Plant Ecology and Evolution 147 (3): 374–391, 2014
http://dx.doi.org/10.5091/plecevo.2014.979

REGULAR PAPER

Revision of the genus *Halamphora* (Bacillariophyta) in the Antarctic Region

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Background and aims – The limnoterrestrial and aquatic diatom flora of the entire Antarctic Region (sub-Antarctic islands, Maritime Antarctic Region, Antarctic Continent) is currently under revision. One of the genera that still needed a thorough analysis is the genus *Halamphora*, recently split off from *Amphora*. *Halamphora* species are a typical constituent of the lake diatom flora in the Antarctic region.
Methods – Using both Light Microscopical (LM) and Scanning Electron Microscopical (SEM) techniques, the morphology of a large number of *Halamphora* taxa, present in the samples from the Antarctic Region, has been analysed. Each taxon is properly described, illustrated and compared with other morphologically similar *Halamphora* taxa, known worldwide.
Key results – A total of seven *Halamphora* taxa has been found. Two taxa could be identified using the currently available literature: *Halamphora veneta* (Kütz.) Levkov and *H. oligotraphenta* (Lange-Bert.) Levkov. Five new *Halamphora* species are described: *Halamphora ausloosiana* Van de Vijver & Kopalová sp. nov., *H. compereana* Van de Vijver & Levkov sp. nov., *H. dagmarobbelsiana* Van de Vijver & Levkov sp. nov., *H. lateantarctica* Van de Vijver, Kopalová, Zidarova & Levkov sp. nov. and *H. vyvermaniana* Van de Vijver, Kopalová, Zidarova & Levkov sp. nov.
Conclusions – The obtained results confirm the presence of a typical and highly specific limnoterrestrial diatom flora in the Antarctic Region and contradict the generally accepted idea about the worldwide distribution of diatoms.

Key words – Antarctic Region, Bacillariophyta, *Halamphora*, new species, morphology, taxonomy.

INTRODUCTION

The genus *Halamphora* (Cleve) Levkov was originally described by Cleve (1895) as a subgenus of *Amphora* Ehrenb. ex Kütz. In 2009, Levkov raised the subgenus to the genus level and recombined many *Amphora* taxa that presented all morphological features of the new genus to *Halamphora*. The genus is characterized by moderately to strongly dorsiventral valves with a shallow ventral mantle, uniseriate or biseriate striae comprised of round, elliptical to transversely elongated areolae occluded by hymenes, an eccentric raphe system and a girdle composed of numerous open copulae. Widespread species in this genus, often occurring in large abundances, are for instance all species belonging to the species complexes around the former *Amphora veneta* Kütz., *A. coffeaeformis* C.Agardh and *A. normanii* Rabenh.

In the Antarctic Region, almost all records of *Halamphora* species were attributed to *H.* (cf.) *veneta* (Kütz.) Levkov giving this presumably cosmopolitan species a very broad biogeographical distribution with records ranging from the Antarctic Continent to the sub-Antarctic islands in the southern Indian and Atlantic Oceans (Kellogg & Kellogg 2002). It was however quickly clear that species drift and force-fitting (Tyler 1996) increased the taxonomic uncertainty about this presumably cosmopolitan species. A first superficial analysis of some of the Antarctic populations revealed distinct differences between some of these populations making a revision of the genus *Halamphora* in all parts of the Antarctic Region highly necessary, especially in the light of further biogeographical and ecological research.

In this paper, we present the first revised species list of the genus *Halamphora* present in Sub-Antarctic and Antarc-

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tic inland waters, compiled on the basis of a critical revision of literature reports (Kellogg & Kellogg 2002) and, where necessary, (re)analysis of slides and samples from our own Antarctic collections (see table 1). Ile Amsterdam, although located just north of the sub-Antarctic Region is included as it is part of the French Antarctic Territories. Five new *Halamphora* taxa are described from aquatic materials. In addition, information is provided for two other, previously described, *Halamphora* taxa with notes on their morphology, ecology and biogeography.

MATERIAL AND METHODS

Samples used in this study were collected from different aquatic habitats during several field trips on the South Shetland Islands (Livingston Island), James Ross Island and the sub-Antarctic Islands in the southern Indian (Ile Amsterdam, Iles Crozet). Additional material from the Antarctic Continent (Bunger Hills and Vestfold Hills) was acquired in collaboration with Dr. J.A.E. Gibson (Gibson et al. 2006 and unpublished data). Details on sampling methods and physico-chemical analyses can be found in Van de Vijver et al. (2002), Gibson et al. (2006), Kopalová et al. (2013), Kopalová & Van de Vijver (2013) and Chattová et al. (2014). All sampling localities are indicated on fig. 1 whereas all samples and slides used in the present study are listed in table 1.

Diatom samples for LM observation were prepared following the method described in Van der Werff (1955). Subsamples of the original material were oxidized using 37% H_2O_2 and heating to 80°C for approximately 1h. The reaction was further completed by the addition of $KMnO_4$. Following digestion and centrifugation (three times 10 minutes at 3700x g), the material free of organic matter was diluted with distilled water for sample mounting to avoid excessive concentrations of diatom valves and frustules on the slides. A subsample from the organic-free material was mounted in Naphrax® for diatom community studies. The slides were analysed using an Olympus BX53 microscope, equipped with Differential Interference Contrast (Nomarski) and an Olympus UC30 digital camera. 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 20 nm and studied in a ZEISS Ultra SEM microscope at 3 kV (Natural History Museum London, UK). Diatom terminology follows Ross et al. (1979), Round et al. (1990) and Levkov (2009). Comparisons with other Antarctic, South American and northern Hemisphere taxa, are based on Sabater et al. (1990), Carter & Round (1993), Lange-Bertalot et al. (1996) and Levkov (2009).

OBSERVATIONS

A total of seven *Halamphora* taxa has been found in the samples collected from the investigated sub-Antarctic (including Ile Amsterdam) and Antarctic localities. Two of them could be identified up to species level using the currently available literature: *Halamphora oligotraphenta* (Lange-Bert.) Levkov and *H. veneta*. A complete morphological and ecological characterisation is provided below.

Five taxa are described as new for science. These are described below and compared with similar taxa from the Northern hemisphere and from South America.

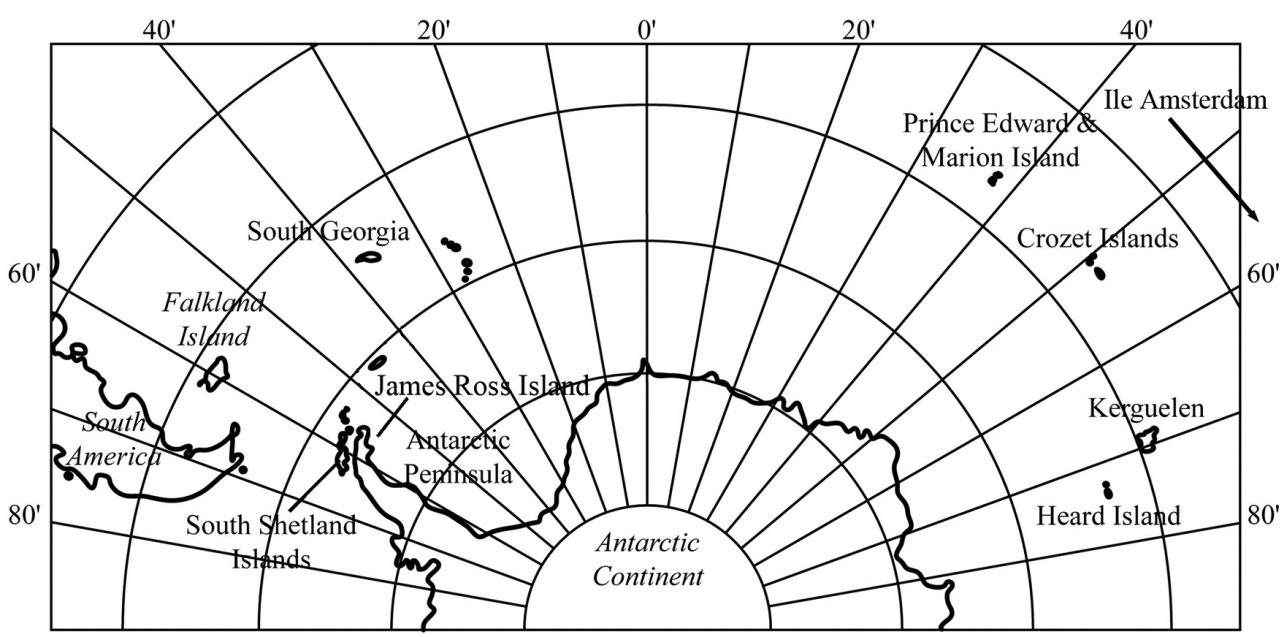

Figure 1 – The Antarctic Region with the location of the different islands and archipelagos discussed in this paper. Ile Amsterdam is positioned outside the map (arrow).

Table 1 – List of samples used in this study.

Sample ID	Geographic locality	Source
C-W581	Crozet	Van de Vijver et al. 2002
AMS-W121	Ile Amsterdam	Chattová et al. 2014
AMS-W033	Ile Amsterdam	Chattová et al. 2014
AMS-W041	Ile Amsterdam	Chattová et al. 2014
AMS-BM050	Ile Amsterdam	unpublished data
SG-W369	South Georgia	Van de Vijver & Beyens 1996
LIV-BY049	Livingston Island	Kopalová & Van de Vijver 2013
LIV-BY055	Livingston Island	Kopalová & Van de Vijver 2013
LIV-BY062	Livingston Island	Kopalová & Van de Vijver 2013
JRI-032	James Ross Island	Kopalová et al. 2013
JRI-063	James Ross Island	unpublished data
VH003	Vestfold Hills (Ant. Continent)	unpublished data
VH005	Vestfold Hills (Ant. Continent)	unpublished data
BH022	Bunger Hills (Ant. Continent)	Gibson et al. 2006

Previously described taxa

Halamphora veneta (Kütz.) Levkov
Figs 2 & 3

LM: morphological observations – Frustules elliptic with obtusely rounded ends (fig. 2O). Valves semi-lanceolate, dorsi-ventral with convex dorsal margin and slightly concave to straight ventral margin; valve apices rounded, weakly separated from the rest of the valve, sub-protracted and slightly ventrally bent; valve dimensions (n = 30): length 13–38 µm, width 3.5–6.5 µm, frustule width 9–13 µm. Axial area narrow, wider on the ventral valve side. Central area on the dorsal side almost indiscernible, wider on the ventral side. Raphe sternum broad, gradually narrowing towards the valve ends; raphe biarcuate with straight to slightly dorsally bent proximal endings, slightly expanded into small central pores. In some specimens central pores distantly spaced (fig. 2A–D & O). Dorsal striae 22–26 in 10 µm, distinctly punctate, radiate throughout, composed of round to elongated areolae. Ventral striae indistinct, hard to resolve in LM, 26–30 in 10 µm.

