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Two new *Gomphonema* species (Bacillariophyta) from the Maritime Antarctic Region

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Abstract

Two new diatom taxa belonging to the genus *Gomphonema* were recorded during a survey of the Maritime Antarctic freshwater and limno-terrestrial diatom flora: *Gomphonema jamesrossense sp. nov*. and *G.maritimo-antarcticum sp. nov*. Detailed light (LM) and scanning electron microscope (SEM) observations are used to characterize the morphology and ultrastructure of the two new *Gomphonema* taxa. Comparisons with similar taxa and the ecological preferences of each species are added. The revision of these species confirmed the endemic nature of the Antarctic diatom flora.

Key-words: Maritime Antarctica, *Gomphonema*, new species, morphology

Introduction

The genus *Gomphonema* Ehrenberg (1832: 87) is an important constituent of the Maritime Antarctic diatom flora. Despite numerous records of the genus in Antarctic diatom surveys, the number of typical Antarctic taxa remains very low. In total, 26 *Gomphonema* taxa have been reported from the Maritime Antarctic Region (including South Orkney Islands, South Shetland Islands, James Ross Island). Kellogg & Kellogg (2002) list all taxa reported in the Antarctic literature but the list of records merely comprises observations of northern hemisphere taxa such as *Gomphonema parvulum* (Kützing 1844: 84) Kützing (1849: 65), *G. angustum* Agardh (1831: plate 24, Fig. 47) or *G. gracile* Ehrenberg (1838: 217). Of these, only two taxa were originally described from this region: *Gomphonema charcotii* M.Peragallo (1921: 63) and *G. signyensis* Kociolek & Jones (1995: 270), the first probably being a marine taxon that should be transferred to another genus. This low number of typical Antarctic endemic *Gomphonema* taxa is in clear contrast with the current, generally accepted view that the Antarctic region is home to a highly specific diatom flora (Sabbe *et al*. 2003, Van de Vijver *et al*. 2005, Vanormelingen *et al*. 2008, Vyverman *et al*. 2010) and raises questions regarding the correct taxonomic identity of the recorded populations. Revisions of, for instance, the genera *Navicula* Bory (1822: 128) (Van de Vijver *et al*. 2011a), *Muelleria* (Frenguelli 1924: 256) Frenguelli (1945: 172) (Van de Vijver *et al*. 2010, 2014), *Luticola* D.G.Mann in Round *et al*. (1990: 670) (Van de Vijver & Mataloni 2008, Van de Vijver *et al*. 2011b, Kopalová *et al*. 2011, Zidarova *et al*. 2014), *Pinnularia* Ehrenberg (1843: 45) (Van de Vijver & Zidarova 2011, Zidarova *et al*. 2012), *Hantzschia* Grunow (1877: 174) (Zidarova *et al*. 2010) and *Surirella* Turpin (1828: 362–363) (Van de Vijver *et al*. 2013a) clearly showed that the diversity of the Antarctic diatoms has been largely underestimated in the past due to species drift and force-fitting (Tyler 1996) the Antarctic diatoms into European or North-American names.

The present paper reports on the results of the revision of the genus *Gomphonema* in samples from the Maritime Antarctic Region. Two new taxa are described based on detailed light and scanning electron microscopy observations. *Gomphonema jamesrossense* sp. nov. was found on James Ross Island, an island situated in the southern part of the Maritime Antarctic Region. The second species, *G. maritimo-antarcticum* sp. nov., was described from Livingston Island, one of the main islands of the South Shetland Islands. The two taxa are compared with similar taxa worldwide and notes on their ecological preferences are added.

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Material and Methods

During several austral summers (2008–2012), material for diatom analysis has been sampled from various lakes and ponds on Livingston Island (mainly from the Byers Peninsula) and from James Ross Island (mainly the Ulu Peninsula). Details about sampling localities and samples are given in Kopalová *et al*. (2012, 2013, 2014) and Kopalová & Van de Vijver (2013).

Diatom samples for LM observation were prepared following the method described in Van der Werff (1955). Small parts of the sample 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®. The slides were analyzed using an Olympus BX53 microscope, equipped with Differential Interference Contrast (Nomarski) and the Olympus UC30 Imaging System. Samples and slides are stored at the BR-collection, property of the Belgian federal government and given in permanent loan to the Botanic Garden Meise (Belgium). For scanning electron microscopy (SEM), parts of the oxidized suspensions were filtered through a 1-µm Isopore™ polycarbonate membrane filter (Merck Millipore). The stubs were sputter-coated with a Gold-Palladium layer of 10 nm and studied in a ZEISS Ultra SEM microscope at 3 kV (Natural History Museum London, UK). Diatom terminology follows Ross *et al*. (1979) and Round *et al*. (1990). The morphology of the new taxa has been compared with morphologically similar known species described worldwide (Kociolek & Jones 1995, Lange-Bertalot & Metzeltin 1996, Reichardt 1999, Rumrich *et al*. 2000).

