described from the subantarctic Ile de la Possession (Crozet archipelago), located in the southern Indian Ocean (Van de Vijver et al. 2011).

During a survey of the freshwater diatom flora of Macquarie Island (southern Pacific Ocean), we observed an unknown freshwater *Navicula* taxon showing strong similarities to *Navicula gottlandica* Grunow (often misspelled as *N. gothlandica* or *N. gotlandica*), originally described by Grunow (in Van Heurck 1880: pl. 8, fig. 8). Grunow's drawing (no description or type locality were provided) was most probably based on material collected by Cleve, as the name *N. gottlandica* was first introduced (but invalidly, as no description or illustration were provided) in Cleve & Möller (1878), who listed it as present in their collection slide 161 ('Diatoms from Fårön, Gottland, Sweden'). They also mentioned that this slide was verified by Grunow. Grunow's handwritten list of materials (and the species they contain) in the Grunow collection (W) suggest that his sample 2222 ('Alnäsa Träsk, Fårön, Gottland' (Cleve No. 72)) was used to make slide 161 in the Cleve & Möller collection, as reference to this slide is made three times in the species list of sample 2222 (A. Igersheim, Grunow Collection, Naturhistorisches Museum Wien, Austria, pers. comm.). Curiously, however, the species list does not mention *N. gottlandica*. Cleve (1895) published the first full morphological description of the species and added Cleve & Möller 161 as reference slide, together with reference to Grunow's drawing in Van Heurck (1880). Interestingly, Cleve (1895) also mentioned Tasmania as a locality for the distribution of the species.

In order to verify the identity of the Macquarie diatom, we studied the type and other materials belonging to *N. gottlandica* from Europe, and also re-examined our own materials of *N. gottlandica* from Tasmania, Australia (Vyverman et al. 1995, Hodgson et al. 1997, John 2018).

Based on these analyses, it is clear that we are dealing with three morphologically similar but separate species, *N. gottlandica* and two new species, *N. eileencoxiana* Van de Vijver & Sabbe sp. nov., and *N. bergstromiana* Van de Vijver & Verleyen sp. nov., which are here described on the basis of light and scanning electron microscopy. *N. gottlandica* is formally lectotypified. Concise notes on the taxonomic identity, biogeography and ecology of *N. gottlandica* and the new species are added.

MATERIAL AND METHODS

During the austral summer of 2013, diatom samples were collected from the littoral zone of 25 lakes and ponds on Macquarie Island. On the days of measurement the salinities of the sample sites were 0.05–0.75 psu, pH 6.3–9.9, and temperatures 5.1–15.3°C. Macquarie Island (54°30′S, 158°57′E) is a small subantarctic island (total surface area c. 120 km²) located in the southern Pacific Sector of the Southern Ocean, about 1500 km southeast from Tasmania and 1130 km southwest of New Zealand. The island is 34 km long and up to 5 km wide and largely consists of a high plateau of between 150 and 300 m a.s.l., with the highest point being Mt Hamilton (433 m). The plateau is bounded by steep cliffs plunging straight into the ocean or onto a narrow coastal terrace. Macquarie is amongst a small number of subantarctic islands that were not formed as a result of volcanic activity (such as for instance the Crozet archipelago) but is entirely composed of emergent ocean crustal material uplifted at the Miocene Macquarie Ridge formed at the confluence of two crustal plates. Adamson et al. (1996) estimated the emergence of Macquarie Island as being as old as 700 000 years ago, and there is no evidence of Quaternary glaciations (Hodgson et al. 2014). The island has a typical oceanic climate (cool, moist and windy) with little variation in the principal climatic parameters. The vegetation reflects its strong oceanic character with a low number of vascular plants (only 46 species recorded: Copson 1984), 134 species of mosses and hepatics (Seppelt 2004) and about 100 lichen species (Kantvilas & Seppelt 1992). There is a marked west to east salinity gradient in lakes across the island as a result of sea spray carried by the prevailing westerly winds (Saunders et al. 2009). It is an important breeding ground for large numbers of seabirds and seals, locally resulting in heavy nutrient enrichment. One sample, from a small pond close to Square Lake, containing a fairly large population of *Navicula bergstromiana*, was used in the present study (table 1).

In addition, benthic samples from a large set (the TASDI-AT data set) collected in 1994 and 1995 from 76 Tasmanian highland lakes were reanalysed. Tasmania is situated at about 240 km to the South of the Australian mainland and has a surface area of about 68 000 km². It has a maritime, temperate-cool climate and is characterized by a marked west-

Table 1 – **Overview of the slides and other materials examined.**

Slide/material nr.	Locality	Coordinates	Date	Herbarium reference
Cleve & Möller slide 161	Alnäsa Träsk, Fårön, Gottland (Cleve No. 72)	57°56′29.2″N, 19°10′03.1″E	–	slide n° II-6-B11 (Van Heurck collection, BR)
Brun slide 183	Lac Leman, Geneva, Switzerland	–	4 May 1879	Slide 183, eau du lac, prise du 4 mai 1879 (Brun collection, Geneva)
MAC9 LIT1	Macquarie Island, Australia	54°41′59.4″S, 158°50′45.4″E	29 Nov. 2013	
Dobson 940314	Dobson Lake, Tasmania, Australia	42°41′01.4″S, 146°35′29.3″E	14 Mar. 1994	
Perry 940312	Lake Perry, Tasmania, Australia	43°12′49.8″S, 146°45′17.9″E	12 Mar. 1994	
Lake Barterand 30-07-2015 UO1	Lake Barterand, France	45°47′23″N, 5°44′41″E	30 Jul. 2015	

east gradient in precipitation, which roughly coincides with a west-east gradient in geology. The western part is dominated by Precambrian to Ordovician siliceous rocks, while the east has Jurassic dolerite, Permian mud- and sandstone and Tertiary basalt. Most lakes in Tasmania originated by Pleistocene glacial activity. The marked west-east gradients in precipitation and geology are equally reflected in contrasting aquatic and terrestrial biota (Vyverman et al. 1995). The western lakes are dystrophic and characterized by a chemical composition close to that of seawater (with higher sodium and chloride) but with high amounts of soluble humic substances (Gilvin), while the eastern lakes are oligotrophic and have higher pH, calcium concentrations and alkalinity. These limnological differences underlie marked differences in benthic diatom species composition between the west and east (Vyverman et al. 1996). For a more detailed description and overview of the sampling and slide preparation methods used, the limnological characteristics and the benthic diatom communities of the TASDIAT data set, we refer to Vyverman et al. (1995, 1996). Two samples containing large populations of the new species *Navicula eileencoxiana* (formerly identified as *N. gottlandica* in Vyverman et al. 1995, 1996) were used in the present study (table 1).

Slide Cleve & Möller 161 (made from sample 2222 in the Grunow collection in Vienna (W)) from the Van Heurck collection (slide n° II-6-B11) at the Meise Botanic Garden (Belgium) was analysed as the original illustration and description of *N. gottlandica* is most probably based on this material. Unfortunately, no unmounted material was available for making SEM analyses of this material. As *N. gottlandica* is a very rare species, even in Scandinavian countries (A. Jarlman, Jarlman Konsult AB, Lund, Sweden & I. Sundberg, Medins Havs och Vattenkonsulter AB, pers. comm.), we could not find a population close to Gotland (Sweden) for SEM analysis. In France, several larger populations were observed (cf. for instance Bey & Ector 2013). Therefore, a population from Lake Barterand (Ain department, France, sample 30-07-2015 UO1 on *Nymphaea*, leg. R. Chavaux), located close to Lake Geneva, was chosen for SEM analysis.