SEM: morphological observations, external and internal view – Transition between dorsal valve side and dorsal mantle abrupt (figs 2R, 3B & C). Narrow, thickened marginal ridge present along the junction of valve face and dorsal margin (figs 2Q, 3A & B). Marginal ridge strongly thickened at the apices (figs 2R, 3B). In some specimens, raphe sternum ornamented with round or irregularly-shaped depressions, variable in size and not internally penetrating (fig. 3A–C). Internally, distal raphe endings slightly ventrally deflected and terminating onto developed helictoglossae (fig. 2S). Proximally, raphe terminating onto fused central helictoglossae (figs 2S, 3E). Dorsal striae uniseriate, interrupted at the marginal ridge and continuing onto the valve mantle (figs 2R, 3C). Ventral striae not interrupted near the central nodule, composed of one single rounded to elongated areola (figs 2P, 3D). Internally, areolae occluded by hymens (fig. 3E). Girdle bands open, each bearing at least one row of large, round poroids similar in size as the ventral areolae (fig. 2P).

Habitat and distribution – Despite the large number of literature records in (sub-)Antarctica (Kellogg & Kellogg 2002: 33 records), *Halamphora veneta* s.s. was so far only confirmed from the sub-Antarctic islands Ile Amsterdam and Ile de la Possession in the southern Indian Ocean. The largest populations were found in rather alkaline (pH > 7.5) lakes and pools with a moderately high conductivity value (100–500 µS/cm). Only a very few valves (< 10 valves) were found in soils and wet mosses (Van de Vijver et al. 2002). On South Georgia, in the southern Atlantic Ocean, one small population was found in a small pool with a very alkaline pH (9.7) and low conductivity values (> 50 µS /cm) (Van de Vijver & Beyens 1996).

Taxonomical remarks – The population of *H. veneta* from Ile Amsterdam (fig. 3A–E) has a more prominent ornamentation of the raphe ledge, a higher stria and areola density than European (Hustedt 1930: 345, Levkov 2009: 242) and North American (Patrick & Reimer 1975: 73) populations. However, all other dimensional, morphological and ultrastructural features fit entirely with the description of *H. veneta* making conspecificity more than likely.

Halamphora oligotraphenta (Lange-Bert.) Levkov
Figs 4A–R & 5

LM: morphological observations – Valves semi-lanceolate, dorsi-ventral with a convex dorsal margin and a straight to weakly tumid in mid-valve ventral margin. Valve apices protracted and slightly ventrally bent, capitate in larger specimens to rostrate in smaller specimens. Valve dimensions (n = 30): length 17–31 µm, width 3.5–4.5 µm. Axial area narrow, wider on ventral valve side. Central area absent on dorsal side, longitudinally elongated on ventral side. Raphe biarcuate, raphe branches slightly curved, with proximal endings weakly expanded and slightly dorsally deflected and distal fissures dorsally deflected. Dorsal striae with fine punctation in LM, radiate throughout, 26–30 in 10 µm. Ventral striae almost indistinct, hard to resolve with LM, 28–36 in 10 µm.

SEM: morphological observations, external and internal view – Transition between dorsal valve side and dorsal mantle abrupt (fig. 5B & C). Narrow, very weakly developed marginal ridge present along junction of valve face and dorsal margin (fig. 5B). Raphe ledge flat, narrow, linear, slightly

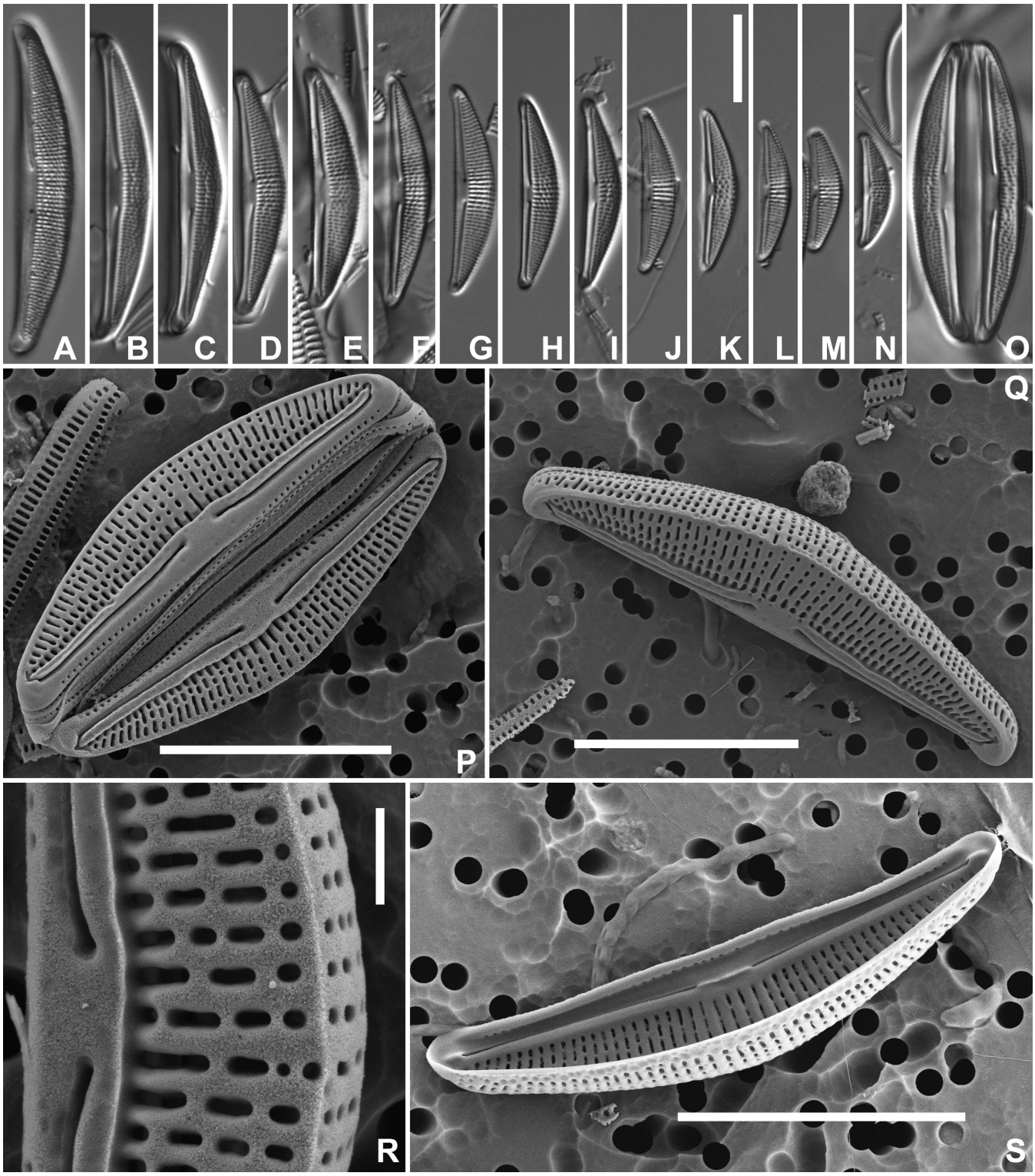

Figure 2 – *Halamphora veneta*: A–O, LM micrographs of largest population on Ile de la Possession (Iles Crozet) (sample C-W581). O represents a frustule in girdle view; P, Scanning electron micrograph (SEM), entire frustule showing two connected valves and some girdle elements; Q, SEM, entire valve in valve view; R, SEM, external detail of the central area; S, SEM, internal overview of an entire valve with the fused proximal helictoglossae. Scale bars represent 10 µm except for R where scale bar = 1 µm.

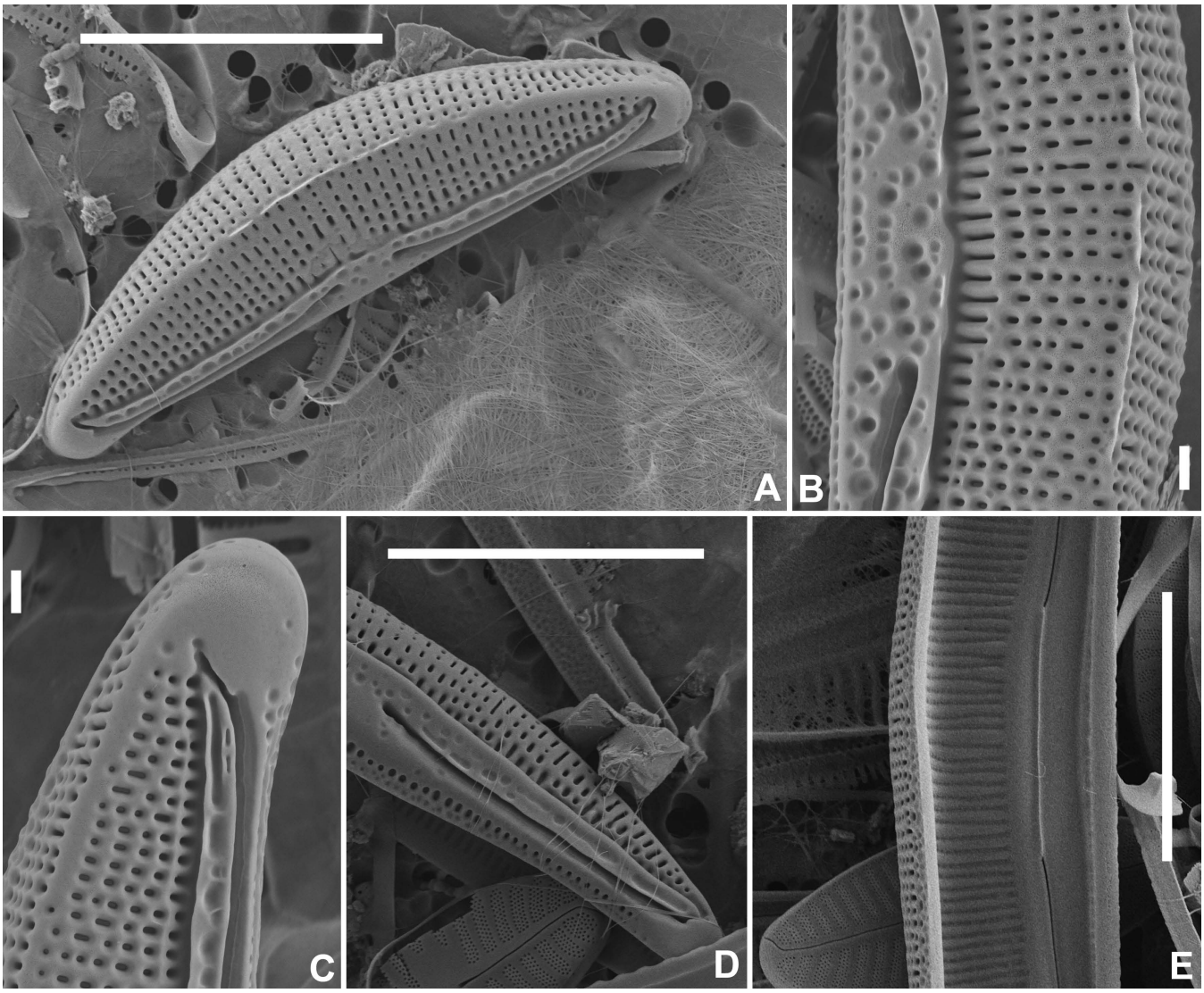

Figure 3 –Scanning electron micrographs (SEM) of the largest population of *Halamphora veneta* on Ile Amsterdam (sample AMS-W041): A, entire valve showing the ornamentation on the raphe ledge; B, external detail of the central area with the proximal raphe endings and the typical ornamentation; C, external detail of a valve apex showing the prominent raphe ledge; D, external detail of a valve apex in oblique view showing the mantle areolae; E, internal detail of the central area with fused helictoglossae. Scale bars represent 10 µm except for B & C where scale bars = 1 µm and E where scale bar = 5 µm.

wider in mid-valve, without ornamentation (fig. 5A & B). Internally (fig. 5G), distal raphe endings slightly ventrally deflected (fig. 5G), terminating onto developed helictoglossae. Proximally, raphe endings terminating onto fused central helictoglossae (fig. 5F). Dorsal striae uniseriate, composed of round to elongated areolae (fig. 5B & C). Ventral striae continuing onto the valve mantle, not interrupted in the region of the central nodule, composed of round to elongated areolae (fig. 5A). Internally, areolae occluded by hymenes (fig. 5F).