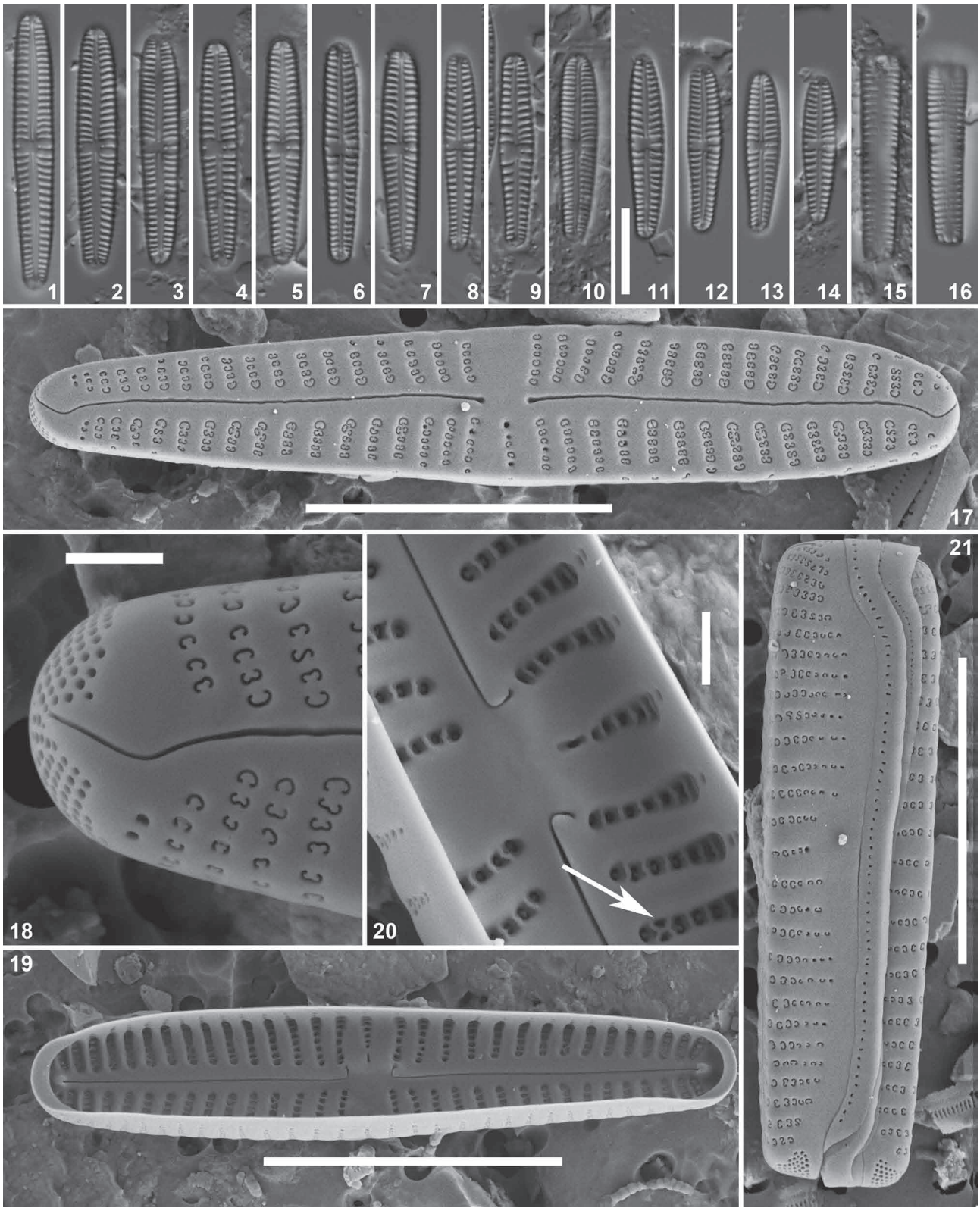
Observations

Division **Bacillariophyta**
Class **Bacillariophyceae**
Subclass **Bacillariophycidae**
Order **Cymbellales**
Family **Gomphonemataceae**
Genus ***Gomphonema***

Gomphonema jamesrossense **Van de Vijver, Kopalová, Zidarova & Kociolek, *sp. nov*. (Figs 1–21)**

LM (Figs 1–16): Frustules in girdle view almost rectangular, weakly clavate with narrower footpole (Figs 15, 16). Valves linear-clavate with almost parallel margins and broadly rounded obtuse head- and footpole. Valves occasionally asymmetrical to the apical axis. Valve dimensions (n=25): length 20–37 µm, width 3.5–4.5 µm, the greatest width being almost in the middle of the valve. Axial area narrow, linear to linear-lanceolate, almost 1/6 of the total valve width, never widened until the central area. Central area asymmetrical, rectangular. One side with one very shortened stria, other side with one longer stria. Stigmoid present at the end of the longer stria, almost not separated from the last areola. Raphe branches undulate, weakly lateral with straight to slightly deflected, simple proximal raphe endings and hooked distal fissures. Striae clearly radiate near the central area becoming almost parallel towards the headpole, 11–14 in 10 µm. Near the apices, striae positioned more closely together, up to 17 in 10 µm. Areolae almost not discernible in LM. SEM (Figs 17–21): Striae uniseriate composed of "C"- to "3"-shaped areolae (Figs 17, 18). Striae continuing uninterruptedly onto the mantle, eventually terminating in one small rounded areola (Fig. 21). Mantle edge forming a relatively broad hyaline zone (Fig. 21). Footpole with a hyaline tip, bordered by a large apical pore field composed of up to 8 rows of very small pores (Fig. 18). Apical pore field bisected by the distal raphe fissures (Fig. 18). External raphe branches clearly undulate (Fig. 17). External proximal endings weakly deflected terminating in simple, almost non-expanded pores (Fig. 17). Distal raphe fissures (strongly) hooked, almost not continuing onto the mantle (Fig. 18). External stigmoid opening rounded, not more distantly separated from the last areola of the central stria (Fig. 17). Foot- and headpole with small pseudoseptum (Fig. 19). Internally, central nodule raised. Internal proximal raphe endings positioned closely together, clearly recurved (Fig. 20). Distal raphe endings terminating on small helictoglossae (Fig. 19). Striae internally bearing vimines, oriented perpendicularly to the striae. Occasionally, areolae subdivided by transapical vimines (Fig. 20, arrow). Internal stigmoid opening slit-like (Fig. 20).

Type:—JAMES ROSS ISLAND. Ulu Peninsula: Lake Katia II, sample D15 (63° 52' 15.9" S, 57° 58' 32.5"), *L. Nedbalová*, *1 February 2008* (holotype BR! slide no. 4444, isotype PLP! slide 299, University of Antwerp, Belgium).



FIGURES 1–21. *Gomphonema jamesrossense*. LM & SEM pictures taken from the holotype population (sample D15) from Katia II Lake, James Ross Island. 1–16. Light microscopy observations. 17. External view of an entire valve with focus on the proximal raphe endings, the apical pore field and the position of the stigmoid. Note the variation in areola shapes. 18. External detail of the footpole with the apical pore field and the distal raphe ending. 19. Internal view of an entire valve with focus on the proximal raphe endings and the position of the stigmoid. 20. Internal detail of the central area with the proximal raphe endings and the position of the stigmoid. 21. Girdle view of an entire frustule. Note the presence of the apical pore field almost entirely on the mantle, the hyaline mantle edge and the small areolae terminating the mantle striae. Scale bar represents 10 µm except for Figs 18 & 19 where scale bar = 1 µm.

Ecology and distribution:—The highest relative abundance of *Gomphonema jamesrossense* was found in an epilithon sample, collected from Katia II Lake, on the Ulu Peninsula, at an altitude of 45 m a.s.l. The lake has circumneutral pH (7.3) with a moderate conductivity (580 µS/cm), very low nutrient but higher salinity levels (Cl^- 106 mg/l, SO_4^{2-} : 66 mg/l). The species was likewise found in several other samples of James Ross Island but always in very low abundances. On other investigated localities of the Maritime Antarctic Region, the species seems to be absent so far.

Etymology:—The species is named after James Ross Island where several populations were found.