As *Navicula helvetica* Brun (1895) is regarded as a synonym of *N. gottlandica* (Lange-Bertalot 1979, 2001), slide n°

183 ("eau du lac, prise du 4 mai 1879") from the Brun collection in Geneva (Switzerland), containing a small population of *N. helvetica*, was investigated to establish whether the two species are truly conspecific.

Subsamples of the Macquarie Island and Tasmania material were prepared for light microscopy (LM) observations 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 min at $3700 \times g$), cleaned material was diluted with distilled water to avoid excessive concentrations of diatom valves on the slides. Cleaned diatom material was mounted in Naphrax. All slides were analysed using an Olympus BX53 microscope, equipped with Differential Interference Contrast (Nomarski) optics and the Olympus UC30 Imaging System. Samples and slides are stored at the BR-collection (Meise Botanic Garden, Belgium) and at the Lab for Protistology and Aquatic Ecology (Ghent University, Belgium). For scanning electron microscopy (SEM), parts of the oxidized suspensions were filtered through a 2-µm Isopore™ polycarbonate membrane filter (Merck Millipore). The stubs were sputter-coated with a Gold-Palladium layer of 20 nm and studied using a Zeiss Ultra SEM microscope at 3 kV (Natural History Museum London, UK), a JEOL-JSM-7100F (Meise Botanic Garden, Belgium) and a Hitachi SU-70 at 5 kV (LIST, Belvaux, Luxemburg). Terminology used in the description of the structures of the siliceous cell wall is based on Anonymous (1975), Ross et al. (1979), Barber & Haworth (1981: valve outlines and structural types), Cox & Ross (1981) and Round et al. (1990: cingulum and raphe structures).

RESULTS

Navicula gottlandica Grunow (in Van Heurck 1880: pl. 8, fig. 8)

Figs 1 & 2

Synonym – *Navicula helvetica* Brun.

Used material – Cleve & Möller slide 161 (LM) and Lake Barterand (SEM) (see table 1 for details).

Typification – As outlined above, no slide or locality was mentioned with Grunow's original drawing of *N. gottlandica* in Van Heurck (1880). As it is highly likely (cf. Introduction) that Grunow's drawing is based on material from his sample 2222 and that this sample was used to make slide 161 in the Cleve & Möller collection, we propose Grunow slide 2222 present in the W collection as the lectotype, and Cleve & Möller slide 161 (Van Heurck collection, II-6-B11) as isolectotype.

Description: LM – See fig. 1A–G: valves strictly lanceolate with clearly convex margins and rostrate to apiculate, produced apices. Valve dimensions (n = 10): length 40–56 µm, width 7–9 µm. Axial area narrow except for a distinct widening towards the centre of the valve on the secondary side only; central area small, more or less round on both sides but asymmetric. As a result, the raphe sternum has an overall asymmetric appearance. Raphe branches straight. Central raphe endings pore-like and weakly deflected towards the secondary side. Terminal raphe fissures deflected. Striae distinctly radiate and slightly more widely spaced near the valve centre, becoming parallel to convergent near the apices, 18–19 in 10 µm. Central striae weakly geniculate with shorter striae inserted in between. Lineolae distinct, apically elongated, c. 25 in 10 µm. Distinct longitudinal lines present, curved around the valve centre and more prominent near the valve margins.