Habitat and distribution – At present *H. oligotraphenta* is only confirmed from James Ross Island (Kopalová et al. 2012, 2013 as *Amphora* sp.) Reported populations from other Antarctic localities in the Maritime Antarctic Region need to be carefully examined using SEM to distinguish them from for instance *Halamphora ausloosiana* Van de Vijver & Kopalová sp. nov. (see below). The largest populations were found in lakes on Ulu Peninsula and Clearwater Mesa with a very alkaline pH (between 8.0 and 8.8) and rather low to high conductivity values (up to 1000 µS/cm). In seepage areas and streams, the species, though present, was less frequently observed.

Taxonomical remarks – The populations of *H. oligotraphenta* from James Ross Island fit the protologue (Haworth 1974: 48, figs 6 & 19) and share comparable morphological features as European (Lange-Bertalot & Metzeltin 1996, Levkov 2009) populations. A small proportion of the analysed populations showed heavily silicified valves, the so-called ghost valves (figs 4Q & R, 5E). It is unclear how and why these valves are formed. For the separation from *H. ausloosiana*, see below.

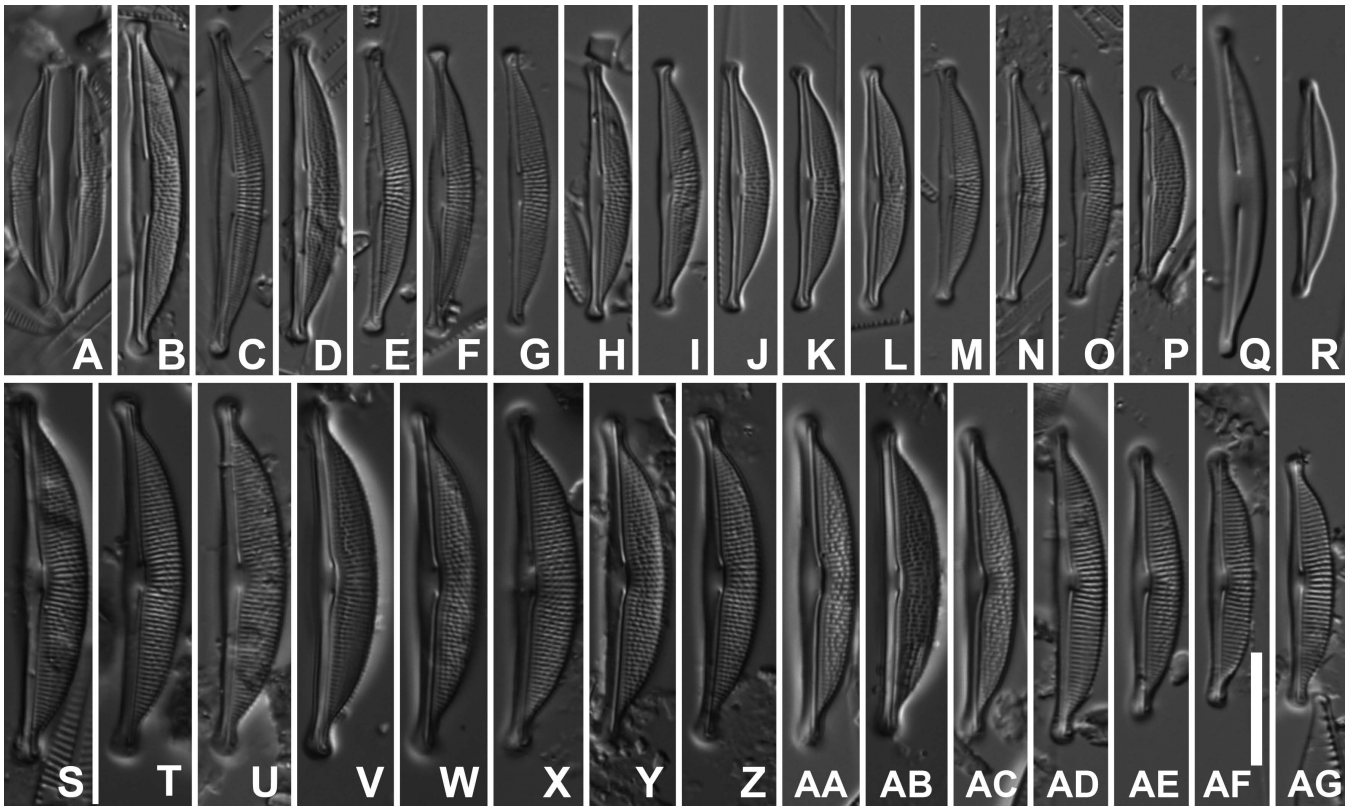

Figure 4 – *Halamphora oligotraphenta* (A–R) and *H. ausloosiana* (S–AG): A–R, LM micrographs of a population of *H. oligotraphenta* from James Ross Island (sample JRI-D032). A represents a frustule in girdle view; Q & R represent so-called ghost valves; S–AG, LM micrographs of the population of *H. ausloosiana* from Livingston Island (sample LIV-BY049). Scale bar represents 10 µm.

New taxa

Halamphora ausloosiana Van de Vijver & Kopalová, **sp. nov.**

Figs 4S–AG & 6

Type: holo-: BR-4370 (Botanic Garden Meise, Belgium); iso-: PLP-258 (University of Antwerp, Belgium), BRM-ZU9/75 (Hustedt Collection, Bremerhaven, Germany). – Type locality: Byers Peninsula, Livingston Island, South Shetland Islands, sample BY049 (62°38'43.1"S, 61°06'22.9"W), (coll. B.Van de Vijver, coll. date 14 Jan. 2009).

LM: description – Valves semi-lanceolate, dorsi-ventral. Dorsal margin convex to almost straight (fig. 4Y, AA, AD & AF) in mid-valve, ventral margin straight (fig. 4AB & AD) to weakly tumid in mid-valve (fig. 4E, Z, AE–AG). Valve ends distinctly set-off, slightly ventrally bent, sub-capitate in larger specimens to rostrate and slightly rounded in smaller specimens. Valve dimensions (n = 25): length 22–34 µm, valve width 4.0–6.5 µm. Axial area narrow, more expressed on the ventral valve side. Central area almost absent on the dorsal side, sometimes weakly semi-elliptical (fig. 4U, Z, AD, AF& AG), longitudinally elongated on the ventral side. Raphe biarcuate with slightly curved branches. Proximal ends distantly spaced, weakly expanded and slightly dorsally bent; distal fissures dorsally deflected. Dorsal striae showing a fine punctation in LM, 22–28 in 10 µm. Ventral striae indistinct, hard to resolve with LM, not interrupted in the region of the central nodule, 28–32 in 10 µm.

SEM: description, external and internal view – Transition between dorsal valve side and dorsal mantle abrupt (fig. 6A & C). Raphe ledge flat, wide, linear, distinctly wider in mid-valve, without ornamentation (fig. 6A–C). Internal distal raphe endings slightly ventrally deflected terminating onto developed helictoglossae (fig. 6F). Proximally, raphe terminating onto fused central helictoglossae (fig. 6E). Dorsal striae biseriate throughout. Areolae appearing as 'complex' with small circular foramina laying in two rows (fig. 6D) giving them a biseriate character. Biseriate character of striae also internally clearly visible (fig. 6F). Recessed sieve plates present within areolae. Areolae internally occluded by hymenes. Ventral striae composed of one single elongated areola, becoming smaller near the central area (figs 6A & C).

Etymology – The specific epithet '*ausloosiana*' is given in honour of our late colleague and dear friend Dr. Gert Ausloos (Botanic Garden Meise), head of Public Awareness of the Botanic Garden who passed away too early on March 2nd 2014.

Distribution and ecology – At present, *H. ausloosiana* has only been with certainty identified from the South Shetland Islands (Kopalová & Van de Vijver 2013 as *Amphora* cf. *veneta* Kütz.). It is however very likely that the distribution of this species is much larger but due confusion with similar taxa such as *H. veneta* and *H. oligotraphenta*, it is distribution is unclear. It has so far not been recorded during the revision of *H.* cf. *veneta* populations from the Antarctic Continent (see below). On Livingston Island (South Shetland