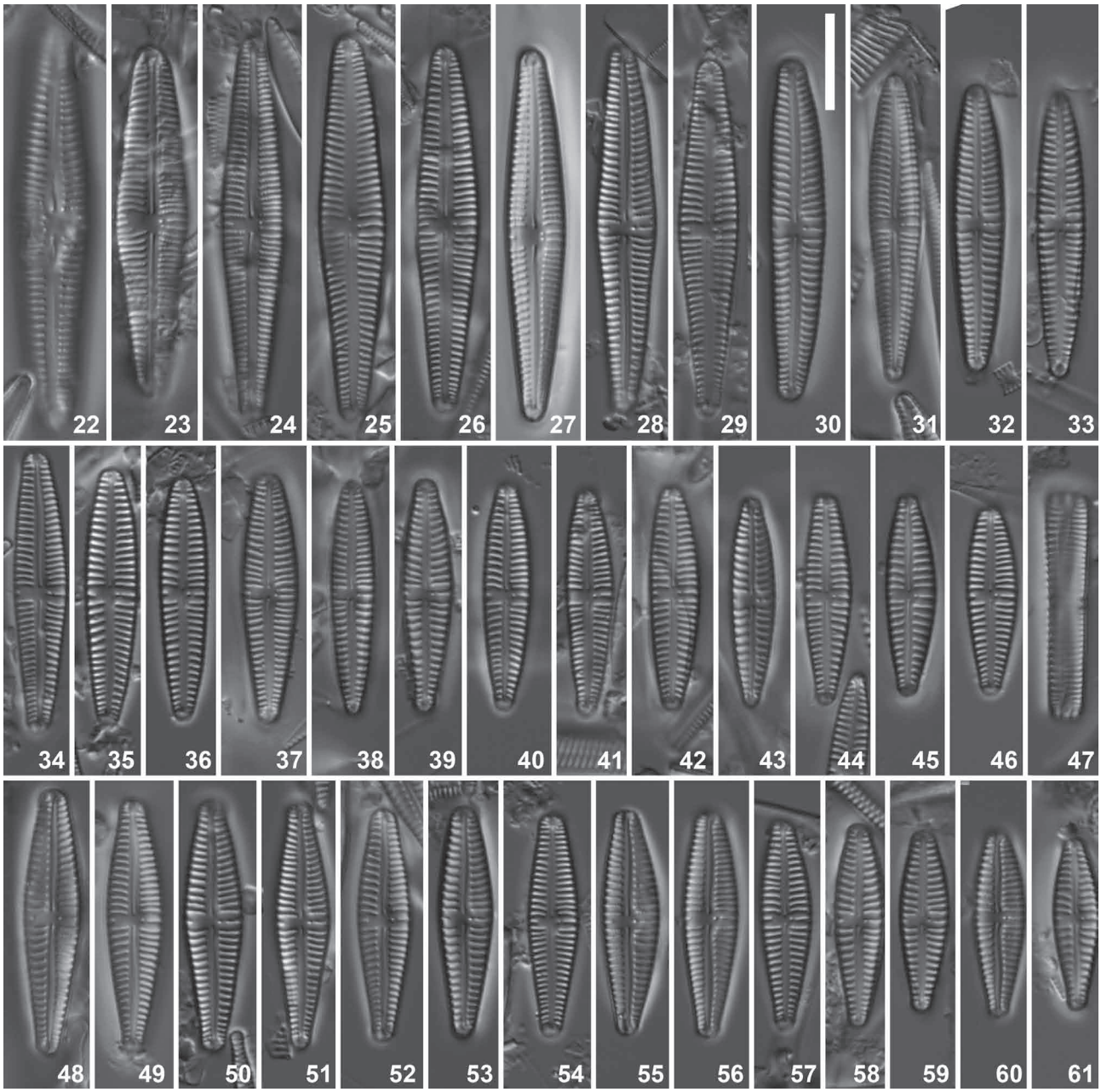
Taxonomic remarks:—Although *Gomphonema jamesrossense* shows a typical gomphonemoid structure and outline, there are hardly any *Gomphonema* taxa that can be confused with the new species. *Gomphonema clavatulum* Reichardt (1999: 25) shows a slight resemblance in valve outline although the footpole in the later is more acutely rounded giving the valve a more clavate outline compared to the almost linear valves in *G. jamesrossense*. *Gomphonema sarcophagus* Gregory (1856: 13) has a similar linear outline, but with clearly protracted, rostrate headpoles and footpoles. The Antarctic *Gomphonema signyensis* has a less linear valve outline with a narrower headpole, compared to *G. jamesrossense*, a larger valve width of more than 5 µm (Kociolek & Jones 1995), whereas the valves of *G. jamesrossense* do not exceed 4.5 µm in width, and a finer striation of up to 18 striae in 10 µm (instead of up to 14 in *G. jamesrossense*).

***Gomphonema maritimo-antarcticum* Van de Vijver, Kopalová, Zidarova & Kociolek, *sp. nov*. (Figs 22–74)**

LM (Figs 22–61): Frustules in girdle view almost rectangular, weakly clavate with a slightly narrower footpole. Valves lanceolate to rhombic-lanceolate, often asymmetrical to the apical axis. Headpole either not or only weakly protracted, acutely rounded in larger specimens, rostrate to truncated in mid-size to smaller specimens. Footpole always acutely rounded, pointed. Valve dimensions (n=100): length 20–50 µm, width 4.5–7.0 µm. Axial area rather narrow, broader in longer specimens, 1/4–1/5 of the total valve width, linear to linear-lanceolate, not widening towards the central area. Central area asymmetrical, rectangular to slightly wedge-shaped with one shortened stria on one side and one normal stria on the other side. Stigmoid rounded, at the end of the central stria, slightly separated from the last areola. Raphe clearly lateral, undulate. Proximal raphe endings deflected, weakly expanded. Distal raphe fissures hooked. Striae radiate to weakly moderate, becoming parallel near the headpole, 12–14 in 10 µm, more densely spaced near the head- and foothpole (up to 18 in 10 µm). In smaller specimens striae even parallel throughout the entire valve. Areolae weakly discernible in LM. SEM (66–74): Striae uniseriate composed of "C"- to "3"-shaped areolae (Figs 64, 66, 67, 70). Occasionally striae biseriate due to doubling of the areolae (Fig. 67). Striae continuing uninterruptedly onto the mantle, terminating in one small rounded areola (Fig. 62). Mantle edge forming a relatively broad hyaline zone (Fig. 62). Mantle of initial valves bearing a large series of rounded areolae per stria (Fig. 63). Girdle bands perforated by one series of rounded pores (Fig. 62). Footpole with a hyaline tip (Fig. 64). Large apical pore field present at the footpole composed of up to 8 rows of relatively large pores (Figs 62, 64, 66, 67). Initial valves and larger specimens showing an (often reduced) apical pore field at the headpole (Figs 63, 64, 65). Apical pore field bisected by the distal raphe fissures (Fig. 68). External raphe branches undulate with clearly deflected external proximal endings terminating in enlarged, drop-like pores (Figs 66, 67, 73). Distal raphe fissures (strongly) hooked, almost not continuing onto the mantle (Figs 69, 72). External stigmoid opening rounded to transapically enlarged (including in initial valves), clearly larger than the areolae, weakly separated from the last areola of the central stria (Figs 64, 66, 67, 73). Foot- and headpole with small pseudoseptum (Fig. 68). Internally, central nodule weakly raised. Internal proximal raphe endings clearly distant from each other, distinctly recurved (Fig. 71). Distal raphe endings terminating on small helictoglossae (Fig. 68). Striae internally bearing vimines, oriented perpendicularly to the striae. Doubling of areolae occasionally visible (Fig. 74). Areolae internally with round foramina. Internal stigmoid opening slit-like, well separated from the last areola in the central striae (Fig. 71).

Type:—LIVINGSTON ISLAND (SOUTH SHETLAND ISLANDS). Byers Peninsula, sample BY15 (62° 39' 24.1" S, 61° 06' 48.9"), *B. Van de Vijver*, *11 January 2009* (holotype BR! slide no. 4445, isotype PLP! slide 300, University of Antwerp, Belgium).

Ecology and distribution:—*Gomphonema maritimo-antarcticum* is a very common diatom in large lakes and ponds of James Ross Island and the South Shetland Islands, including Livingston Island and other major islands (King George Island and Nelson Island, Zidarova, pers. obs.). Large populations have been found in slightly to very alkaline lakes, ponds and streams (pH 7.78–9.30) with a low to moderate conductivity (<33000 µS/cm). Based on the available iconographic data from earlier studies in other areas in Antarctica, the species might also be present further south, on Horseshoe Island, Antarctic Peninsula (Wasell & Håkansson 1992, figs 28–33, 36, 84, as *Gomphonema* cf. *angustatum/parvulum*) and on the Antarctic Continent (Sabbe *et al*. 2003, p. 237, fig. 50, as *Gomphonema* sp.).