Description: SEM – See fig. 2A–F: valve surface almost entirely covered by parallel, continuous longitudinal strips, which have the same width across the whole valve face (fig. 2A–C). Lineolae only visible where ribs are eroded or incompletely formed (fig. 2B, arrows). External raphe branches weakly curved, showing a slight notch on both sides of the central area (fig. 2A, arrows). External central raphe endings expanded, pore-like and hooked towards the secondary side (fig. 2B). Terminal raphe fissures continuing onto the valve mantle, strongly hooked towards the secondary side (fig. 2A & C). Internally, striae composed of large, square to rectangular lineolae in between narrow, slightly thickened virgae (fig. 2D). Raphe sternum well developed, raised. Accessory rib only weakly developed on the secondary side, almost absent in the centre of the valve (fig. 2D & E). Internal raphe branches opening laterally to the secondary side (fig. 2D). Internal central raphe endings clearly separated from each other, slightly expanded (fig. 2E). Internal terminal raphe endings end in small helictoglossae (fig. 2F). At the apex, the raphe-sternum is transapically expanded, creating a hyaline area around the helictoglossa (fig. 2D & F).
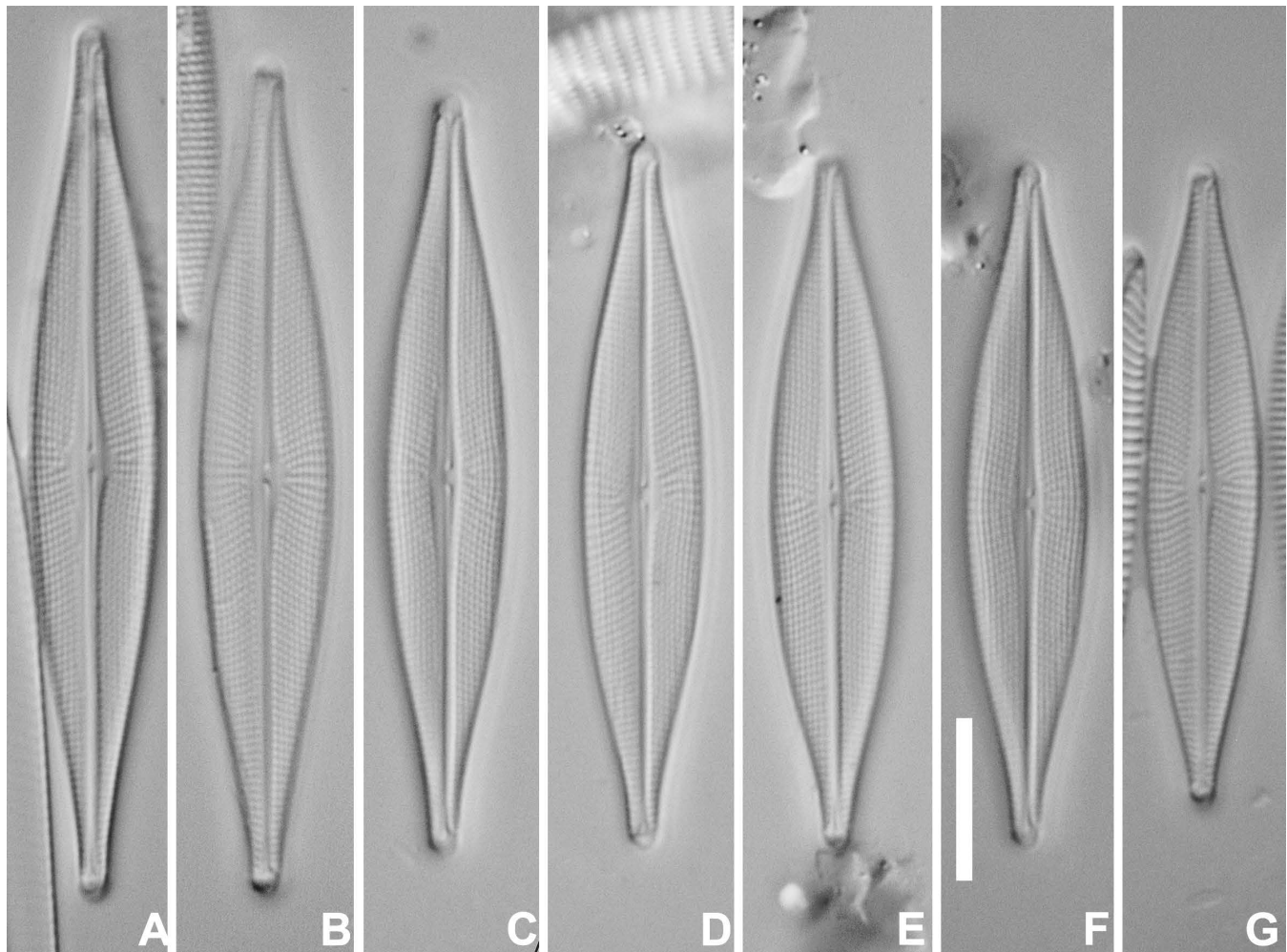
Figure 1 – *Navicula gottlandica*, LM of the isolectotype slide BR II-6-B11 (Cleve & Möller slide 161). Scale bar = 10 µm.
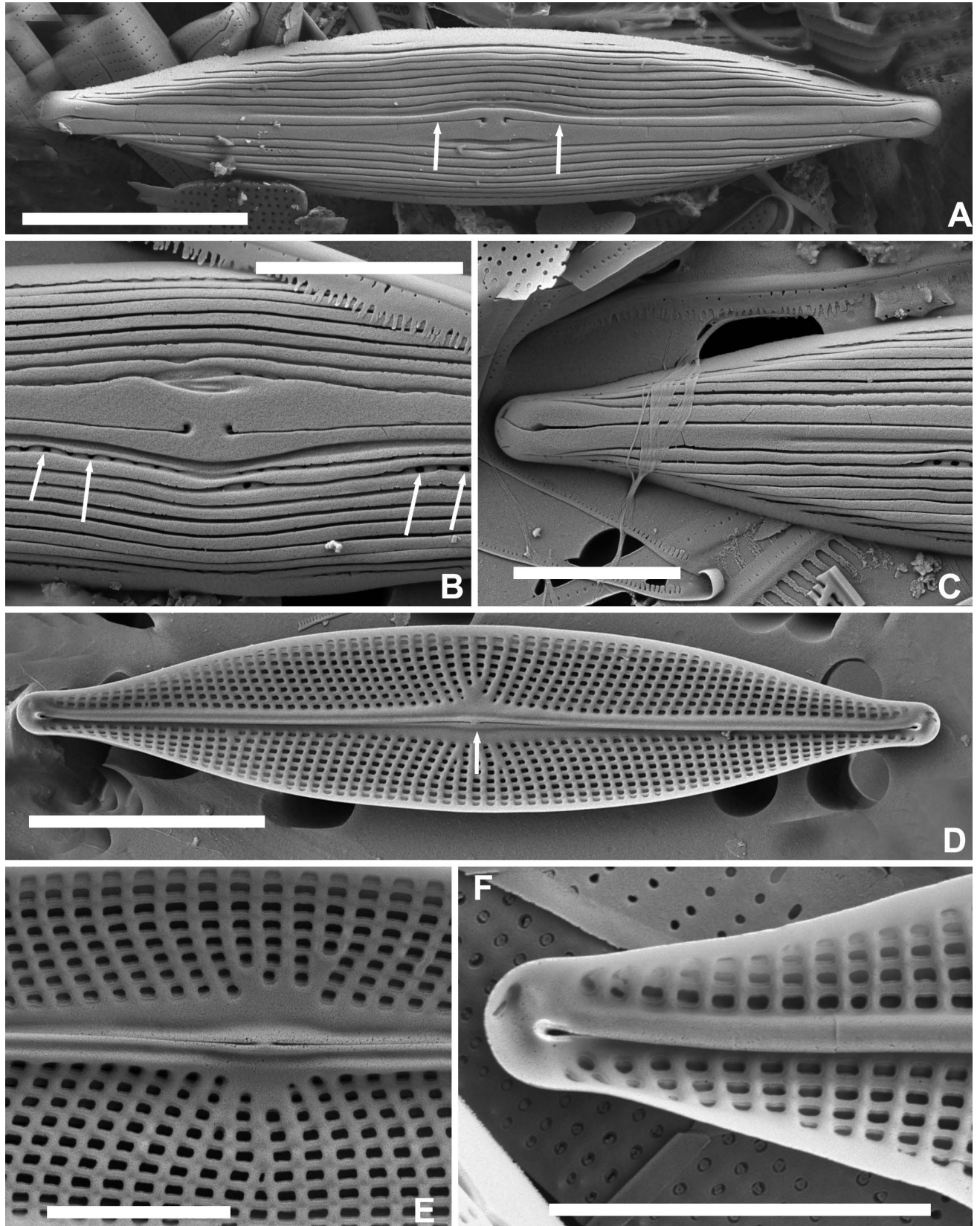
Figure 2 – *Navicula gottlandica*, SEM of a population of Lake Barterand, France (30-07-2015 UO1): A, entire external valve view; arrows indicate notches in raphe branches; B, detail external valve centre. Arrows show areolae; C, detail of external valve apex; D, entire internal valve view, arrow indicating separated central raphe endings; E, detail of internal valve centre; F, detail of internal valve apex. Scale bars: A & D= 10 µm; B, C & F = 5 µm; E = 4 µm.

Ecology – *Navicula gottlandica* was originally described from Alnäsa Träsk which is a lake on the island of Fårö (Fårön) at the northern tip of Gotland, the main Swedish Baltic island. The species has been reported from localities worldwide but unfortunately only a few records could be verified as usually no LM or SEM micrographs were provided. Analysis of these records shows that in several cases, the species was misidentified and represents a different species (e.g. Hall (1986) shows *N. trivialis*). Nahar et al. (2015) reported the presence of *N. gottlandica* in Bangladesh but the illustrated specimen appears to represent a *Frustulia*. The records from Japan (Haraguchi 1997, 1998) represent a species that shows some similarities with *N. gottlandica* but has a different central area with isolated striae and a clearly rhombic valve outline. In France, *N. gottlandica* can be confirmed from small pools (Germain 1981) and several rivers and canals in the Rhône-Alpes region (Bey & Ector 2013). Other verified European observations are from Spain (Ortiz Lerín 2011), Poland (Rakowska 1996) and Germany (especially in lakes with good water quality at higher altitudes, Hofmann et al. 2011). One record from India (Tripathi et al. 2012) could also be confirmed; the species was observed there in the region of Saharanpur, close to the Himalayan region. Patrick & Reimer (1966) reported the species from fresh and brackish waterbodies in several states of the USA, but it is not possible to verify these records as the only illustrated specimen was drawn after the isotype slide from Fårön and did not represent a valve from the USA. Several records of *N. gottlandica* exist from the southern hemisphere. Foged (1978) reported the species (as '*N. gothlandica*') from Eastern Australia but showed a specimen of *N. trivialis*. Other reports (e.g. Crosby & Wood 1959, also from Australia) could not be verified. Given the close similarity with the two new species (and other species from the *N. gottlandica* complex, see discussion), it is clear that all reports of *N. gottlandica* outside Eurasia need to be carefully checked.