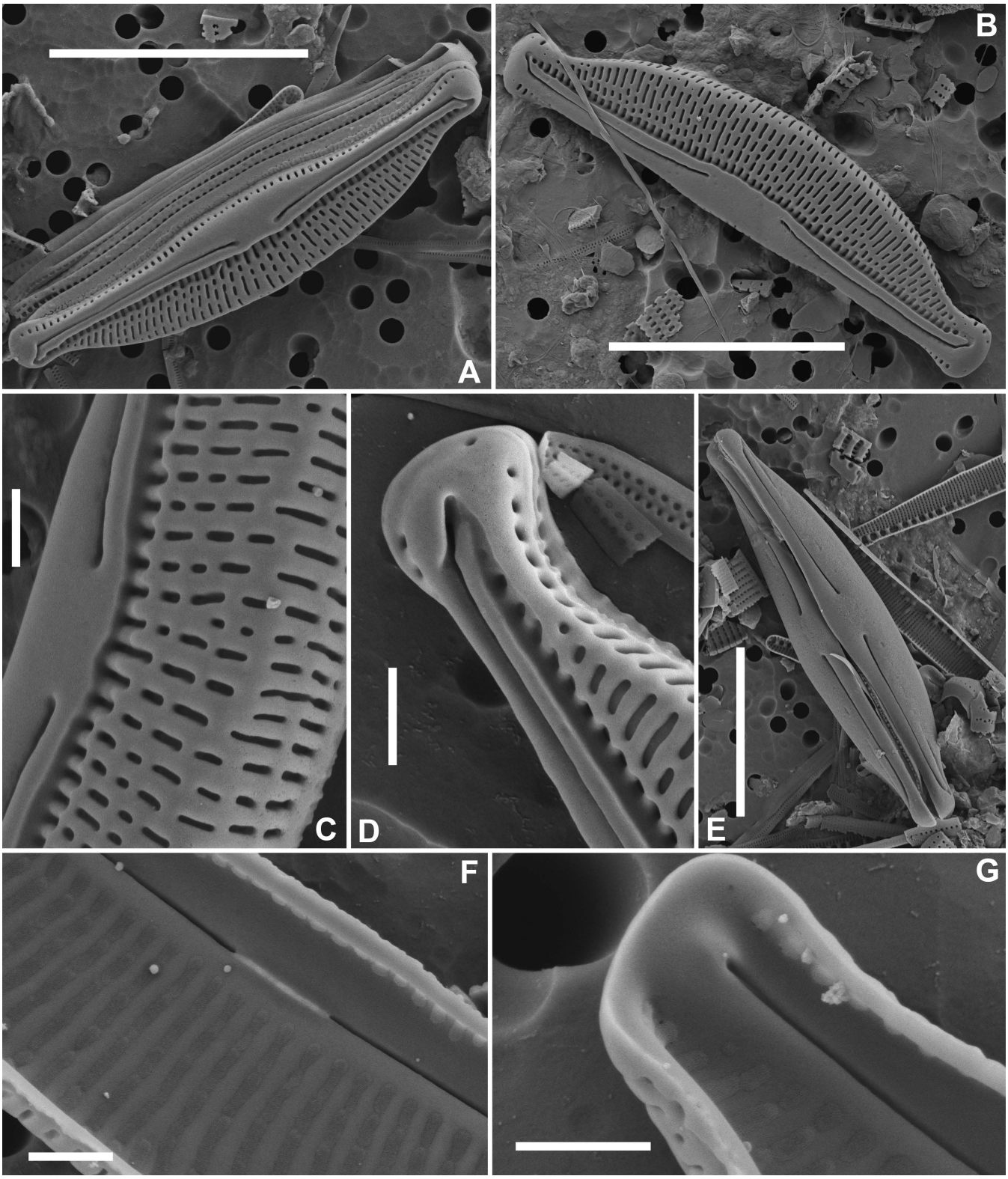

Figure 5 –Scanning electron micrographs (SEM) of a population of *Halamphora oligotraphenta* from James Ross Island (sample JRI-D032): A, entire valve with parts of the girdle bands; B, entire valve; C, external detail of the central area with the proximal raphe endings; D, external detail of a valve apex with the distal raphe fissure; E, external view of an entire frustule of the so-called ghost-valves lacking any ornamentation apart from the raphe branches; F, internal detail of the central area with fused helictoglossae; G, internal detail of a valve apex. Scale bars represent 1 µm except for A, B & E where scale bars = 10 µm.

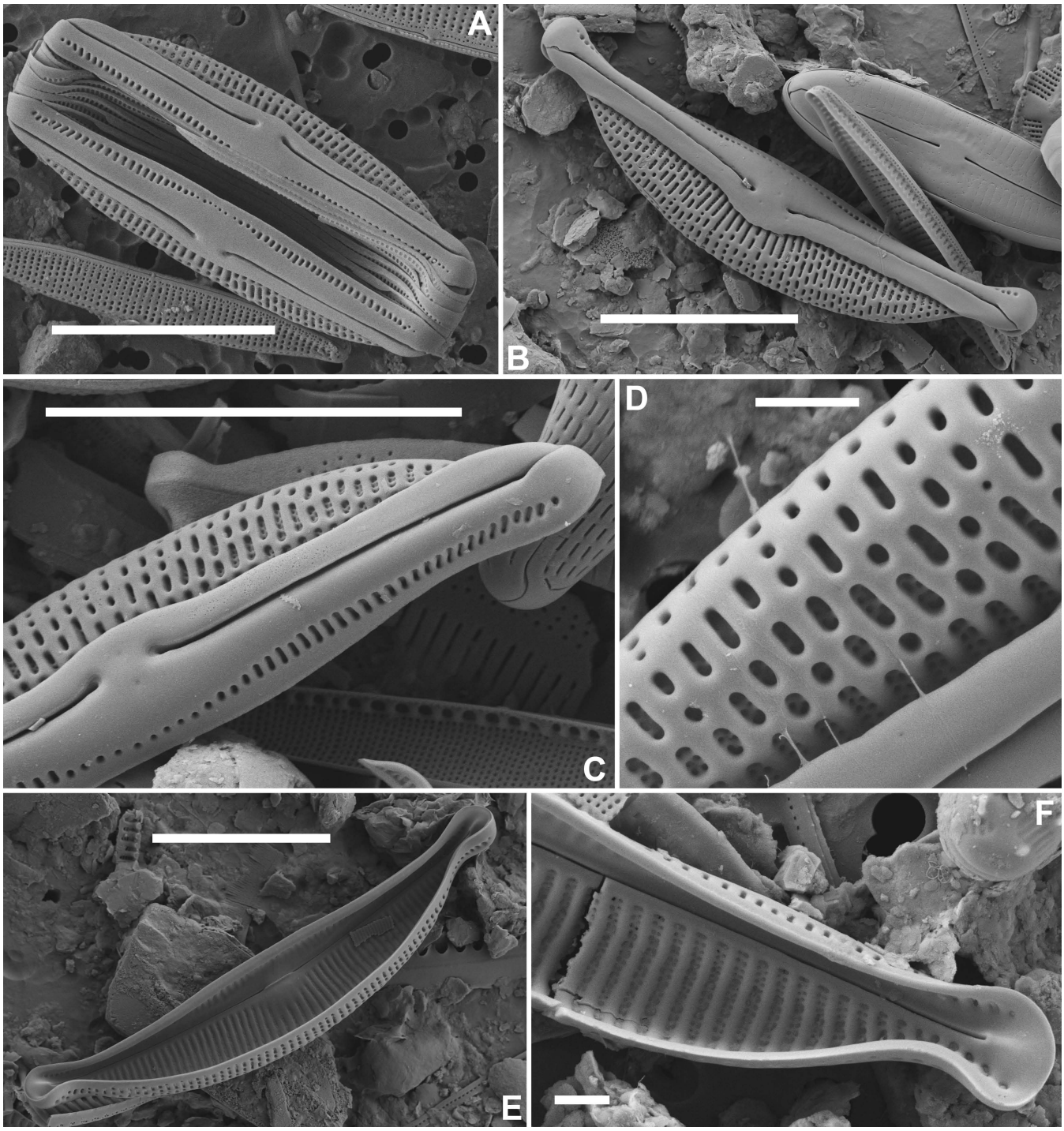

Figure 6 – Scanning electron micrographs (SEM) of the population of *Halamphora ausloosiana* from Livingston Island (sample LIV-BY049): A, entire frustule with parts of the girdle bands; B, entire valve; C, external detail of half a valve in oblique view showing the mantle striae composed of one single areola; D, external detail of the biseriate striae showing clearly the doubling of the areolae inside the striae ; E, internal overview of an entire valve with fused helictoglossae; F, internal detail of a valve apex with the covered biseriate striae. Scale bars represent 10 µm except for D & F where scale bars = 1 µm.

Islands), *H. ausloosiana* often forms rather large populations in the lakes and pools on Byers Peninsula. The type population was found in a small pool (10 m diameter) close to Limnopolar Lake. On one side of the pool water was dripping from a rock surface in the pool while on the other side, water was flowing out in a small braided river. The bottom was covered with fine sediment and larger pebbles. Thin algal mats were present in the pool. The pool had a rather alkaline pH (7.6) with a low specific conductance value (58 µS/cm). Dominant taxa in the pool include *Fragilaria capucina*

s.l., *Planothidium frequentissimum* (Lange-Bert.) Round & Bukht. and an at present unidentified *Staurosirella* taxon.

Taxonomical remarks – Based on valve size and shape, *Halamphora ausloosiana* resembles *H. coraensis* (Foged) Levkov (Foged 1964: fig. 16/11, Levkov 2009: plate 107: figs 33–37), but can be differentiated from latter by the shape of the valve ends (capitate and dorsally bent in *H. coraensis*), the ventral margin (distinctly concave in *H. coraensis*) and the dorsal margin (strongly convex in *H. coraensis*). *Halamphora acutiuscula* (Kütz.) Levkov shares similar morphological features as *H. ausloosiana* such as the valve outline. Additionally, *H. acutiuscula* has a similar areola structure with recessed sieve plates within (Levkov 2009: plate 234: figs 1–4). Differences between these two species are based on several morphological features: The areolae in *H. acutiuscula* have small round to slightly elongated external apertures, making the striae appearing as finely punctate. The proximal raphe fissures in *H. acutiuscula* are distinctly dorsally bent and positioned very closely to each other. The central nodule (central internal costae) in *H. acutiuscula* is inwards thickened and elevated compared to the rest of the valve.

Several *Halamphora* species with 'complex' areolae (areolae with recessed sieve plates) have been observed such as *H. aponina* (Kütz.) Levkov, *H. ghanensis* Levkov and *H. sydowii* (Cholnoky) Levkov (Levkov 2009). *Halamphora aponina* is characterized by narrower valves (3.0–4.5 µm vs. 4.0–6.5 µm), and entirely biseriate striae. *Halamphora ghanensis* has shorter valves (24–27 µm vs. 22–34 µm) and more finely punctated striae with lower stria density (14–16 vs. 22–28 in 10 µm). In *H. sydowii*, a single row of areolae close to the raphe is bordered by an internal longitudinal rib. This feature is not present in the *H. ausloosiana*. Moreover, the proximal raphe fissures in *H. sydowii* are distinctly dorsally bent and positioned very closely to each other contrary to *H. ausloosiana* that has distant proximal raphe fissures. Differences between *H. sydowii* and *H. ausloosiana* can also be observed in the stria density (17–19 vs. 22–28 in 10 µm).

Halamphora oligotraphenta differs in lacking the biseriate striae and having narrower valves (3.5–4.5 µm vs. 4.0–6.5 µm).

Halamphora compereana Van de Vijver & Levkov, **sp. nov.** Fig. 7

Type: holo-: BR-4371 (Botanic Garden Meise, Belgium); iso-: PLP-259 (University of Antwerp, Belgium), BRM-ZU9/76 (Hustedt Collection, Bremerhaven, Germany). – Type locality: Grand Tunnel, Île Amsterdam, TAAF sample AMS-W033 (37°48'47.1"S, 77°33'42.6"E), (leg. B. Van de Vijver, coll. date 4 Dec. 2007).