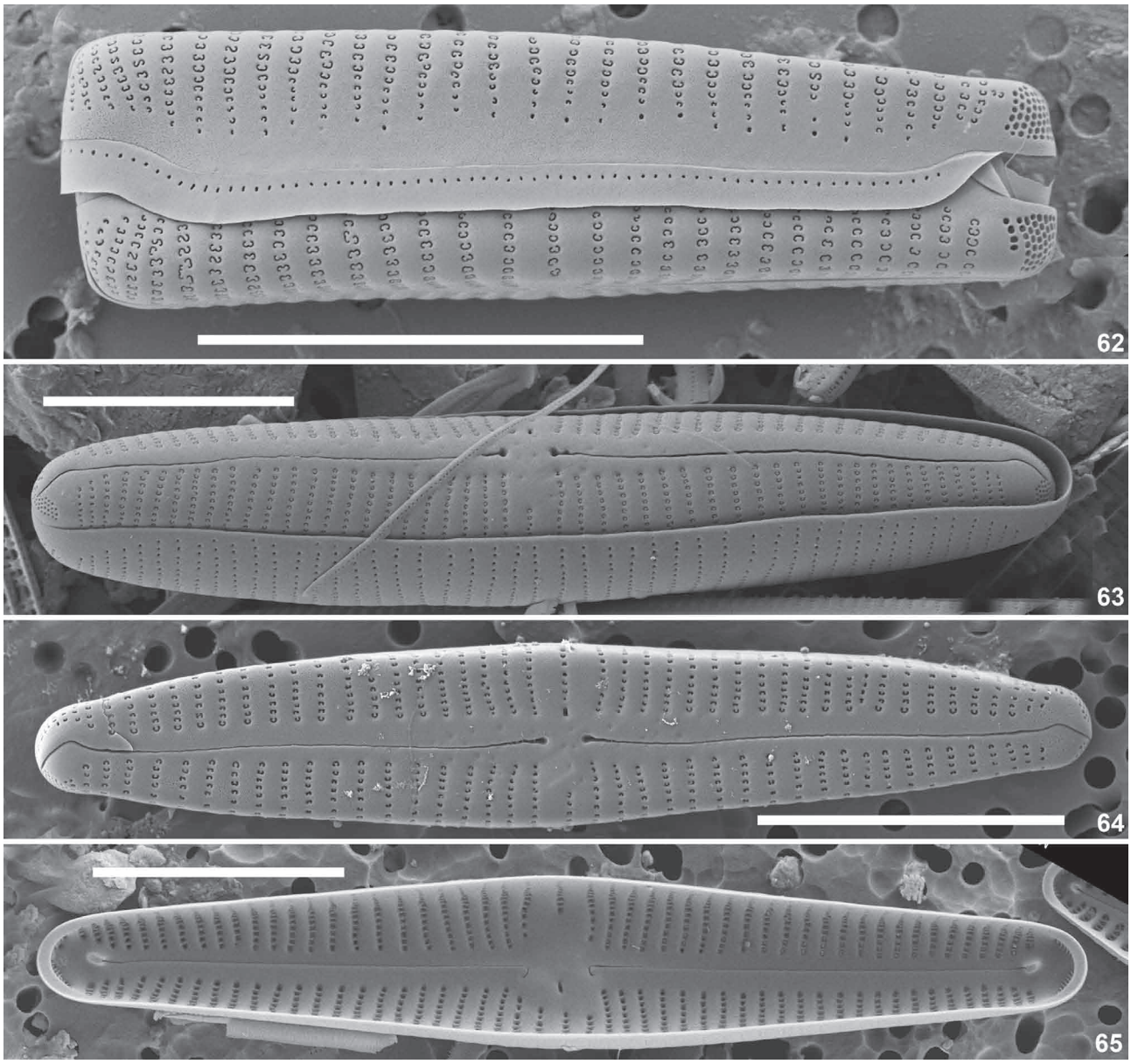
FIGURES 22–61. *Gomphonema maritimo-antarcticum*. LM pictures taken from the holotype population (sample BY015) from Byers Peninsula, Livingston Island. 48–61. Valves with a more rhombic-lanceolate valve outline and protracted, rostrate apices. Scale bar represents 10 µm.

Etymology:—The specific epithet refers to the biogeographical distribution area of the new species: Maritime Antarctic Region. The hyphen can and should be maintained in the species name based on art. 60.9 of the International Code of Nomenclature for algae, fungi and plants (McNeill *et al*. 2012).

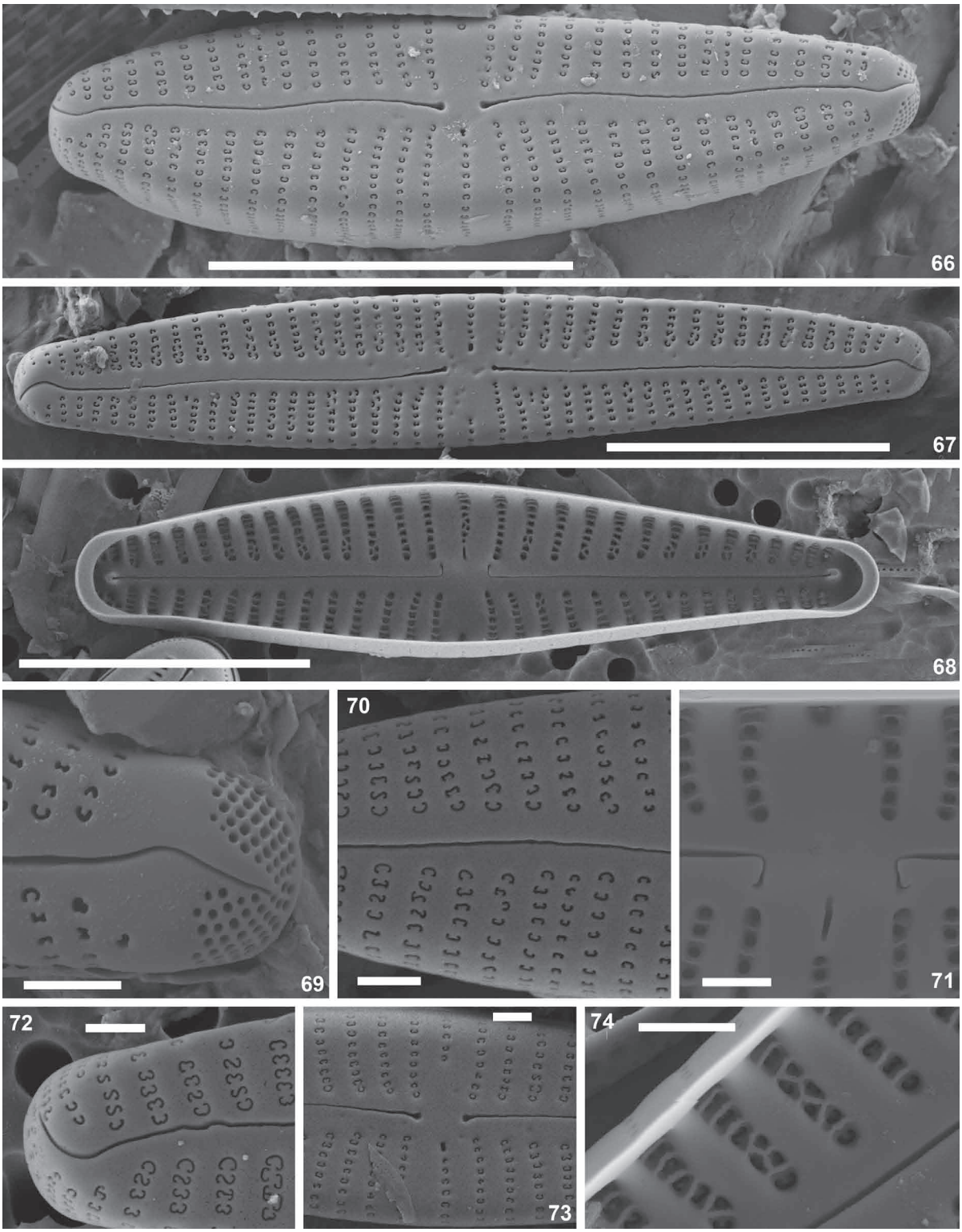
Taxonomic remarks:—Shorter valves of *Gomphonema maritimo-antarcticum* with a more rhombic-lanceolate outline can be confused with *G. punae* Lange-Bertalot & Rumrich in Rumrich *et al*. (2000: 140) and *G. pseudoclavatum* Lange-Bertalot & Reichardt in Lange-Bertalot *et al*. (1996: 92). Both taxa were described from southern Chile but can be separated from *G. maritimo-antarcticum*. Both Chilean taxa have a different striation pattern with equidistant striae throughout the entire valve. When considering the entire cell cycle, conspecificity is to be excluded based on the variable valve outline in *G. maritimo-antarcticum* (ranging from linear-lanceolate to rhombic-lanceolate) compared to the typical clavate, broadly lanceolate outline in *G. punae* and *G. pseudoclavatum*. *Gomphonema punae* was described from high elevations (1600–4300 m) in southern Chile, including Patagonia. The new species from Maritime Antarctica is proportionately narrower, being approximately the same width but nearly twice the valve length reported for *G. punae*. *Gomphonema punae* is usually shorter (14–26 µm) although no clear difference in valve width could be