Navicula bergstromiana Van de Vijver & Verleyen, **sp. nov.**
Figs 3 & 4

Type material – Macquarie Island, small pond near Square lake, sample MAC9 LIT1 (54°41′59.4″S, 158°50′45.4″W), 29 Nov. 2013, *W. Van Nieuwenhuyze* s.n. (holo-: BR, slide BR-4537; iso-: University of Antwerp, Belgium, slide PLP-352).

Description: LM – See fig. 3A–I: valves linear-elliptical to narrowly lanceolate with almost parallel to weakly convex margins and clearly produced, rostrate apices. Valve dimensions (n = 10): length 39–50 μm, width 6.5–7.5 μm. Axial area narrow but clearly asymmetrically wider towards the centre of the valve, on the secondary side only. Central area small and likewise asymmetric, wedge-shaped on the primary side and more rounded to semi-elliptical on the secondary side. Raphe sternum distinct; raphe branches weakly curved. Central raphe endings expanded to pore-like, slightly deflected towards the secondary side. Terminal raphe endings deflected. Striae strongly radiate and slightly more widely spaced in the centre of the valve, becoming parallel to convergent near the apices, 15–16 in 10 μm. Voigt discontinuity clearly visible (fig. 3B, arrow). Areolae distinct, ca. 20–25 in 10 μm. Longitudinal lines more or less distinct, slightly curved around the centre of the valve.

Description: SEM – See fig. 3J–L & 4: valve surface very smooth because of the presence of wide longitudinal strips, continuous near the valve margins but interrupted in the centre of the valve by an asymmetric hyaline zone (fig. 3J). Lineolae only slightly visible near the axial area where strips are slightly narrower (fig. 3K, arrows). External raphe branches weakly curved, showing a slight notch close to the central area (fig. 3J, arrow). External central raphe endings hooked to the secondary side, each expanded 'pore' containing two small opposed teeth projecting into the opening, one projecting from the centre and pointing towards the apex, the other opposite it, pointing towards the centre (fig. 3K). As in *N. eileencoxiana* (see below), this creates the impression of satellite pores (see fig. 5J, arrow), adjacent to the central raphe endings and connected to these via a narrow slit. Terminal raphe fissures continuing onto the valve mantle, strongly hooked (fig. 3L). Girdle bands plain, unperforated, open (fig. 3L). Internally, striae composed of large, more or less square lineolae covered by hymenes, with narrow virgae (fig. 4A). Raphe sternum with well-defined accessory rib on the primary side, distinctly thicker in the centre (fig. 4A & B). Raphe branches opening laterally to the secondary side (fig. 4A). Internal central raphe endings clearly separated from each other, only slightly expanded (fig. 4B). Internal terminal raphe endings end in small helictoglossae (fig. 4C). At the apex, raphe sternum transapically and asymmetrically (to the primary side) expanded, creating a hyaline area around the helictoglossa (fig. 4C).

Etymology – This new species is named in honour of Dr. Dana Bergstrom (Australian Antarctic Division, Kingston, Australia) for her outstanding work on the botany and ecology of Antarctic and subantarctic ecosystems, and more specifically for her work in identifying and managing the impacts of humans and invasive species on Macquarie Island, and for the leading role she played in initiating and coordinating several international SCAR (Scientific Committee on Antarctic Research) science programmes.

Ecology and associated diatom flora – *Navicula bergstromiana* was present, but always in low abundances, in a large number of lakes on Macquarie Island. The largest populations were found in rather alkaline (pH 7.3–8.1) lakes with a low conductivity (72–150 μS cm^{-1}). So far, the species was not observed on the other subantarctic islands in the southern Indian and southern Atlantic Ocean (Van de Vijver, pers. obs.). Dominant taxa co-occurring with *N. bergstromiana* include *Psammothidium abundans* (Manguin) Bukht. & Round, *P. confusum* (Manguin) Van de Vijver, *Achnanthidium sieminskae* Witkowski, Kulikovskiy & Riaux-Gob., *A. modestiforme* (Lange-Bert.) Van de Vijver and *Fragilaria capucina* s.l. Desm.