LM: description – Valves semi-lanceolate with convex dorsal margin and weakly concave to weakly inflated in mid-valve ventral margin. Valve apices distinctly set-off, capitate in larger specimens to rostrate in smaller specimens. Valve dimensions (n = 15): length 21–31 µm, width 4.0–5.5 µm. Central area on dorsal side variable in shape, rectangular (i.e. fig. 7H & I) to semi-elliptical (i.e. fig. 7C, J, L & N), bordered near the valve margin by 3–5 central striae. Central area on the ventral side wide not distinctly separated from the axial area. Raphe ledge narrow, linear, distinctly wider near the valve ends, fused with the valve face in mid-valve. Raphe biarcuate with slightly curved raphe branches. Proximal ends clearly dorsally bent and distal ends dorsally deflected. Dorsal striae showing fine punctation in LM, radiate throughout, 19–21 in 10 µm. Ventral striae indistinct, hard to resolve in LM, not interrupted near the central nodule 24–26 in 10 µm.

SEM: description, external and internal view – Transition between dorsal valve side and dorsal mantle abrupt (fig. 7P). Marginal ridge along the junction of valve face and dorsal margin absent (fig. 7P). Raphe ledge flat without ornamentation (fig. 7P & R). Internally (fig. 7S), distal raphe endings slightly ventrally deflected, terminating onto developed helictoglossae. Proximal raphe endings terminating onto fused central helictoglossae. Dorsal striae biseriate throughout, towards the dorsal margin, striae becoming uniseriate (fig. 7P& R). Areolae visible as 'complex' with small circular foramina arranged in two rows (7R). Recessed sieve plates present within the areolae which are clearly punctate (typically biseriate). Biseriate character of the striae also visible internally (fig. 7S). Areolae internally occluded by hymenes. Ventral striae composed of round to elongated areolae, smaller near the central area (fig. 7Q).

Etymology – This new species is dedicated to our dear colleague Pierre Compère (Botanic Garden Meise) on the occasion of his 80th birthday.

Distribution and ecology – *Halamphora compereana* was found in a lava cavern on Ile Amsterdam, which 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 very small, probably temporary pools, was continuously fed by water dripping from the cavern's ceiling, with a pH of 5.8 and a specific conductance of 239 µS cm^{-1}. The sample was dominated by several *Diadesmis* species (among others *D. vidalii* Van de Vijver & Ledeganck and *D. crozetikerguelensis* Le Cohu & Van de Vijver), *Planothidium subantarcticum* Van de Vijver & C.E.Wetzel, *Karayevia oblongella* (Østrup) Aboal, *Melosira* sp., *Orthoseira verleyenii* Van de Vijver, *Sellaphora barae* Van de Vijver & E.J.Cox, *Mayamaea cavernicola* Van de Vijver & E.J.Cox and *Chamaepinnularia aerophila* Van de Vijver & Beyens.

Taxonomical remarks – *Halamphora compereana* resembles *H. fontinalis* (Hust.) Levkov. Both taxa share the same valve outline and size, but can be differentiated by the shape of the central area. The central area on the dorsal side in *H. fontinalis* forms a broad fascia reaching the dorsal margin (Hustedt 1937: figs 24: 4, 5; Sala et al. 2006: figs 4, 6, 8, Levkov 2009: plate 222: figs 1–5) whereas in *H. compereana* the central area is always bordered by shortened striae, therefore never forming a fascia. *Halamphora rugosa* (Hust.) Levkov has longer valves (35–47 µm vs. 21–31 µm) with a distinctly convex ventral margin. Further differences between *H. compereana* and *H. rugosa* can be found in the position of the ventral striae, the shape of the central and axial areas, and the shape of the proximal raphe endings. *Halamphora compereana* has a comparable size as *H. schroederi* (Hust.) Lev-

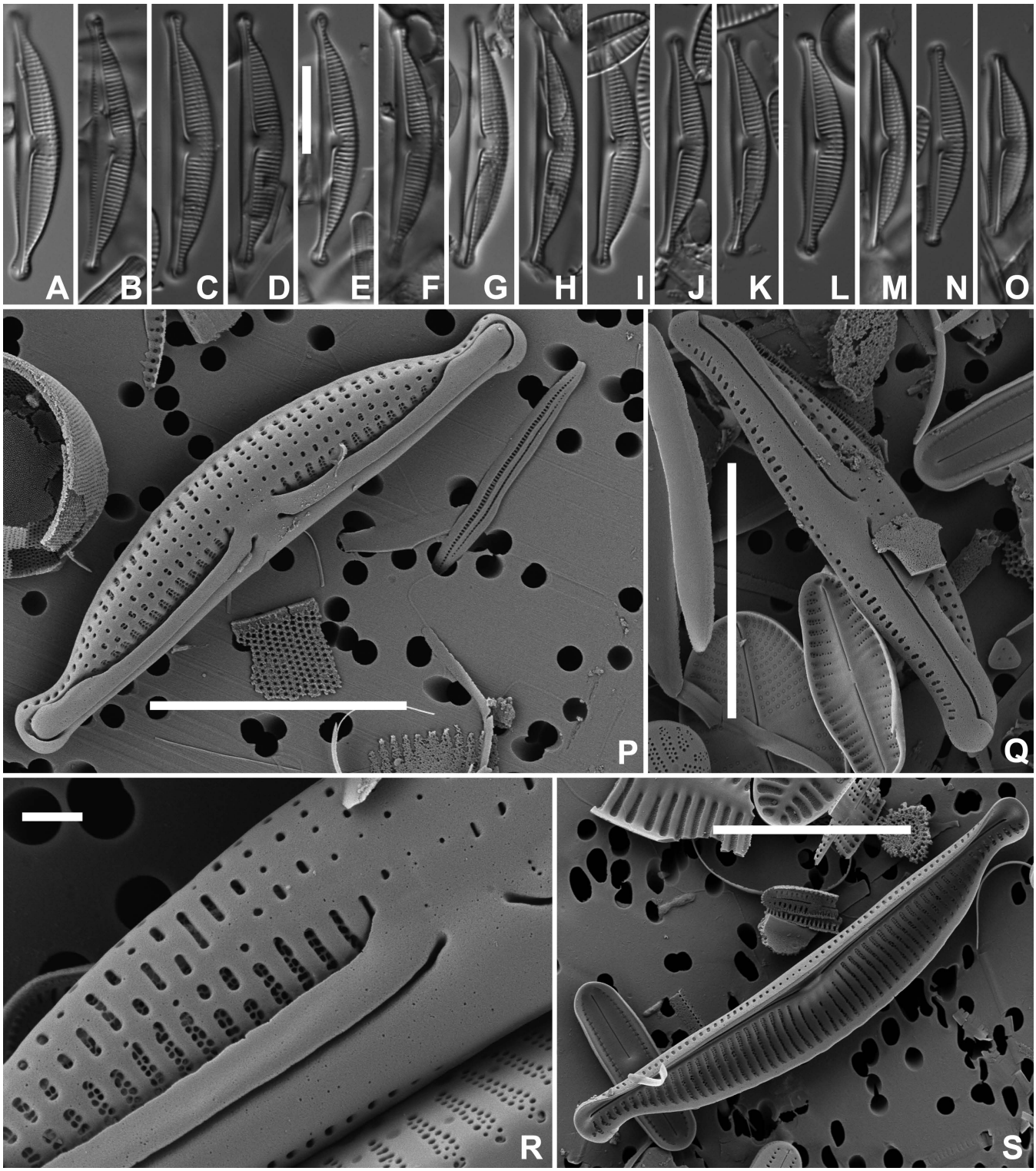

Figure 7 – *Halamphora compereana*: A–O, LM micrographs of the type population on Ile Amsterdam (sample AMS-W033); P, Scanning electron micrograph (SEM), entire valve with typical doubling of the areolae and the central area; Q, SEM, external view of a valve in oblique view showing the mantle areolae; R, SEM, external view of the central area showing the striae with a doubling of the areolae inside; S, SEM, internal overview of an entire valve. Scale bars represent 10 µm except for R where scale bar = 1 µm.

kov but can be differentiated from the latter by the shape of the central area on the dorsal valve side (Hustedt 1921: figs 16–18) which is absent in *H. schroederi* with the dorsal striae reaching the raphe ledge (partial conopeum sensu Levkov 2009). Additionally, in *H. schroederi* the internal virgae are strongly thickened, observable even with LM. From other taxa observed in the Antarctic and sub-Antarctic region, such as *H. ausloosiana* and *H. oligotraphenta*, *H. compereana* can be easily separated by the shape of the central area on the dorsal side and the proximal raphe endings. The central area on the dorsal side in *H. ausloosiana* and *H. oligotraphenta* is absent or almost absent, whereas in *H. compereana* it is rectangular to semi-elliptic in shape. Other differences include the proximal raphe endings that are distantly spaced and only slightly dorsally deflected in *H. oligotraphenta* and *H. ausloosiana* contrary to the clearly dorsally bent proximal raphe endings in *H. compereana*.

Halamphora dagmarobbelsiana Van de Vijver & Levkov, **sp. nov.**
Fig. 8

Type: holo-: BR-4372 (Botanic Garden Meise, Belgium); iso-: PLP-260 (University of Antwerp, Belgium), BRM-ZU9/77 (Hustedt Collection, Bremerhaven, Germany). – Type locality: Grand Tunnel, Île Amsterdam, TAAF sample AMS-M050 (37°48'47.1"S, 77°33'42.6"E), (leg. B. Van de Vijver, coll. date 4 Dec. 2007).