found, thus it has a more squat valve outline. Other reported (and illustrated) populations always show the same squat valve outline (Morales *et al*. 2007, Alvial *et al*. 2008, Sala *et al*. 2008) as shown in the type population of *G. punae*. More elongate valves as could be found in populations of *G. maritimo-antarcticum* have never been seen in illustrated records of *G. punae* of South America.

The Antarctic *Gomphonema signyense* can be separated again by having linear to linear-clavate valves with broader and obtusely rounded headpole, which were not observed in any of the studied populations of *G. maritimo-antarcticum*, as well as by the comparatively more radiate striae in *G. maritimo-antarcticum*.



FIGURES 62–65 *Gomphonema maritimo-antarcticum*. SEM pictures taken from various maritime Antarctic populations including the type population (sample BY015, Figs 64, 65) from Byers Peninsula, Livingston Island. 62. Girdle view of an entire frustule. Note the presence of the apical pore field almost entirely on the mantle, the hyaline mantle edge and the small areolae terminating the mantle striae. 63. Girdle view of an initial valve. Note the apical pore fields on both head- and footpole, the small, rounded areolae on the mantle and the domed overall shape of the valves. 64. External view of an entire valve, most likely from the early cell cycle with an apical pore field on both head- and footpole. 65. Internal view of an entire valve, most likely from the early cell cycle with an apical pore field on both head- and footpole. Scale bar represents 10 µm.



FIGURES 66–74. *Gomphonema maritimo-antarcticum*. SEM pictures taken from various maritime Antarctic populations including the type population (sample BY015, Figs 66, 68, 74) from Byers Peninsula, Livingston Island. 66. External view on an entire valve with more rhombic-lanceolate valve outline showing the raphe, the apical pore field, the variation in areola shape and the position of the stigmoid. 67. External view on an entire valve with more narrowly lanceolate valve outline showing the raphe, the apical pore field, the variation in areola shape and the position of the stigmoid. 68. Internal view of an entire valve with the helictoglossae and the position of the stigmoid. 69. External detail of the apical pore field and the distal raphe ending at the footpole. 70. External detail of the striae showing the variation in areola shape. 71. Internal detail of the central area with the proximal raphe endings and the internal stigmoid opening. 72. External detail of the headpole with the distal raphe ending. 73. External detail of the central area with the proximal raphe endings and the external stigmoid opening. 74. Internal detail of the occasional doubling of the areolae per stria. Scale bar represents 10 µm except for Figs 69–74 where scale bar = 1 µm.

Discussion

Gomphonema is a large genus with species that can be assigned to different morphological groups. Kociolek & Kingston (1999) and Kociolek *et al*. (2016) have discussed some of these groups, based on the presence or absence of stigmoids, the ultrastructure of striae, the size and shape of the central nodule, the degree of curvature of the internal proximal raphe endings and the position of the apical pore field. The ultrastructure of the valves of these two new species from Antarctica shows them to be members of the "classical" species of the genus, by having the characteristic "C"- or "3"-shaped areolae, broadly recurved internal proximal raphe endings, a small mound-shaped central nodule and the position of the apical pore field almost entirely on the mantle. The majority of the species in this genus occur in this "classical" group, which includes amongst many others *G. parvulum* (Dawson 1972), *G. acuminatum* Ehrenberg (1832: 88) (Reichardt 1999, Kulikovskiy *et al*. 2015) and *G. augur* Ehrenberg (1840: 211) (Van de Vijver *et al*. 2013b).

An interesting observation was made on the initial valves of *G. maritimo-antarcticum*, which are asymmetrical to the apical axis, having simple stigmoids and bear apical pore fields at both poles. A similar observation was made on species of the closely related genus *Gomphoneis* Cleve (1894:73) (Kociolek & Stoermer 1988). We can see the differences in structure between the initial valves and others in the life cycle from the point of view of ontogenetic changes. In the case of *Gomphonema maritimo-antarcticum*, ontogeny shows a cymbelloid symmetry in terms of the position of the apical pore fields at both poles, a simple stigmoid opening internally, and asymmetry about the apical axis early in development. Later in development, an apical pore field at one pole, differentiation of the stigmoids between exterior and interior, and symmetry about the transapical axis are found in typical valves. Kociolek and Williams (1987) discussed how features of the initial valves that are early in the ontogenetic sequence of size diminution series might reflect the phylogenetic history of the taxa, in this case, the close relationship with cymbelloid diatoms, and perhaps with groups such as *Reimeria* Kociolek & Stoermer (Kociolek & Stoermer 1987, Sala *et al*. 1993, Kermarrec *et al*. 2011, Nakov *et al*. 2014).