Navicula eileencoxiana Van de Vijver & Sabbe, **sp. nov.**
Figs 5 & 6

Type material – Australia, Tasmania, Lake Perry, sample 940312 (43°12′49.8″S 146°45′17.9″E), *W. Vyverman* s.n. (holo-: BR, slide BR-4538; iso-: University of Antwerp, Belgium, slide PLP-353).
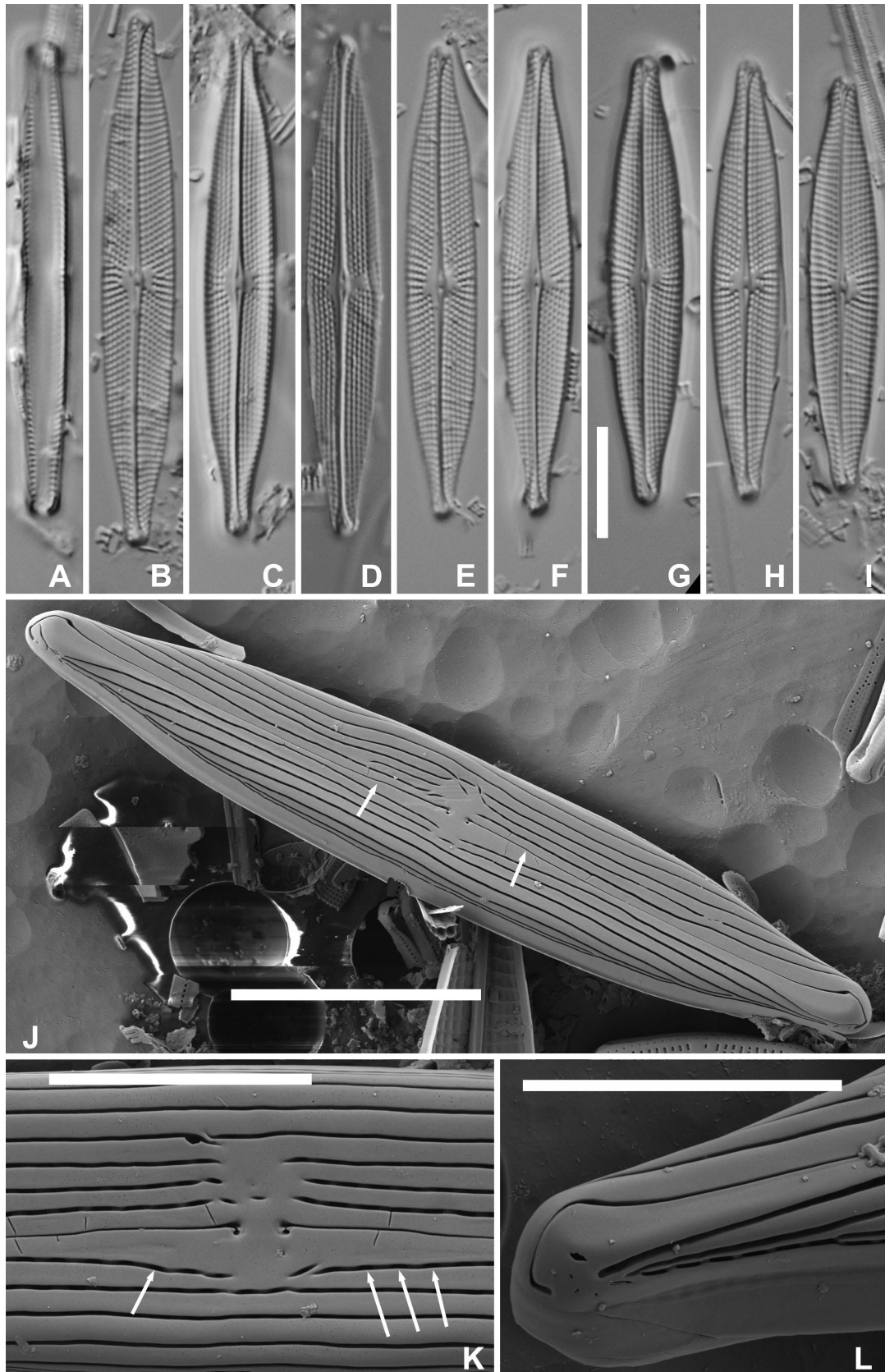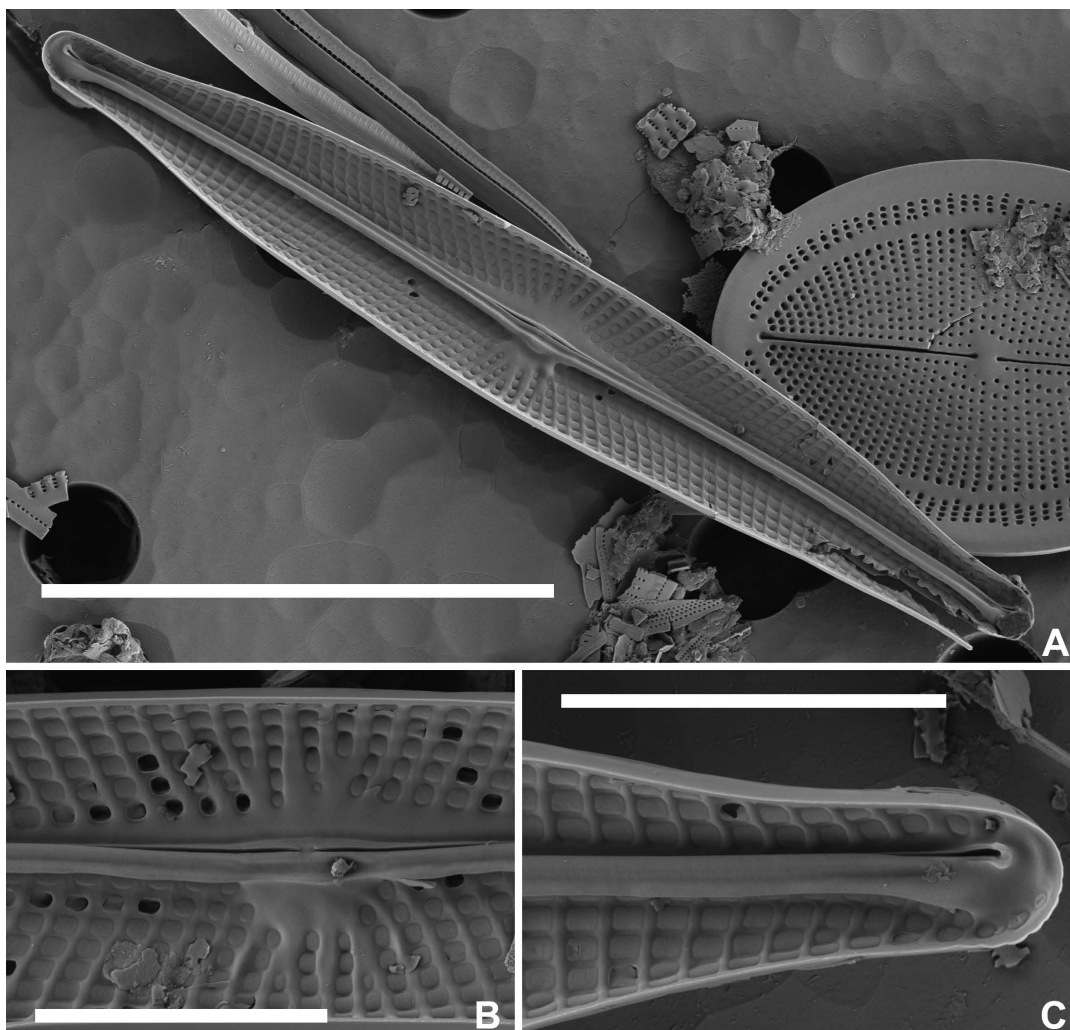
Figure 3 – *Navicula bergstromiana*, LM & SEM of the type population (Macquarie Island, sample MAC9 LIT1): A, LM girdle view; B–I, LM valve views; the arrow in B shows the Voigt discontinuity; J, entire external valve view; arrows indicate notches in raphe branches; K, detail of external valve centre; arrows show areolae; L, detail of external valve apex. Scale bars: A–J = 10 µm; K & L = 5 µm.

Description: LM – See fig. 5A–H (and John 2018: pl. 289, figs H–S): valves linear-lanceolate to moderately broadly lanceolate with always slightly convex margins and weakly produced, substrate apices. Valve dimensions (n = 25): length 47–62 μm, width 6.5–7.5 μm. Axial area narrow, asymmetrically widening towards the centre of the valve on the secondary side only. Central area small, asymmetrical, rounded to wedge-shaped to irregularly shaped on the primary side and semi-elliptical on the secondary side. Raphe sternum well-developed. Raphe branches weakly curved. Central raphe endings slightly expanded to pore-like, weakly deflected towards the secondary side. Terminal raphe endings slightly deflected to the secondary side. Striae strongly radiate and slightly more widely spaced near the central area with several shorter striae inserted, becoming equidistant and parallel to clearly convergent near the apices, 15–16 in 10 μm. Voigt discontinuity occasionally visible (fig. 5A, arrows). Areolae distinct, ca. 20–25 in 10 μm. Longitudinal lines distinct, slightly curved around the central area.

Description: SEM – See fig. 5I–K & 6: longitudinal strips covering the whole valve, continuous near the valve margins but interrupted in the centre of the valve by an asymmetric hyaline zone (fig. 5I & J). The strips are narrower closer the axial area, making the underlying lineolae here more clearly visible (fig. 5I & J, John 2018: pl. 290, figs B, C). Striae composed of apically elongated lineolae (fig. 5I & J). External raphe branches weakly curved (fig. 5I). External central raphe endings expanded, hooked to the secondary side with two small opposite teeth across the opening (fig. 5J, double arrow), creating the impression of satellite pores (fig. 5J, arrow). Terminal raphe fissures continuing onto the mantle, clearly hooked (fig. 5K). Internally, striae composed of very large, square-shaped to rounded lineolae with hymenes, virgae clearly much narrower than the striae (fig. 6A). Raphe sternum with well-defined accessory rib on the primary side, distinctly thicker in the centre (fig. 6A & B). Raphe branches opening laterally to the secondary side (fig. 6A & B). Internal central raphe endings appear to be continuous, only slightly expanded (fig. 6B). Internal terminal raphe endings end in small helictoglossae (fig. 6C). At the apex, raphe sternum transapically and asymmetrically (to the primary side) expanded, creating a hyaline area around the helictoglossa (fig. 6C).