LM: description – Valves semi-lanceolate with convex dorsal margin and weakly concave to straight ventral margin. Valve apices in larger specimens distinctly set-off, subcapitate and ventrally bent, in smaller specimens rounded and not separated from rest of valve. Valve dimensions (n = 13): length 9–18 µm, width 2.0–3.0 µm. Axial area very narrow, indistinct. Central area on both valve sides very small, semi-elliptical (fig. 8A & D–F) to almost indistinct and hardly separated from the axial area. Raphe biarcuate with slightly curved raphe branches. Proximal endings slightly expanded, straight to weakly dorsally bent and distal fissures dorsally deflected. Dorsal and ventral striae not recognizable in LM.
SEM: description, external and internal view – Transition between dorsal valve side and dorsal mantle gradual. Marginal ridge along the junction of valve face and dorsal margin absent (fig. 8L). Raphe ledge broad, linear, without ornamentation and slightly wider near mid-valve (fig. 8K& L). Raphe biarcuate with expanded and slightly dorsally bent proximal endings, distal fissures dorsally deflected (fig. 8K & L). Internally (fig. 8M), distal raphe endings straight, terminating onto weakly developed helictoglossae. Proximal raphe endings terminating onto fused central helictoglossae. Externally (fig. 8L), dorsal striae uniseriate throughout, 46–54 in 10 µm, composed of two transversally elongated to round areolae. Areolae near the valve margin appearing longer, due to a large portion of the first row of areolae next to the raphe being covered by the raphe ledge. Internally (fig. 8M), areolae next to the raphe apparently longer and occluded by hymenes. Ventral striae (fig. 8K) composed of round

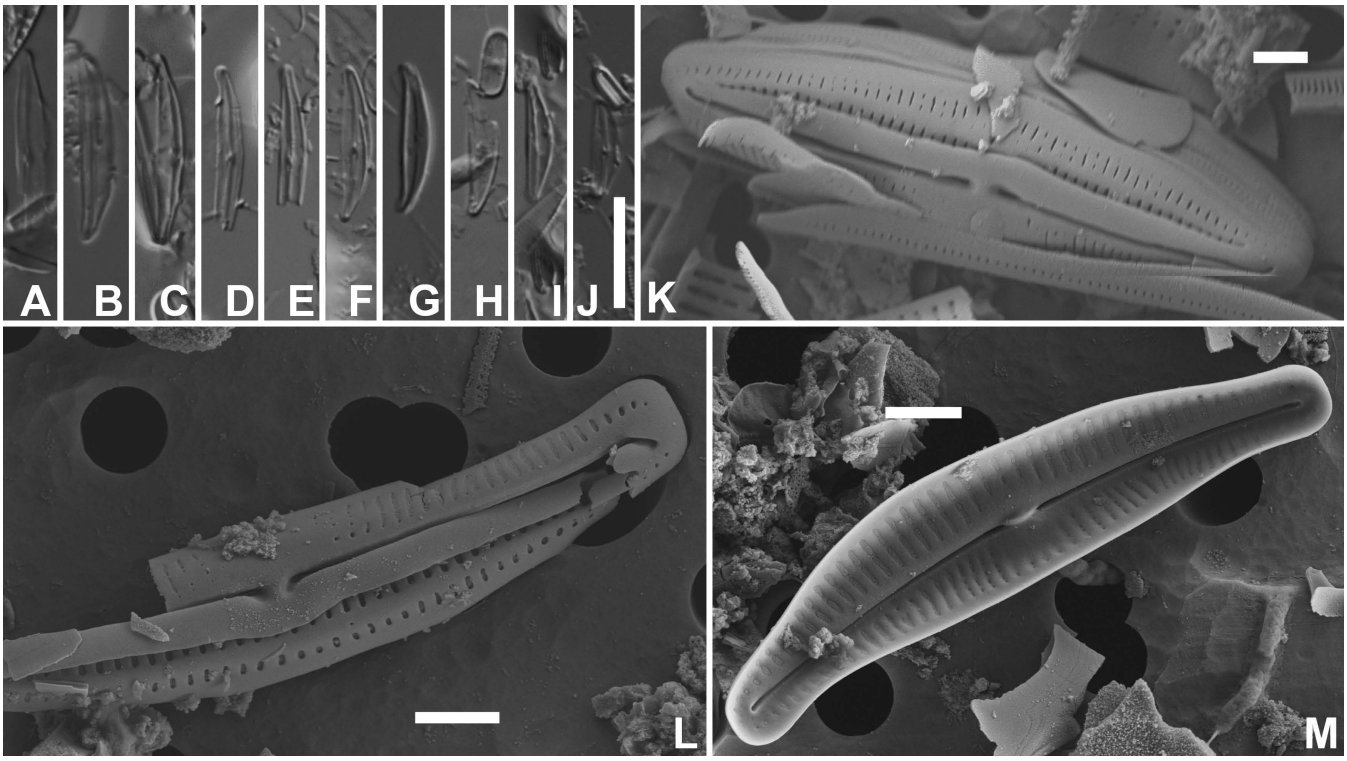

Figure 8 – *Halamphora dagmarobbelsiana*: A–J, LM micrographs of the type population on Ile Amsterdam (sample AMS-M050); K, Scanning electron micrograph (SEM), external detail of a frustule in oblique view showing the mantle and some girdle elements; L, SEM, entire (broken) valve showing the raphe course and the striae; M, SEM, internal overview of an entire valve. Scale bars represent 10 µm except for K–M where scale bars = 1 µm.

to elongated areolae, longer towards mid-valve, 54–60 in 10 µm. In some specimens (fig. 8L) ventral areolae appearing as externally occluded. Near the central area ventral striae composed of small round areolae (fig. 8L).

Etymology – The new species is dedicated to Mrs. Dagmar Obbels (Ghent University, Belgium) in recognition of her algological work in the polar regions.

Distribution and ecology – The lava cavern in which *Halamphora dagmarobbelsiana* was 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 mosses growing on the wall of the cavern, close to the entrance, in a population of the fern *Blechnum australe* L. The sample was entirely dominated by a centric diatom species belonging at present to an undescribed new genus (Van de Vijver et al., unpubl. data), closely related to *Melosira* C.Agardh.

Taxonomical remarks – *Halamphora dagmarobbelsiana* has a unique set of characters (size, valve outline, shape of the central area and stria density) and is easy to distinguish from other species. *Amphora micrometra* Giffen (1967: figs 16, 17) share some morphological features as *H. dagmarobbelsiana* such as valve size and stria density. Smaller valves of *H. dagmarobbelsiana* can be confused with *A. micrometra*, but clear differences can be noticed with SEM. The dorsal striae in *A. micrometra* are composed of a single elongated areola that continues on the valve mantle. The raphe ledge in *A. micrometra* is absent, opposite to *H. dagmarobbelsiana* where the raphe ledge on the dorsal valve side is well developed and thick. Additionally, a single portula-like opening is present in *A. micrometra* (see Ács et al. 2011: figs 19, 21, 24, 25), while such portula in *H. dagmarobbelsiana* is absent.

Amphora exilissima Giffen (1967: 251, fig 1: 8, 9) has a similar valve size (length 9–10 µm; width 2.5–3 µm) as *H. dagmarobbelsiana*, but can be easily differentiated from the latter by the presence of a well-developed, conspicuous central stauros (see Ács et al. 2011: figs 13, 14). *Amphora exilitata* Giffen (1971: figs 5–7) has a similar valve size as *H. dagmarobbelsiana* (length 6–11 µm, width 2.5 µm) but most probably belongs to *Amphora* sensu stricto, since the girdle bands on the dorsal side are 'apparently simple' (Giffen 1971: 2). Images depicted in Witkowski et al. (2000: plate 164: figs 11–13) clearly show a species from the genus *Amphora* sensu stricto.

Two small-sized *Amphora* sensu lato taxa have been depicted in Rumrich et al. (2000): *Amphora* (?nov.) spec. sensu Rumrich et al. (2000: plate 123: figs: 15–18) and *Amphora* spec. sensu Rumrich et al. (2000: plate 123: figs 24, 25). Both taxa can be easily differentiated from *H. dagmarobbelsiana* by the shape of the central area and the stria density. *Catenula adherens* Mereschkowsky shows a similar valve size and stria morphology as *H. dagmarobbelsiana*, but can be easily distinguished from the latter by the position of the raphe (clearly observed in LM), its raphe structure and stria morphology. *Lunella bisecta* Snoeijs (Snoeijs 1996: 145, figs 1–34) has a similar appearance as *H. dagmarobbelsiana*, but can be easily differentiated by the raphe and stria morphology and structure (compare also with Witkowski et al. 2000: plate 170: figs 20–22).

Halamphora lateantarctica Van de Vijver, Kopalová, Zidarova & Levkov, **sp. nov.**
Fig. 9

Type: holo-: BR-4373 (Botanic Garden Meise, Belgium); iso-: PLP-261 (University of Antwerp, Belgium), BRM-ZU9/78 (Hustedt Collection, Bremerhaven, Germany). – Type locality: Lake 22, Bunger Hills, Antarctic Continent, sample BH-22 (66°16'36"S, 100°41'06"E), (leg. J.A.E. Gibson, coll. date 4 Dec. 2007).

LM: description – Frustules elliptic with truncate ends (fig. 9A). Valves semi-elliptical to nearly semi-circular in smaller specimens, dorsi-ventral with strongly convex dorsal margin and weakly concave (fig. 9B–D) to straight ventral margin (fig. 9E), sometimes weakly inflated in mid-valve (fig. 9G). Valve ends distinctly protracted and sub-capitate in larger specimens to weakly protracted and rounded in smaller specimens. Valve dimensions (n = 25): length 26–47 µm, width 7.0–10.0 µm, frustule width 13–21 µm. Axial area narrow, more expressed on ventral valve side. Central area absent on dorsal side, longitudinally elongated on ventral side. Raphe ledge broad, widened at mid-valve tapering towards valve ends. Raphe biarcuate with slightly dorsally curved proximal endings. Proximal endings expanded into small distantly spaced central pores. Distal raphe fissures dorsally bent. Dorsal striae 22–28 in 10 µm, with distinct punctation, radiate throughout. Ventral striae hard to resolve with LM, not interrupted in the region of the central nodule, 26–32 in 10 µm.

SEM: description, external and internal view – Transition between dorsal valve side and dorsal mantle abrupt (fig. 9I). Externally (fig. 9I), narrow, weakly thickened marginal ridge present along junction of valve face and dorsal margin. Marginal ridge more strongly thickened near poles. In some specimens raphe ledge ornamented with round or irregularly-shaped variable in size depressions which not penetrate internally (fig. 9I & J). Dorsal striae uniseriate, composed of transversally elongated areolae (fig. 9I). Striae interrupted at marginal ridge and continuing on valve mantle. Ventral striae composed of transversally elongated areolae (fig. 9J). Size of areolae increases halfway from center to apex (fig. 9J). Internally (fig. 9K), internal costae (virgae) have the same width as striae, except central virgae which are wider. Internal distal raphe endings slightly ventrally deflected and terminate with developed helictoglossae. Proximal, raphe endings terminate with fused central helictoglossae. Five open girdle bands present, each bearing two rows of large, round poroids (fig. 9H).

Etymology – The specific epithet refers to the broad valve dimensions (Latin= '*late*') and the distribution on the Antarctic Continent.