Our observations on *G. maritimo-antarcticum* showed great morphological variation in valve outline for this species. There were some apparent morphologically-distinct groups (such as those with straight outlines others more lanceolate-clavate (Figs 34–46) and others more rhombic-lanceolate with protracted headpoles (Figs 48–61)), however, in each case we could identify specimens/morphotypes that appeared to be intermediate forms between these groups. One interpretation of this high degree of variability might be that it is a case of incipient species, where polymorphism is related to speciation (*e.g*. Day & McPhail 1996, Skúlason *et al*. 1999, Adams & Huntingford 2004), demonstrated in plants (Nies & Reusch 2005), insects (Drummond *et al*. 2010), fishes (Snorrason & Skúlason 2004) and mammals (Hadid *et al*. 2013). However, active pseudocryptic speciation is another plausible explanation and has been demonstrated by several other freshwater diatoms, including the genus *Gomphonema*. Kermarrec *et al*. (2013) and Abarca *et al*. (2014) recognized new species from morphologically similar populations in the *G. parvulum* species complex based on molecular research, although morphologically the differences between these new species were hardly noticeable. In the past, a similar approach was used to unravel pseudocryptic species complexes in other genera than *Gomphonema* (Vanelslander *et al*. 2009, Beszteri *et al*. 2003). Finally, the environmental conditions that prevail in the Maritime Antarctic Region, with large fluctuations in both temperature and moisture, might also be important drivers of this phenotypic plasticity. As not all populations of *G. maritimo-antarcticum* were found in 100% identical conditions, adaptations to their environment might be advantageous for the species to survive. Further morphological and molecular approaches with diatoms might prove fruitful to determine if this relationship between increased variation and incipient speciation holds across taxa.

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References

Abarca, N., Jahn, R., Zimmerman, J. & Enke, N. (2014) Does the cosmopolitan diatom *Gomphonema parvulum* (Kützing) Kützing have a biogeography? *PLoS ONE* 9: e86885.
http://dx.doi.org/10.1371/journal.pone.0086885

Adams, C.E. & Huntingford, F.A. (2004) Incipient speciation driven by phenotypic plasticity? Evidence from sympatric populations of Arctic charr. *Biological Journal of the Linnaean Society* 81: 611–618.
http://dx.doi.org/10.1111/j.1095-8312.2004.00314.x

Agardh, C.A. (1831) *Conspectus Criticus Diatomacearum*. *Part 3*. Litteris Berlingianis, Lund, pp. 33–48.

Alvial, I.E., Cruces, F.J., Araneda, A.E., Grosjean, M. & Urrutia, R.E. (2008) Estructura comunitaria de diatomeas presentes en los sedimentos superficiales de ocho lagos andinos de Chile central. *Revista Chilena de Historia Natural* 81: 83–94.
http://dx.doi.org/10.4067/S0716-078X2008000100007

Beszteri, B., Acs, E. & Medlin, L.K. (2005) Ribosomal DNA sequence variation among sympatric strains of the *Cyclotella meneghiniana* complex (Bacillariophyceae) reveals cryptic diversity. *Protist* 156: 317–333.
http://dx.doi.org/10.1016/j.protis.2005.07.002

Bory de Saint-Vincent, J.B.M. (1822) *Dictionnaire Classique d'Histoire Naturelle*. Rey & Gravier, libraires-éditeurs, Baudouin Frères, libraires-éditeurs 2, Paris.

Cleve, P.T. (1894) Synopsis of the Naviculoid Diatoms, Part I. *Kongliga Svenska-Vetenskaps Akademiens Handlingar* 26: 1–194.

Dawson, P.A. (1972) Observations on the structure of some forms of *Gomphonema parvulum* Kütz. *British phycological Journal* 7: 255–271.
http://dx.doi.org/10.1080/00071617200650261

Day, T. & McPhail, J.D. (1996) The effect of behavioural and morphological plasticity on foraging efficiency in the threespined stickleback (*Gasterosteus* sp.). *Oecologia* 108: 380–388.
http://dx.doi.org/10.1007/BF00334665

Drummond, C.S., Xue, H-J., Yoder, J.B. & Pellmyr, O. (2010) Host-associated divergence and incipient speciation in the yucca moth *Prodoxus coloradensis* (Lepidoptera: Prodoxidae) on three species of host plants. *Heredity* 105: 183–196.
http://dx.doi.org/10.1038/hdy.2009.154

Ehrenberg, C.G. (1832) Über die Entwicklung und Lebensdauer der Infusionsthiere; nebst ferneren Beiträgen zu einer Vergleichung ihrer organischen Systeme. *Abhandlungen der Königlichen Akademie der Wissenschaften zu Berlin* 1831: 1–154.

Ehrenberg, C.G. (1838) *Die Infusionsthierchen als vollkommene Organismen*. *Ein Blick in das tiefere organische Leben de Natur*. Verlag von Leopold Voss, Leipzig, 548 pp.
http://dx.doi.org/10.5962/bhl.title.58475

Ehrenberg, C.G. (1840) Characteristik von 274 neuen Arten von Infusorien. *Bericht über die zur Bekanntmachung geeigneten Verhandlungen der Königlich-Preussischen Akademie der Wissenschaften zu Berlin* 1840: 197–219.

Ehrenberg, C.G. (1843) Mittheilungen über 2 neue asiatische Lager fossiler Infusorien-Erden aus dem russischen Trans-Kaukasien (Grusien) und Sibirien. *Bericht über die zur Bekanntmachung geeigneten Verhandlungen der Königlich-Preussischen Akademie der Wissenschaften zu Berlin* 1843: 43–49.

Frenguelli, J. (1924) Diatomeas de Tierra del Fuego. *Anales de la Sociedad Científica Argentina* 97: 87–118, 231–266.

Frenguelli, J. (1945) El Platense y sus diatomeas, Las diatomeas del Platense. *Revista del Museo de La Plata (Nueva Serie), Seccion Paleontología* 3: 77–221.

Gregory, W. (1856) Notice of some new species of British Fresh-water Diatomaceae. *Quarterly Journal of Microscopical Science*, *new series*, *London* 4: 1–14.

Grunow, A. (1877) New Diatoms from Honduras, with notes by F. Kitton. *Monthly Microscopical Journal, London* 18: 165–186.
http://dx.doi.org/10.1111/j.1365-2818.1877.tb00123.x

Hadid, Y., Tzur, S., Pavlicek, T., Sumbera, R., Skilba, J., Lövy, M., Fragman-Sapir, O., Beiles, A., Arieli, R., Raz, S. & Nevo, E. (2013) Possible incipient sympatric ecological speciation in blind mole rats (*Spalax*). *Proceedings of the National Academy of Sciences of the United States of America* 110: 2587–2592.
http://dx.doi.org/10.1073/pnas.1222588110

Kellogg, T.B. & Kellogg, D.E. (2002) Non-marine and littoral diatoms from Antarctic and Subantarctic regions. Distribution and updated taxonomy. *Diatom Monographs* 1: 1–795.