Figure 4 – *Navicula bergstromiana*, SEM of the type population (Macquarie Island, sample MAC9 LIT1): A, entire internal valve view; B, detail of internal valve centre; C, detail of internal valve apex. Scale bars: A = 10 μm; B & C = 5 μm.
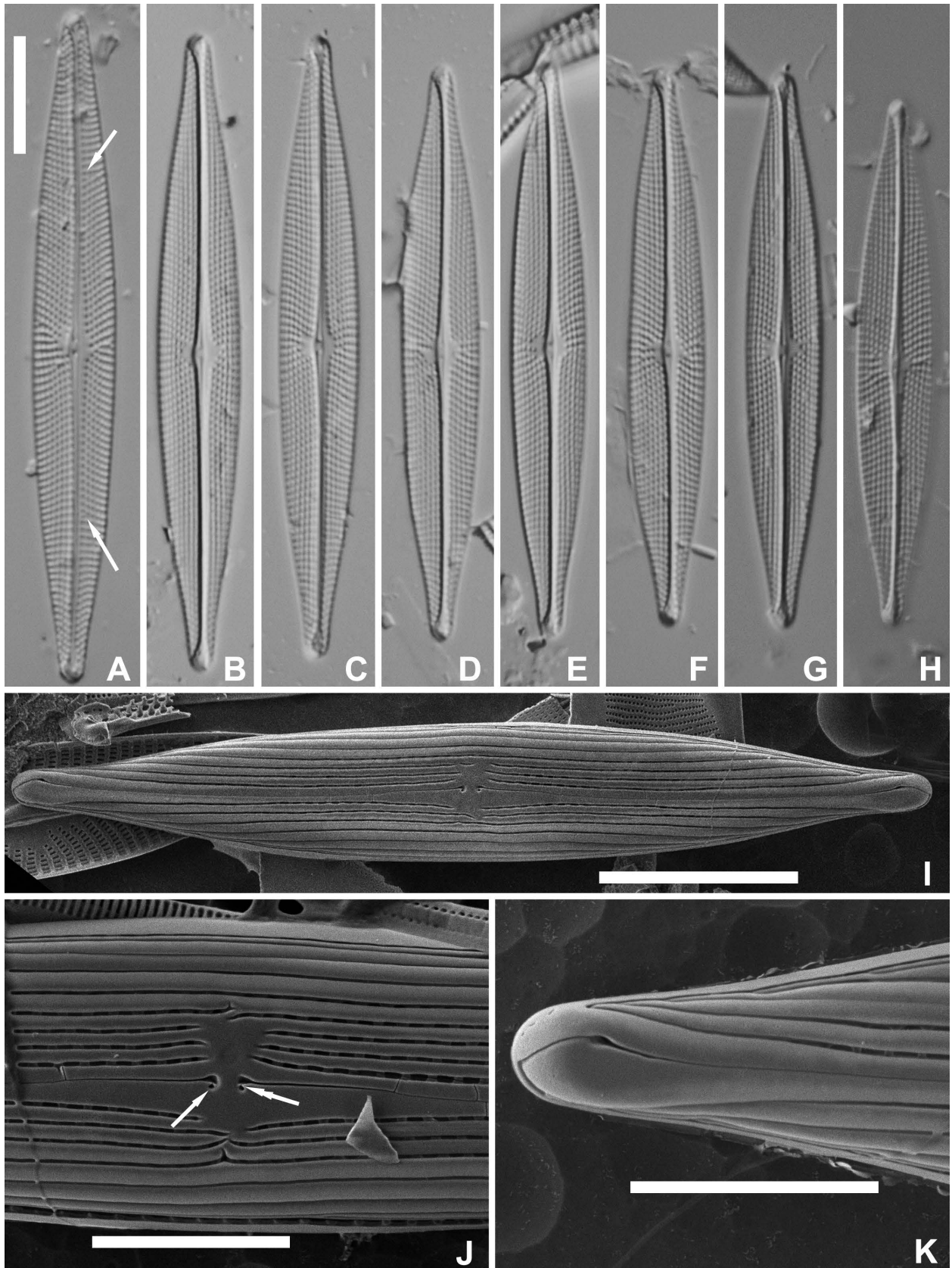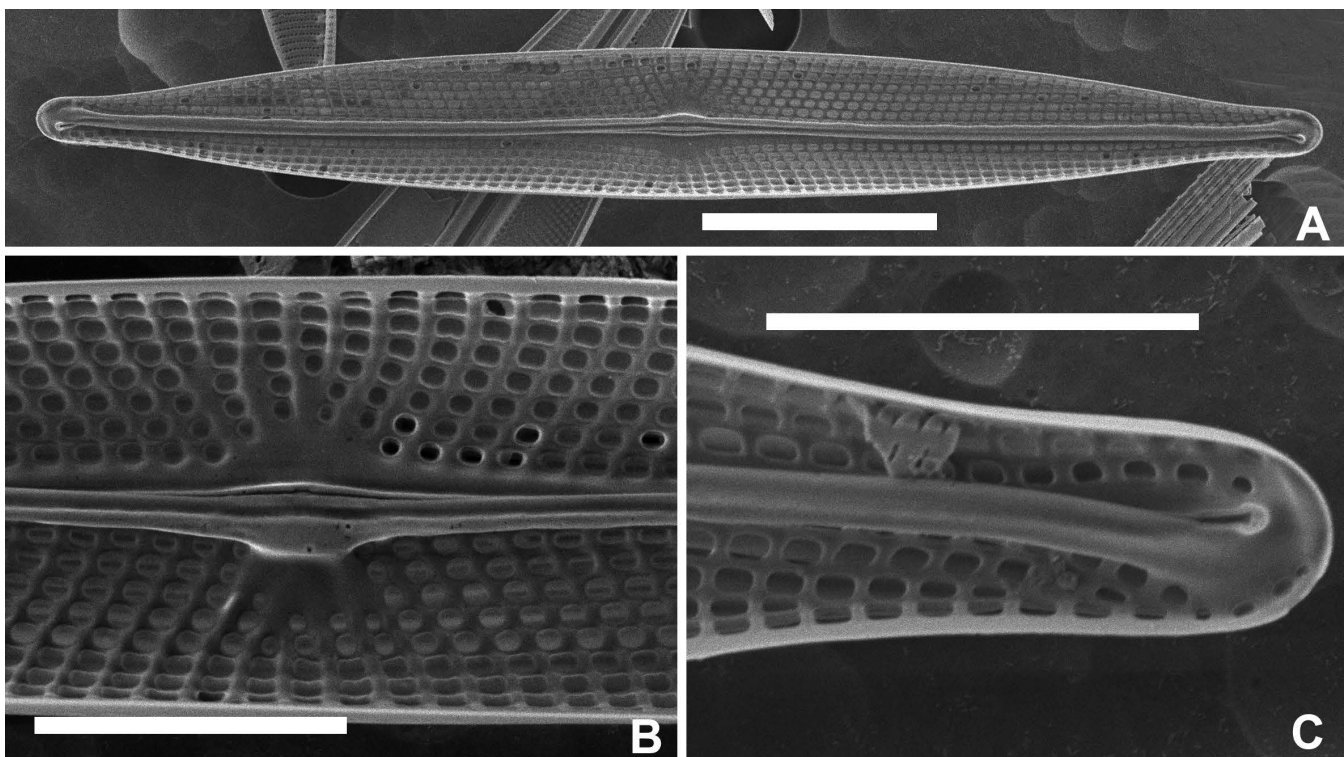
Figure 5 – *Navicula eileencoxiana*, LM & SEM of the type population (Lake Perry, Tasmania, Sample 940312): A–H, LM valve views; arrows in A show Voigt discontinuities; I, entire external valve view; J, detail of external valve centre; K, detail of external valve apex. Scale bars: A–I = 10 µm; J & K = 5 µm.