Distribution and ecology – *Halamphora lateantarctica* is a common species in East-Antarctica with confirmed records from the Windmill Island (Roberts et al. 2001), Amery oasis (Cremer et al. 2004), Bunger Hills (Gibson et al. 2006 as *Amphora* sp. g), Vestfold Hills (Van de Vijver, unpubl. res.) and most likely also from the Skarvsness ice free area (Ohtsuka et al. 2006, as *Amphora* sp., fig. 4). It is quite possible that the taxon is also present on other localities on the Antarctic Continent but confusion with *Halamphora* (*Amphora*) *veneta* obscures its distribution. The type population on Bunger

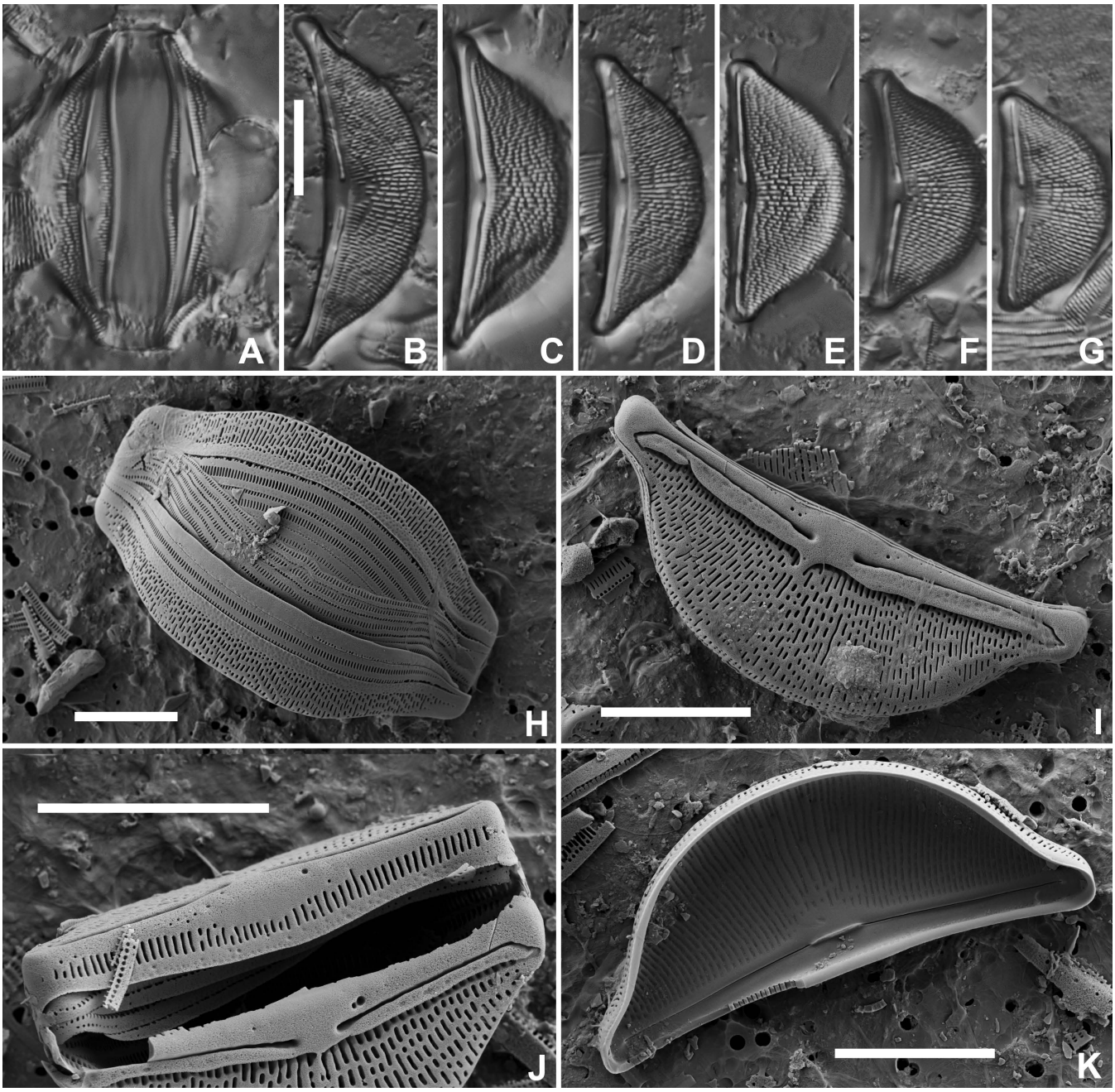

Figure 9 – *Halamphora lateantarctica*: A–G, LM micrographs of the type population on Bunger Hills, Antarctic Continent (sample BH022). A represents a frustule in girdle view; H, Scanning electron micrograph (SEM), external view of an entire frustule showing the girdle and the dorsal mantle; I, SEM, external view of an entire valve showing the raphe ledge and dorsal striae; J, SEM, detail of the ventral mantle and some girdle elements; K, SEM, internal view of an entire valve with the fused proximal helictoglossae Scale bars represent 10 µm.

Hills was collected from a rather large lake (length between 20 and 100 m) covered with an orange-green benthic microbial mat. Other populations in the Bunger Hills were always sampled in low-salinity lakes (Gibson et al. 2006).

Taxonomical remarks – *Halamphora lateantarctica* resembles *H. miroides* Levkov (Levkov 2009: plate 109: figs 45–46; plate 220: figs 1–7) based on the valve shape, but differences can be observed in several ultrastructural features. In *H. miroides* the external openings of areolae are recessed showing a hexagonal shape. The areolae are partially occluded creating slit-like external foramina. The ventral striae near the central nodule are composed of 2–5 small round areolae, opposite to a single elongated areola in *H. lateantarctica*. Internally, the central virgae are strongly thickened, feature clearly visible also with LM. The marginal ridge in *H. miroides* is absent and the transition between dorsal valve side and dorsal mantle is gradual, contrary to the strongly thickened marginal ridge in *H. lateantarctica* that interrupts the dorsal striae. Another species that resembles *H. lateantarctica* is *H. mira* (Krasske) Levkov. However, the

latter species has larger valves (length 40–80 µm, width 9–14 µm), with longer and more subcapitate apices and a lower stria density (dorsal striae 17–21 in 10 µm; ventral striae 18–24 in 10 µm). Additionally, *H. mira* is a brackish, subtropical species, opposite to *H. lateantarctica* which occurs in low-salinity polar lakes. *Halamphora lateantarctica* can be easily differentiated from *H. tucumana* (Herbst & Maidana) Levkov by the absence of strongly thickened virgae (Herbst & Maidana 1988: figs 1–17).

Halamphora vyvermaniana Van de Vijver, Kopalová, Zidarova & Levkov, **sp. nov.**
Figs 10 & 11

Type: holo-: BR-4374 (Botanic Garden Meise, Belgium); iso-: PLP-262 (University of Antwerp, Belgium), BRM-ZU9/79 (Hustedt Collection, Bremerhaven, Germany). –Type locality: Tarnya Lake 1a, Vestfold Hills, sample VH003, (leg. J.A.E. Gibson).

LM: description – Frustules broadly elliptical with short protracted and truncated ends (fig. 10A). Valves broadly semi-elliptical, dorsi-ventral with a strongly convex dorsal margin and weakly concave ventral margin, sometimes almost straight (fig. 10N, T & V) to slightly inflated in the middle (fig. 10H & U). Valve ends variable, long protracted and capitate in larger specimens to shortly subrostrate in mid-sized and small-sized specimens. Valve dimensions (n = 22): length 14–47 µm, width 5–10 µm. Axial area narrow, more expressed on the ventral valve side. Central area absent on the dorsal side, longitudinally elongated on the ventral side. Raphe ledge broad, widened at mid-valve tapering towards the valve ends. Raphe biarcuate with slightly expanded, straight to dorsally bent proximal endings. Dorsal striae radiate throughout, distinctly punctate, 24–30 in 10 µm. Areolae in the mid-valve larger. Ventral striae indistinct, hard to resolve with LM, 28–32 in 10 µm. Ghost valves often observed (fig. 10I).

SEM: description, external and internal view – Transition between the dorsal valve side and the dorsal mantle abrupt (fig. 11A–C). Distinct marginal ridge present along the dorsal margin (fig. 11B & C). Raphe ledge broad, arched, elevated from valve face and ornamented with small, round depressions (fig. 11C & D). Proximal endings expanded and slightly dorsally bent, distal fissures dorsally deflected (fig. 11A & C). Striae uniseriate, radiate throughout, composed of elongated areolae of different size (fig. 11C). Ventral striae placed on the ventral mantle, composed of a single areola and not interrupted near the central area (fig. 11A & D). Areolae on the ventral striae slit-like, having a variable size, smaller towards the central area and the apices (fig. 11D). Dorsal and ventral girdle bands with a row of small, elongated poroids (fig. 11B & C). Internally (fig. 11E), central virgae slightly

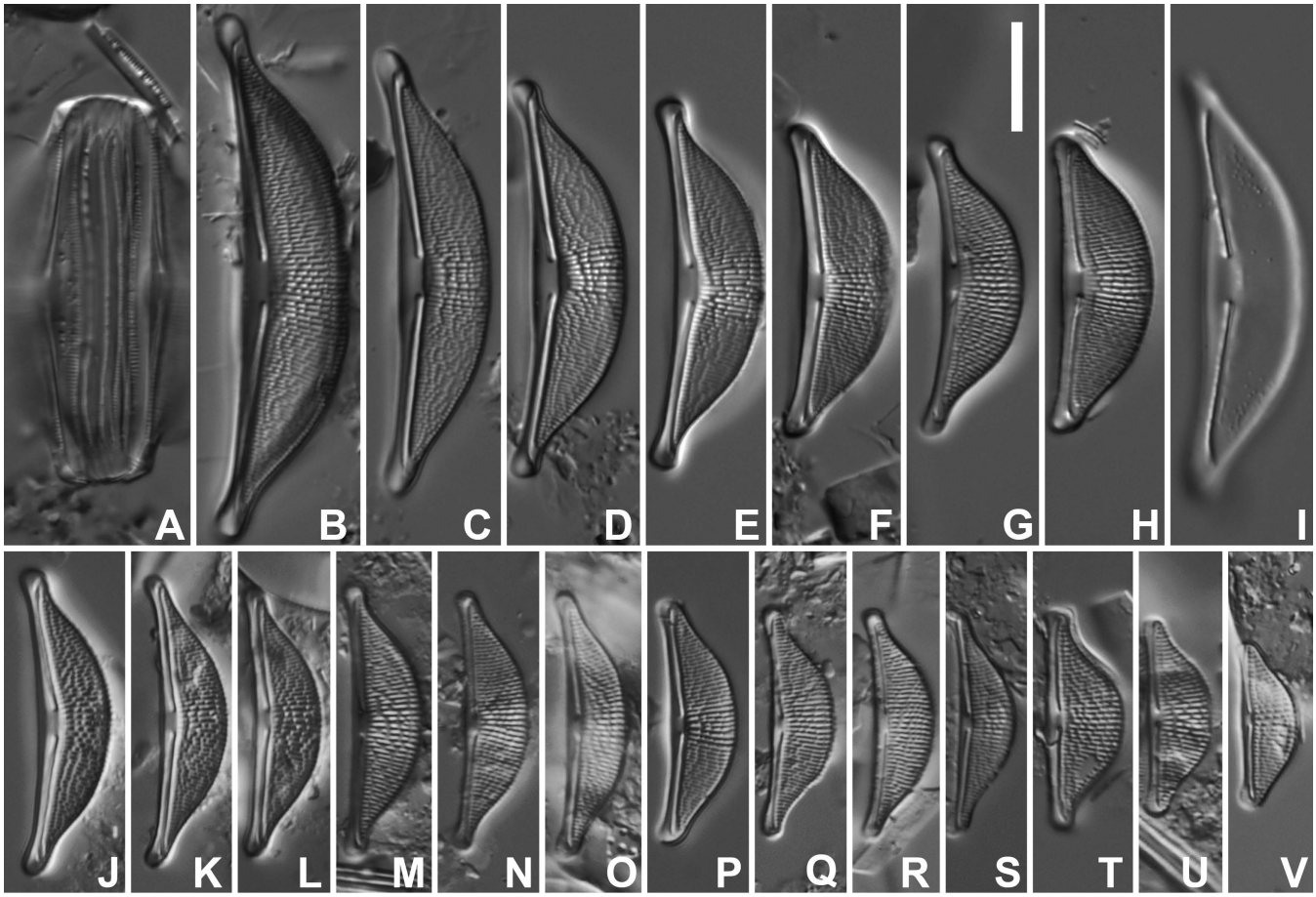

Figure 10 – LM micrographs of the type population of *Halamphora vyvermaniana* on the Vestfold Hills, Antarctic Continent (sample VH003). I represents a ghost valve. Scale bar represents 10 µm.