Kermarrec, L., Ector, L., Bouchet, A., Rimet, F. & Hoffmann, L. (2011) A preliminary phylogenetic analysis of the Cymbellales based on 18S rDNA gene sequencing. *Diatom Research* 26: 305–315.
http://dx.doi.org/10.1080/0269249X.2011.633255

Kermarrec, L., Bouchez, A., Rimet, F. & Humbert, F. (2013) First evidence of the existence of semi-cryptic species and of a phylogeographic structure in the *Gomphonema parvulum* (Kützing) Kützing complex (Bacillariophyta). *Protist* 164: 686–705. http://dx.doi.org/10.1016/j.protis.2013.07.005

Kociolek, J.P. & Jones, V.L. (1995) *Gomphonema signyensis* sp. nov., a freshwater diatom from maritime Antarctica. *Diatom Research* 10: 269–276. http://dx.doi.org/10.1080/0269249X.1995.9705349

Kociolek, J.P. & Kingston, J.C. (1999) Taxonomy, ultrastructure and distribution of gomphonemoid diatoms (Bacillariophyceae: Gomphonemataceae) from rivers of the United States. *Canadian Journal of Botany* 77: 686–705. http://dx.doi.org/10.1139/b99-007

Kociolek, J.P. & Stoermer, E.F. (1987) Ultrastructure of *Cymbella sinuata* and its allies (Bacillariophyceae), and their transfer to *Reimeria*, gen. nov. *Systematic Botany* 12: 451–459. http://dx.doi.org/10.2307/2418882

Kociolek, J.P. & Stoermer, E.F. (1988) Taxonomy, ultrastructure, and distribution of *Gomphoneis herculeana*, *G. eriense* and closely related species. *Proceedings of the Academy of Natural Sciences of Philadelphia* 140: 24–97.

Kociolek, J.P. & Williams, D.M. (1987) Unicell ontogeny and phylogeny: Examples from the diatoms. *Cladistics* 3: 274–284. http://dx.doi.org/10.1111/j.1096-0031.1987.tb00511.x

Kociolek, J.P., Woodward, J.C. & Graeff, C. (2016) New and endemic *Gomphonema* C.G. Ehrenberg (Bacillariophyceae) species from Hawaii. *Nova Hedwigia* 102: 141–171. http://dx.doi.org/10.1127/nova_hedwigia/2015/0296

Kopalová, K. & Van de Vijver, B. (2013) Structure and ecology of freshwater benthic diatom communities from Byers Peninsula (Livingston Island, South Shetland Island). *Antarctic Science* 25: 239–253. http://dx.doi.org/10.1017/S0954102012000764

Kopalová, K., Nedbalová, L., de Haan, M. & Van de Vijver, B. (2011) Description of five new species of the diatom genus *Luticola* (Bacillariophyta, Diadesmidaceae) found in lakes of James Ross Island (Maritime Antarctic Region). *Phytotaxa* 27: 44–60. http://dx.doi.org/10.11646/phytotaxa.27.1.5

Kopalová, K., Veselá, J., Elster, J., Nedbalová, L., Komárek, J. & Van de Vijver, B. (2012) Benthic diatoms (Bacillariophyta) from seepages and streams on James Ross Island (NW Weddell Sea, Antarctica). *Plant Ecology and Evolution* 145: 190–208. http:// dx.doi.org/10.5091/plecevo.2012.639

Kopalová, K., Nedbalová, L., Nývlt, D., Elster, J. & Van de Vijver, B. (2013) Diversity, ecology and biogeography of the freshwater diatom communities from Ulu Peninsula (James Ross Island, NE Antarctic Peninsula). *Polar Biology* 36: 933–948. http:// dx.doi.org/10.1007/s00300-013-1317-5

Kopalová, K., Ochyra, R., Nedbalová, L. & Van de Vijver, B. (2014) Moss-inhabiting diatoms from two contrasting Maritime Antarctic islands. *Plant Ecology and Evolution* 147: 67–84. http://dx.doi.org/10.5091/plecevo.2014.896

Kulikovskiy, M.S., Kociolek, J.P., Solak, C.N. & Kuznetsova, I. (2015) The diatom genus *Gomphonema* Ehrenberg in Lake Baikal. II. Revision of taxa from *Gomphonema acuminatum* and *Gomphonema truncatum-capitatum* complexes. *Phytotaxa* 233: 251–272. http://dx.doi.org/10.11646/phytotaxa.233.3.3

Kützing, F.T. (1844) *Die Kieselschaligen*. *Bacillarien oder Diatomeen*. Nordhausen, 152 pp.

Kützing, F.T. (1849) *Species Algarum*. F.A. Brockhaus, Leipzig, 922 pp.

Lange-Bertalot, H. & Metzeltin, D. (1996) Oligotrophie-Indikatoren. 800 Taxa repräsentativ für drei diverse Seen-Typen. Kalkreich - Oligodystroph - Schwach gepuffertes Weichwasser. *Iconographia Diatomologica* 2: 1–390.

Lange-Bertalot, H., Külbs, K., Lauser, T., Nörpel-Schempp, M. & Willmann, M. (1996) Dokumentation und Revision der von Georg Krasske beschriebenen Diatomeen-Taxa. *Iconographia Diatomologica* 3: 1–358.

McNeill, J., Barrie, F.R., Buck, W.R., Demoulin, V., Greuter, W., Hawksworth, D.L., Herendeen, P.S., Knapp, S., Marhold, K., Prado, J., Prud'homme Van Reine, W.F., Smith, G.F., Wiersema, J.H. & Turland, N.J. (2012) International Code of Nomenclature for algae, fungi, and plants (Melbourne Code). *Regnum Vegetabile* 154: 1–240.

Morales, E.A., Vis, M.L., Fernández, E. & Kociolek, J.P. (2007) Epilithic diatoms (Bacillariophyta) from cloud forest and alpine streams in Bolivia, South America II: A preliminary report on the diatoms from Sorata, Department of La Paz. *Acta Nova* 3: 680–696.

Nakov, T, Ruck, E.C., Galachyants, Y., Spaulding, S.A. & Theriot, E.C. (2014) Molecular phylogeny of the Cymbellales (Bacillariophyceae, Heterokontophyta) with a comparison of models for accommodating rate-variation across sites. *Phycologia* 53: 359–373. http://dx.doi.org/10.2216/14-002.1

Nies, G. & Reusch, T.B.H. (2005) Evolutionary divergence and possible incipient speciation in post-glacial populations of a cosmopolitan aquatic plant. *Journal of Evolutionary Biology* 18: 19–26. http://dx.doi.org/10.1111/j.1420-9101.2004.00818.x

Peragallo, M. (1921) *Diatomées d'eau douce et Diatomées d'eau salée*. *Deuxième Expédition Antarctique Française (1908-1910) commandée par le Dr*. *Jean Charcot*, *Sciences Naturelles: Documents Scientifiques*, *Botanique*. Masson et Cie, Paris, pp. 6–96. http://dx.doi.org/10.5962/bhl.title.64272

Reichardt, E. (1999) Zur Revision der Gattung *Gomphonema*. Die Arten um *G. affine/insigne*, *G. angustatum/micropus*, *G. acuminatum* sowie gomphonemoide Diatomeen aus dem Oberoligozan in Bohmen. *Iconographia Diatomologica* 8: 1–203.

Ross, R., Cox, E.J., Karayeva, N.I., Mann, D.G., Paddock, T.B.B., Simonsen, R. & Sims, P.A. (1979) An amended terminology for the siliceous components of the diatom cell. *Nova Hedwigia*, *Beiheft* 64: 513–533.

Round, F.E., Crawford, R.M. & Mann, D.G. (1990) *The diatoms: Biology and Morphology of the genera*. Cambridge University Press, Cambridge, 747 pp.

Rumrich, U., Lange-Bertalot, H. & Rumrich, M. (2000) Diatomeen der Anden. *Iconographia Diatomologica* 9: 1–649.