Etymology – This species is dedicated to our friend and colleague Dr. Eileen Cox on the occasion of her 70th birthday. The detailed morphological, morphogenetic and plastid analyses of naviculoid diatoms by Dr. Cox lay at the heart of a major revision of the genus *Navicula* s. lat., which since the late 1980s has resulted in the description of numerous new genera and the resurrection of several forgotten genera.

Ecology & associated diatom flora – *Navicula eileencoxiana* (reported as *Navicula gottlandica* in Vyverman et al. 1995, Hodgson et al. 1997, John 2018) is one of the more common benthic diatom species in (ultra)oligotrophic eastern and central ('corridor') lakes of the Tasmanian highlands. Vyverman et al. (1995), on the basis of the TASDIAT data set (cf. above), reported a weighted average pH optimum and tolerance of 5.87 and 0.57, and a calcium (µequiv·L⁻¹) mean and tolerance value of 55.78 and 34.80. John (2018) recorded this species from Great Lake, Pine Lake, Lake St. Clair, Lake Dobson and Lake Rosenberg in Tasmania; pH in these sites mostly ranged from 5.4 to 6.7 and conductivity from 20 to 66 µS cm⁻¹. In the type locality, Lake Perry, it was mainly accompanied by species such as *Psammothidium* cf. *didymum* (Hust.) Bukht. & Round, *P.* cf. *rossii* (Hust.) Bukht. & Round, *Achnanthidium minutissimum* (Kütz.) Czarn., *Frustulia rhomboides* (Ehrenb.) De Toni and *Kobayasiella hodgsonii* Verleyen. Interestingly, *N. eileencoxiana* also appears to be present in New Zealand, where it was reported as *N. helvetica* var. *wolterecki* Hust. from a number of localities in both the North and the South Island (Kilroy & Sorrell 2013: fig. 14o).

DISCUSSION

Due to the presence of distinct longitudinal striae (corresponding to longitudinally aligned areolae partly covered by external longitudinal silica strips in SEM), *Navicula gottlandica*, *N. eileencoxiana* and *N. bergstromiana* resemble species belonging to the genus *Haslea*, in which such longitudinal striae are one of the defining features (Simonsen 1974, Round et al. 1990, Sterrenburg et al. 2015, Li et al. 2017). However, the exact identity of *Haslea*, and how it is related to similar genera with longitudinal strips such as *Craticula* (see e.g. Morales et al. 2014), *Gyrosigma* (Sterrenburg et al. 2015), but also representatives of *Navicula* such as *N. duerrenbergiana* Hust. (e.g. Krammer & Lange-Bertalot 1986) and *N. gottlandica* (this study), is as yet unclear. Li et al. (2017), using a combination of morphological and molecular-phylogenetic data, convincingly showed that the concept of the genus *Haslea* needs to be more precisely defined. They showed that some species recently described as belonging to *Haslea* actually belong to *Navicula* [*N. avium* (M.A.Tiffany, Herwig & Sterrenburg) Yuhang Li & Kuidong Xu and *N. tsukamotoi* (Sterrenburg & F.Hinz) Yuhang Li & Kuidong Xu]. Moreover, these species appear to be closely related to *N. duerrenbergiana* and *N. ramosissima* (C.Agardh) Cleve, which are also characterized by distinct longitudinal striae in LM. On the basis of their study, they suggested that the following features distinguish *Navicula* s. str. from *Haslea*: small helictoglossae (vs long helictoglossae in *Haslea*), internally thickened areas at the valve apices, and strongly hooked terminal raphe fissures extending onto the valve mantle. In addition, the external central raphe endings in *Haslea* are slit-like and straight, while in *Navicula* they can be strongly hooked with

Figure 6 – *Navicula eileencoxiana*, SEM of the type population (Lake Perry, Tasmania, Sample 940312): A, entire internal valve view; B, detail of internal valve centre; C, detail of internal valve apex. Scale bars: A = 10 µm; B & C = 5 µm.

Table 2 – Comparison between *Navicula gottlandica*, the two new southern hemisphere species and six species from South America.
[a]according to Lange-Bertalot (2001: pl. 72, figs 3, 4).

	Navicula gottlandica	*Navicula bergstromiana*	*Navicula eileencoxiana*	*Navicula bicuneolus*	*Navicula coraliana*	*Navicula herbstiae*	*Navicula insulsa*	*Navicula maidanae*	*Navicula riotecensis*
Source	this study (type material)	this study (type material)	this study (type material)	Metzeltin & Lange-Bertalot (1998)	Metzeltin & Lange-Bertalot (1998)	Metzeltin & Lange-Bertalot (1998)	Metzeltin & Lange-Bertalot (1998)	Metzeltin & Lange-Bertalot (1998)	Metzeltin & Lange-Bertalot (1998)
Length (μm)	40–56	39–50	47–62	43–60	33–51	45–66	40–57	60–70	70–85
Width (μm)	7.0–9.0	6.5–7.5	6.5–7.5	6–7.5	6–7	6.5–7.5	6–7	12–14	7–8
Length/width ratio	5.2–6.7	6.0–7.2	6.8–9.1						
Valve outline	strictly lanceolate with clearly convex margins	linear-elliptical to narrowly lanceolate with parallel to weakly convex margins	lanceolate with convex margins	linear with more or less concave margins	lanceolate	linear-lanceolate to linear with parallel to slightly concave margins	narrowly linear-lanceolate	lanceolate	strictly linear
Valve apices	elongated, protracted, rostrate, acutely rounded apices	clearly protracted, rostrate apices	weakly protracted, subrostrate	clearly protracted, cuneate	broadly rounded, not protracted	protracted, elongated, cuneate	abruptmy narrowing and broadly rounded	broadly rounded, not protracted	broadly rounded, not protracted
Central area	small, apically elongated, lanceolate clearly asymmetrical central area	rather small, asymmetrical, wedge-shaped on the primary side bordered by several shortened striae and apically elliptical on the secondary side	very small, asymmetrical, rounded on the primary side bordered by several slightly shortened striae and apically elliptical on the secondary side	relatively large, forming wedge-shaped fascia	rather small, moderately widening towards the margins	rather small, moderately widening towards the margins	relatively large, almost forming wedge-shaped fascia	moderately large, transapically enlarged, not forming fascia	transapically enlarged to rhombic-elliptical, almost forming fascia
Striation pattern	distinctly radiate near the valve center, becoming parallel and eventually convergent near the apices	strongly radiate near the central area, parallel and clearly convergent near the apices	strongly radiate near the central area, parallel and clearly convergent near the apices	Radiate near the centre, convergent near apices	clearly radiate near the centre, convergent near apices	radiate near the centre, convergent near apices	radiate near the centre, strongly convergent near apices	radiate near the centre, convergent near apices	radiate near the centre, convergent near apices
Number of striae in 10 μm	18–19	15–16	15–16	16–18	14–15	15–16	14–16	12–14	c. 15
Longitudinal strips	entirely covering the valve face, almost never interrupted[a]	entirely covering the valve face, near the axial area strips interrupted	partly present, zone near axial area lacking strips	only near apices, absent near central area	unknown due to lack of SEM observations	present, interrupted near central area	unknown due to lack of SEM observations	unknown due to lack of SEM observations	entirely covering the valve face, clearly undulating to curved