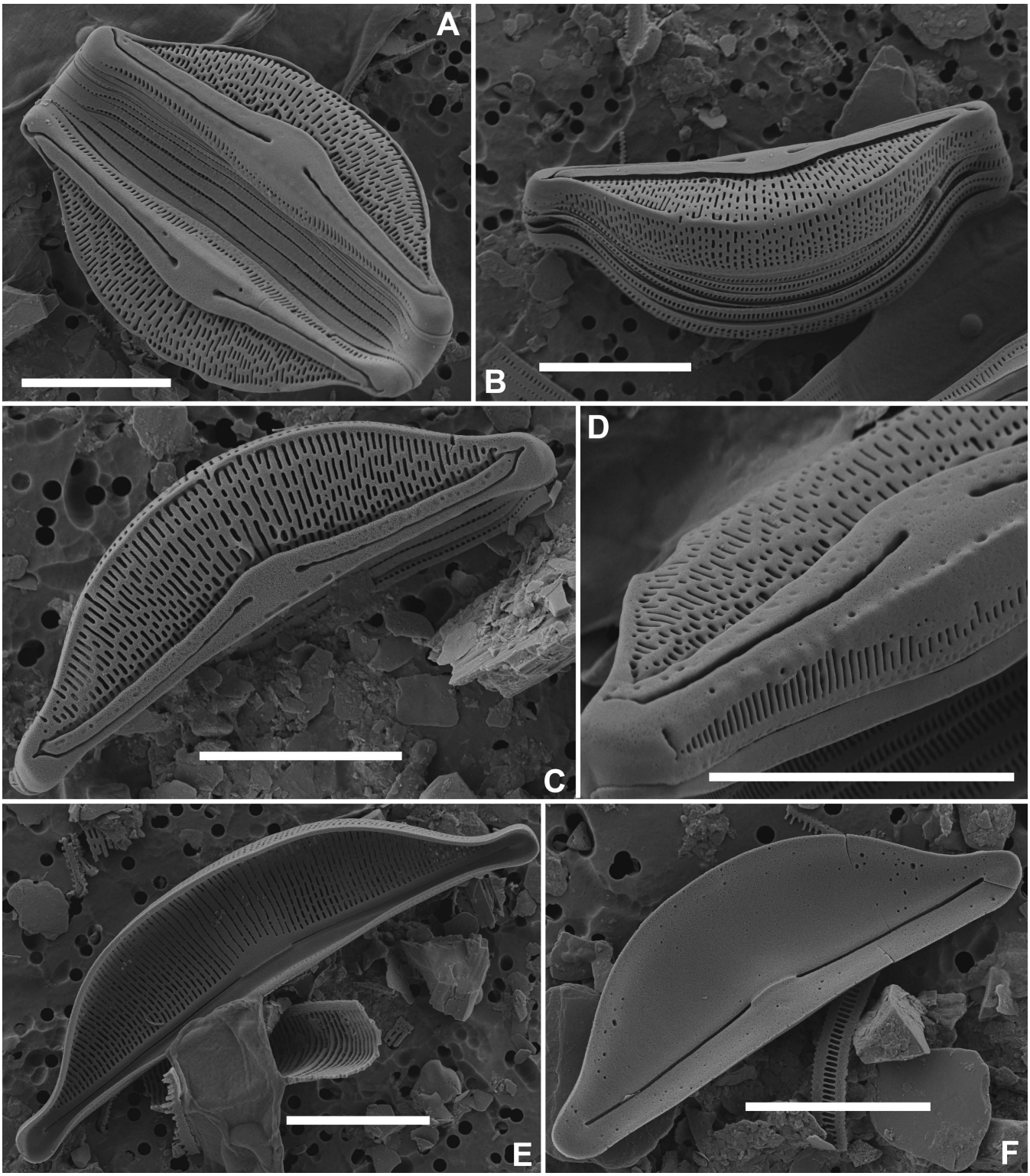

Figure 11 – Scanning electron micrographs (SEM) of the type population of *Halamphora vyvermaniana* on the Vestfold Hills, Antarctic Continent (sample VH003): A, entire frustule with parts of the girdle bands; B, entire valve seen from the dorsal side showing the dorsal mantle and the valve face/mantle margin; C, external view of an entire valve; D, external detail of ventral valve mantle showing the mantle areolae; E, internal view of an entire valve with fused helictoglossae; F, internal view of a heavily silicified valve (ghost valve). Scale bars represent 10 µm.

wider and thickened. Distal raphe endings straight, terminating onto poorly developed helictoglossae. Proximally, raphe endings distantly spaced and terminating onto fused central helictoglossae. Areolae occluded by hymenes. Typical heavily silicified ghost valves occasionally present (fig. 11F).

Etymology – The new species is dedicated to Prof. Dr. Wim Vyverman (Ghent University, Belgium) in recognition of his important contributions to the Antarctic algological research.

Distribution and ecology – Most literature records of *Halamphora veneta* from the Antarctic Continent most likely represent *Halamphora vyvermaniana* (e.g. Sabbe et al. 2003, Ohtsuka et al. 2006, see Kellogg & Kellogg 2002 for more references). Outside the Antarctic Continent, the species has so far not been found. It is a common constituent of different lake ecosystems in Continental Antarctica.

Taxonomical remarks – *Halamphora vyvermaniana* apparently is a quite variable taxon regarding its valve outline and dimensions. All investigated populations show a similar morphological variability. This species was recorded by Ohtsuka et al. (2006: fig. 5) from freshwater lakes of Skarvsnes ice-free area, East Antarctica. However, almost all specimens depicted in Ohtsuka et al. (2006: figs 1–8), labeled as "*Amphora* sp." most probably belong to several different species, differing among each other with respect to mainly the valve shape and size but also to stria density.Whether they all belong to different species is at present unclear and molecular research most likely will be necessary to separate these morphologically different forms. *Halamphora vyvermaniana* has a similar outline and size compared to *H. subcapitata* (Kisselew) Levkov [= *Amphora veneta* var. *subcapitata* Kisselew (Kisselew1932: fig. 22)], but can be easily differentiated by the shape of valve apices (broadly rounded and not protracted in *H. subcapitata*) less pronounced central virgae and higher striae density (20–22 in 10 µm in *H. subcapitata*). Additionally, the external foramina of poroids on girdle bands in *H. subcapitata* appear complex with elaborate invaginations (cf. Levkov 2009: plate 199: figs 5, 6). Larger specimens of *H. vyvermaniana* may be confused with smaller specimens of *H. mira*, but the latter species has usually larger valves (length 40–80 µm) with lower striae density (17–21 in 10 µm). *Halamphora mira* is has larger width than *H. vyvermaniana* (width 9–14 vs. 5–10 µm) for any given valve length and possesses stronger curvature of the dorsal margin. Another species that resembles *H. vyvermaniana* is *H. miroides* (Levkov 2009: plate 109: figs 45–46; plate 220: figs 1–7). *Halamphora vyvermaniana* can be easily differentiated from the latter species by the morphology, structure and shape of areolae on the ventral striae and the less pronounced central virgae. From *H. tucumana* (Herbst & Maidana) Levkov [=*Amphora tucumana* Herbst & Maidana (Herbst & Maidana 1988: figs 1–17)] it can be easily differentiated by the absence of strongly thickened virgae, which are clearly visible with LM. *Amphora inaequistriata* De Toni & Forti (De Toni & Forti 1913: 39–40, fig. 1), has more distantly spaced striae in the mid-valve and broadly rounded (not subcapitate) apices.

BIOGEOGRAPHICAL REMARKS

The taxonomic revision of the genus *Halamphora* with the description of five new species entirely changes our vision on the distribution of this genus in Antarctica. Whereas based on the literature list in Kellogg & Kellogg (2002) *H. veneta* was considered a widespread, cosmopolitan taxon, its distribution in the Antarctic Region is now restricted to the sub-Antarctic islands. In the Maritime Antarctic Region, the species seems to be replaced by *H. ausloosiana* (South Shetland Islands) and *H. oligotraphenta* (James Ross Island). A reanalysis of the original material will be necessary to clarify whether the published records of *H. veneta* and *H. oligotraphenta* from the South Orkney Islands or the South Shetland Islands (e.g. Oppenheim 1990, Oppenheim & Greenwood 1990, Håkansson & Jones 1994) belong to either *H. ausloosiana* or *H. oligotraphenta*. For soil diatoms, it was already clear that a typical regionalization existed within the Antarctic Region as demonstrated by the high number of endemic taxa in the genera *Luticola* (e.g. Van de Vijver et al. 2011a, Kopalová et al. 2011), *Hantzschia* (Zidarova et al. 2010) and *Muelleria* (Van de Vijver et al. 2010, 2014). The revision of *Halamphora* confirms now that a similar regionalization is also present in aquatic genera, as was shown already for *Stauroneis* (Van de Vijver et al. 2005) or *Navicula* (Van de Vijver et al. 2011b), both typical lake ecosystem constituents.

ACKNOWLEDGEMENTS

Sampling on Crozet and Amsterdam has been made possible thanks to the logistic and financial support of the French Polar Institute-Paul-Emile Victor in the framework of the terrestrial program 136 (Marc Lebouvier & Yves Frenot). Samples on Byers Peninsula were taken in the framework of the IPY-Limnopolar Project POL2006-06635 (Prof. Dr. Antonio Quesada, Ministerio de Ciencia y Tecnología, Spain). The authors would also like to thank the members of expeditions to the Czech J.G. Mendel Antarctic Station for field support and assistance. K. Kopalová benefited from grant GA UK grant nr. 394211. Part of the research was funded within the Belspo CCAMBIO project and an EU Synthesys grant to BVDV to visit the National History Museum in London, UK. Alex Ball, the staff of the EMMA laboratory and Eileen J. Cox at the Natural History Museum are thanked for their help with the scanning electron microscopy.

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Manuscript received 14 Feb. 2014; accepted in revised version 10 Apr. 2014.

Communicating Editor: Elmar Robbrecht.