Sabbe, K., Verleyen, E., Hodgson, D.A., Vanhoutte, K. & Vyverman, W. (2003) Benthic diatom flora of freshwater and saline lakes in the Larsemann Hills and Rauer Islands, East-Antarctica. *Antarctic Science* 15: 227–248. http://dx.doi.org/10.1017/S095410200300124X

Sala, S.E., Guerrero, J.M. & Ferrario, M.E. (1993) Redefinition of *Reimeria sinuata* (Gregory) Kociolek & Stoermer and recognition of *Reimeria uniseriata* nov. sp. *Diatom Research* 8: 439–446. http://dx.doi.org/10.1080/0269249X.1993.9705273

Sala, S.E., Ramírez, J.J. & Plata, Y. (2008) Diatoms from lentic and lotic systems in Antioquia, Chocó and Santander Departments in Colombia. *Revista de Biología Tropical* 56: 1159–1178.

Skúlason, S., Snorrason, S.S., Jónsson, B. (1999) Sympatric morphs, populations and speciation in freshwater fish with emphasis on Arctic charr. *In*: Magurran, A.E. & May R. (Eds.) *Evolution of biological diversity*. Oxford University Press, Oxford, pp. 70–91.

Snorrason, S.S. & Skúlason, S. (2004) Adaptive speciation in northern freshwater fishes. *In*: Dieckmann U., Doebeli M., Metz J.A.J. & Tautz D. (Eds.) *Adapative Speciation*. Cambridge University Press, Cambridge, pp. 210–228. http://dx.doi.org/10.1017/cbo9781139342179.012

Turpin, P.J.F. (1828) Observations sur le nouveau genre *Surirella*. *Mémoires du Museum d'Histoire Naturelle, Paris* 16: 361–368.

Tyler, P.A. (1996) Endemism in freshwater algae, with special reference to the Australian region. *Hydrobiologia* 336: 127–135. http://dx.doi.org/10.1007/BF00010826

Van de Vijver, B. & Mataloni, G. (2008) New and interesting species in the genus *Luticola* D.G. Mann (Bacillariophyta) from Deception Island (South Shetland Islands). *Phycologia* 47: 451–467. http://dx.doi.org/10.2216/07-67.1

Van de Vijver, B. & Zidarova, R. (2011) Five new taxa in the genus *Pinnularia* sectio *Distantes* (Bacillariophyta) from Livingston Island (South Shetland Islands). *Phytotaxa* 24: 39–50. http://dx.doi.org/10.11646/phytotaxa.24.1.6

Van de Vijver, B., Gremmen, N.J.M., & Beyens, L. (2005) The genus *Stauroneis* (Bacillariophyceae) in the Antarctic region. *Journal of Biogeography* 32: 1791–1798. http://dx.doi.org/10.1111/j.1365-2699.2005.01325.x

Van de Vijver, B., Mataloni, G., Stanish, L. & Spaulding, S.A. (2010) New and interesting species of the genus *Muelleria* (Bacillariophyta) from the Antarctic Region and South Africa. *Phycologia* 49: 22–41. http://dx.doi.org/10.2216/09-27.1

Van de Vijver, B., Zidarova, R., Sterken, M., Verleyen, E., de Haan, M., Vyverman, W., Hinz, F. & Sabbe, K. (2011a) Revision of the genus *Navicula* s.s. (Bacillariophyceae) in inland water of the Sub-Antarctic and Antarctic with the description of 5 new species. *Phycologia* 50: 281–297. http://dx.doi.org/10.2216/10-49.1

Van de Vijver, B., Zidarova, R. & de Haan, M. (2011b) Four new *Luticola* taxa (Bacillariophyta) from the South Shetland Islands and James Ross Island (Maritime Antarctic Region). *Nova Hedwigia* 92: 137–158.

Van de Vijver, B. Cocquyt, C., de Haan, M., Kopalová, K. & Zidarova, R. (2013a) The genus *Surirella* (Bacillariophyta) in the sub-Antarctic and Maritime Antarctic Region. *Diatom Research* 28: 93–108. http://dx.doi.org/10.1080/0269249X.2012.739975

Van de Vijver, B., Jarlman, A., De Haan, M. & Compere, P. (2013b) Ultrastructure of *Gomphonema augur* and *Gomphonema gautieri* (Bacillariophyta). *Cryptogamie Algologie* 34: 103–116.

Van de Vijver, B., Zidarova, R. & Kopalová, K. (2014) New species in the genus *Muelleria* (Bacillariophyta) from the Maritime Antarctic Region. *Fottea* 14: 77–90. http://dx.doi.org/10.5507/fot.2014.006

Van der Werff, A. (1955) A new method of concentrating and cleaning diatoms and other organisms. *Verhandlungen der Internationalen Vereinigung für Theoretische und Angewandte Limnologie* 2: 276–277.

Vanelslander, B., Créach V., Vanormelingen, P., Ernst, A., Chepurnov, V.A., Sahan, E., Muyzer, G., Stal, L.J., Vyverman, W. & Sabbe, K. (2009) ecological differentiation between sympatric pseudocryptic species in the estuarine benthic diatom *Navicula phyllepta* (Bacillariophyceae). *Journal of Phycology* 45: 1278–1289.
http://dx.doi.org/10.11 11/j.1529-8817.2009.00762.x

Vanormelingen, P., Verleyen, E. & Vyverman, W. (2008) The diversity and distribution of diatoms: from cosmopolitanism to narrow endemism. *Biodiversity & Conservation* 17: 393–405.
http://dx.doi.org/10.1007/978-90-481-2801-3_12

Vyverman, W., Verleyen, E., Wilmotte, A., Hodgson, D.A., Willems, A., Peeters, K., Van de Vijver, B., De Wever, A., Leliaert, F. & Sabbe, K. (2010) Evidence for widespread endemism among antarctic organisms. *Polar Science* 4: 103–113.
http://dx.doi.org/10.1016/j.polar.2010.03.006

Wasell, A. & Håkansson, H. (1992) Diatom stratigraphy in a lake on Horseshoe Island, Antarctica: a marine-brackish-freshwater transition with comments on the systematics and ecology of the most common diatoms. *Diatom Research* 7: 157–194.
http://dx.doi.org/10.1080/0269249X.1992.9705205

Zidarova, R., Van de Vijver, B., Quesada, A. & de Haan, M. (2010) Revision of the genus *Hantzschia* (Bacillariophyceae) on Livingston Island (South Shetland Islands, Southern Atlantic Ocean). *Plant Ecology & Evolution* 143: 318–333.
http://dx.doi.org/10.5091/plecevo.2010.402

Zidarova, R., Kopalová, K. & Van de Vijver, B. (2012) The genus *Pinnularia* (Bacillariophyta) excluding the section *Distantes* on Livingston Island (South Shetland Islands) with the description of twelve new taxa. *Phytotaxa* 44 (1): 11–37.
http://dx.doi.org/10.11646/phytotaxa.44.1.2

Zidarova, R., Levkov, Z. & Van de Vijver, B. (2014) Four new *Luticola* taxa (Bacillariophyta) from Maritime Antarctica with an emended description of *Luticola truncata* Kopalová & Van de Vijver. *Phytotaxa* 170 (3): 155–168.
http://dx.doi.org/10.11646/phytotaxa.170.3.2