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opposite teeth (or other tooth-like protrusions) like those we illustrate here in *N. eileencoxiana* and *N. bergstromiana*, such as in *N. avium* but also in other *Navicula* spp. [e.g. *N. subalpina* E.Reichardt (Lange-Bertalot 2001), *N. wunsamiae* Witkowski, Lange-Bertalot & Metzeltin (Witkowski et al. 2009)]. Moreover, the external longitudinal silica strips (at least in *N. avium* and *N. tsukamotoi*) do not have the 'sandwich-type' ultrastructure typical for *Haslea*, with an inner basal layer and an outer tegumental layer (the longitudinal strips) connected to each other by upright rib-like structures (called 'saepes') Sterrenburg et al. (2015). Instead, the strips are fully fused with the underlying vimines (Xi et al. 2017).

Navicula gottlandica, *N. eileencoxiana* and *N. bergstromiana* also possess small helictoglossae, internal plate-like thickenings at the valve apices, and strongly hooked terminal fissures. In addition, a distinct sandwich-type valve ultrastructure is absent. *Navicula gottlandica* should therefore be kept in the genus *Navicula*. The two new species should also be assigned to this genus. Interestingly, they also possess the hooked central raphe endings with opposite tooth-like structures that are present in *N. avium* and *N. tsukamotoi*. This raises interesting questions regarding the relationship of *N. gottlandica*, *N. eileencoxiana* and *N. bergstromiana* with the clade around *N. duerrenbergiana* (Li et al. 2017). All three species have the typical *Navicula* s. str. features and also share the external longitudinal silica strips and the strongly hooked central raphe endings (with or without teeth). However, there are also some pronounced differences: none of the representatives of the *N. duerrenbergiana* clade have a central area, and the central raphe endings are rather indistinct and close together. Moreover, they are all typically found in marine or saline waters. As long as we have no molecular data for representatives of the *N. gottlandica* complex (see also below), it is not possible to assess whether and how the two groups are related.

In the past, there has been some confusion about the true identity of *N. gottlandica*. This was mainly caused by the erroneous interpretation of this species by Germain (1964). His illustrations (plate 1, figs 1–8) most likely represent *N. trivialis* Lange-Bert. (Lange-Bertalot 2001), while he identified true *N. gottlandica* in the Cleve & Möller slide 161 as *N. helvetica* (following the interpretation of this species by Hustedt (1930)). In 1979, Lange-Bertalot corrected the identification by Germain (1964) and added two more pictures of the type of *N. gottlandica*, this time of a slide labelled sample Grunow 2222. Germain (1989) discussed further illustrations of *N. gottlandica* published in 1981 (Germain 1981: pl. 63, fig. 8) and Krammer & Lange-Bertalot (1986: 523, figs 3, 4) comparing it with *N. gregaria* Donkin and *N. cryptocephala* Kütz. To determine its position within the genus *Navicula*, *Navicula helvetica* was indicated as a synonym of *N. gottlandica* (Lange-Bertalot 1979, 2001, John 2018). Examination of Brun slide 183 showed that both species are indeed conspecific (unfortunately the quality of the slide precluded making photographs).

Navicula gottlandica, *N. eileencoxiana* and *N. bergstromiana* mainly differ in valve shape and length-width ratio, stria density, the shape of the central area, the presence or absence of opposite teeth in the external central raphe endings, the presence of a distinct internal accessory rib, and

the relative width of the longitudinal strips with respect to the longitudinal fissures separating these strips (table 2). *Navicula gottlandica* can be separated from the two new species in valve width and shape (strictly lanceolate with almost apiculate apices), a higher stria density, the absence of opposite teeth within the external central raphe endings, a weakly developed internal accessory rib and external longitudinal strips which are not interrupted in the centre of the valve. The difference between *N. eileencoxiana* and *N. bergstromiana* is more subtle and mainly concerns valve shape (with usually less convex to straight valve margins and more distinctly rostrate apices in the latter) and the structure of the longitudinal strips, which are relatively wider in *N. bergstromiana* compared with the narrower strips which differ in width between the axial and marginal area in *N. eileencoxiana*. In addition, the available data suggest ecological differences as well, with *N. eileencoxiana* being more restricted to more acidic waters.

N. gottlandica, *N. eileencoxiana* or *N. bergstromiana* bear a very close resemblance to a group of species that was described from rivers in tropical South America, viz. *N. bicuneolus* Metzeltin & Lange-Bert., *N. coraliana* Metzeltin & Lange-Bert., *N. herbstiae* Metzeltin & Lange-Bert., *N. insulsa* Metzeltin & Lange-Bert., *N. maidanae* Metzeltin & Lange-Bert. and *N. riotecensis* Metzeltin & Lange-Bert. (Metzeltin & Lange-Bertalot 1998). Table 2 shows the main morphological features of these species. Unfortunately, most of these species were described on the basis of LM only. *Navicula riotecensis* and *N. bicuneolus* differ from the three species in this study in having distinctly linear valves. *Navicula maidanae* is generally larger (60–70 µm long) with a lower stria density (12–14 in 10 µm). In *N. coraliana* the longitudinal striae are markedly curved around the central area. The most similar species are *N. insulsa* and *N. herbstiae*: the former has a higher (25–27 in 10 µm) and the latter a lower areola density (c. 20 in 10 µm) and also less well developed longitudinal silica strips (see Metzeltin & Lange-Bertalot 1998, plate 77, fig. 8).

At present, only one other *Navicula* species, viz. *Navicula woltereckii* Hust., described from the Indonesian island Celebes (now Sulawesi), shows some faint resemblance to the new taxa, mainly based on the fine striation pattern and the rather coarse nature of the areolae (Simonsen 1987: pl. 264, figs 1–4). However, *N. woltereckii* lacks the typical longitudinal strips and shows a lanceolate valve outline without protracted apices. *Craticula perotettii* Grunow presents narrow longitudinal strips but has a different areola structure (no lineolae), lacks the satellite pore-like structures near the central raphe endings and possesses a rather broad conopeum that covers the axial area (Lange-Bertalot 2001: pl. 81).

The description of two new species in the group of species which resemble *N. gottlandica* brings the total number in this group up to nine: six of these have hitherto only been reported from rivers in tropical South America (unfortunately no environmental information is available) but appear to be absent from more southern parts of South America (Rumrich et al. 2000 and references therein), two (described in this paper) are as yet only known from dys- to oligotrophic lakes and ponds in the Australo-Pacific region, and one (*N. gottlandica*) may be more widespread but has its main distribution in the

northern hemisphere. Further collections and study, preferably also including molecular analyses, is needed to further resolve the phylogenetic relationships and unravel the biogeography of this intriguing species complex.

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