

THALASSIONEIS SIGNYENSIS (BACILLARIOPHYCEAE) FROM NORTHWEST WEDDELL SEA ICEBERGS, AN EMENDATION OF THE GENERIC DESCRIPTION¹

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We offer an emended description of the genus *Thalassioneis* based on new observations of the type species, *T. signyensis* Round, from material sampled in the northwest Weddell Sea. Specimens from algal communities attached to submerged flanks of several icebergs were collected with a remote-operated vehicle (ROV-Phantom DS 2). The analyses were carried out by LM and SEM. Fresh material and frustules without organic matter allowed us to observe details not included in the original description such as type and structure of colonies and chloroplasts. The frustule shows an asymmetry with respect to the location of the apical pore fields, one of them situated on the valvar face and the other one displaced toward the mantle; the former is involved in joining contiguous cells to form long chains. Furthermore, we present details on the ultrastructure of the cingulum that consists of three to four open copulae with one or more rows of poroids. A brief discussion on the habit and ecology of this taxon, which may be endemic to the northwest Weddell Sea, is also presented. A comparison with similar genera, such as *Brandinia*, *Creania*, *Fossula*, *Fragilaria*, *Rimoneis*, *Synedropsis*, and *Umaria*, is included with an evaluation of morphological characteristics useful to differentiate them.

Key index words: Antarctica; diatom; iceberg; *Thalassioneis*; Weddell Sea

Abbreviations: CTD, conductivity-temperature-depth; HD, high definition; LPC, Herbarium of the

División Científica Ficología, La Plata; ROV, remote-operated vehicle

Sea ice provides an extensive habitat in the Southern Ocean for large populations of microalgae, principally diatoms that play an important role in the marine food web (Garrison 1991, Roberts et al. 2007). Sea-ice microalgal assemblages are composed predominantly of pennate diatoms (Garrison et al. 1987, De Sève and Dunbar 1990, Poulin 1990, Garrison 1991, Hasle et al. 1994) that live in, on, or associated with, sea ice during different times of their life cycle (Horner 1985a, Horner et al. 1992). About 111 species of sea-ice diatoms have been identified (Palmisano and Garrison 1993). New genera are continuously being established (Hasle et al. 1994, Fernandez et al. 2007) as in the case of *Thalassioneis* Round (Round et al. 1990). Despite the numerous studies that exist in the literature, knowledge about living organisms associated with sea ice as well as their life cycles is considered insufficient (Knox 2007).

The microphytobenthos, a habitat related to sea ice, is not well known, but surveys in the Arctic and Antarctic have increased considerably in the past 20–25 years (Garrison et al. 1987, Poulin 1990, Hasle et al. 1994, Fernandes and Prokopiak 2003, Fernandes et al. 2007, Al-Handal and Wulff 2008, Lundholm and Hasle 2008). Microphytobenthic algae are mostly composed of diatoms of cosmopolitan distribution that inhabit surface sediments as well as rocky bottoms in shallow waters.

In this article, we describe the monospecific genus *Thalassioneis*, established for the species

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T. signyensis (Round et al. 1990), which was described from sea-ice samples collected near Signy Island, Antarctic Peninsula. We found this species in a different habitat, more similar to a benthic (non-pelagic) form, attached to underwater iceberg surfaces, adhered to small minerals embedded in glacier ice (Smith et al. 2007).

The general features of *Thalassioneis* are similar to those of *Fragilaria*, but with ecological and morphological differences (Round et al. 1990). Williams and Round (1987) revised the genus *Fragilaria*, creating a number of smaller genera and restricting the definition of *Fragilaria* to freshwater species (i.e., excluding the marine species *Fragilaria striatula*). *Fragilaria* species usually form linear colonies, have simple striae with discoid areolae and with an external velum, a single rimoportula on the valvar surface, usually lying at a pole, and an ocellulimbus (apical pore field) situated at the apex of the mantle. Linking spines are present, usually occurring at the junction of the valvar face and mantle, with a cingulum composed of a few open bands. There are two plastids, one on each side of the cell. In contrast, *Thalassioneis* was described based on valvar features characterized by flat and linear valves, with rounded ends and central inflation, curving into shallow mantles; striae uniseriate, widely separated and somewhat irregular, with areolae occluded externally by hymenes and opening internally in round foramina. A single rimoportula aligned transversally occurs on the central inflation, slightly closer to one pole. The apical pore fields are sunken slightly on the valve face, with a few scattered pores extending on the valve mantle. Description to date is based solely on valve features (Round et al. 1990), and was derived from all material available (F. E. Round, pers. comm.).

Herein, we offer an emended description of the genus *Thalassioneis*. Fresh, live material was collected from icebergs during two cruises to the northwest Weddell Sea in 2005 and 2009. We provide the first data on the structure of plastids and the cingulum ultrastructure based on observation of living cells and clean material by LM and SEM. Brief discussions on the habit and ecology of this taxon are also presented. Its morphology is discussed and compared with other similar genera.

MATERIALS AND METHODS

In the framework of the project “Free-drifting Icebergs as Proliferating Dispersion Sites of Iron Enrichment, Organic Carbon Production and Export in the Southern Ocean,” several icebergs were sampled in the northwest Weddell Sea during austral summer and fall, between $\sim 61^\circ$ S and 63° S and 50° W and 54° W (3–28 December 2005 and 10 March–7 April 2009) on board the ARSV *Lawrence M. Gould* and ARIB *Nathaniel B. Palmer*, respectively (Fig. 1).

Diatom specimens were collected with an ROV-Phantom DS 2 from algal mats attached to the iceberg’s flanks by scraping the vertical surfaces and resuspending the algae. Subsequently, we collected them with a $20\ \mu\text{m}$ net attached to the ROV’s

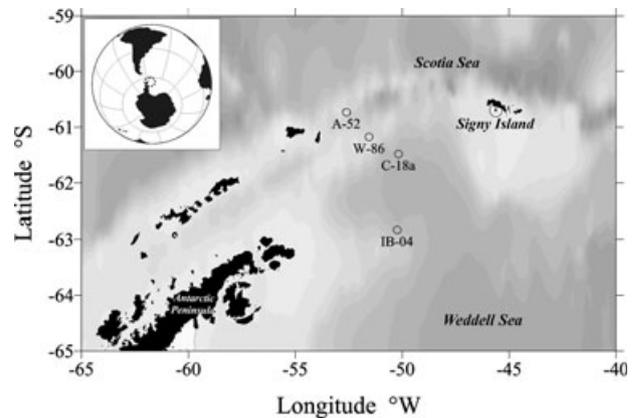


FIG. 1. Map of the northwest Weddell Sea and southern Scotia Sea depicting sampling locations of *Thalassioneis signyensis* associated with icebergs.

front or we pumped the water with the particles and filtered them through a $300\ \mu\text{m}$ net (Robison et al. 2011). Algal presence was documented with a high-definition (HD) camera, the physical structure of the water column was characterized with a conductivity-temperature-depth (CTD) sensor, and water was collected with 12 L Ocean Test Model 110 Sampling Bottles (Ocean Test Equipment Inc., Fort Lauderdale, FL, USA) attached to the ROV. Colony type and chloroplast morphology were examined and photographed from fresh material on-board the ship using a Nikon E-800 compound microscope equipped with a SPOT RT1 Slider camera and Nikon SMZ 1500 stereomicroscope (Nin Instruments Inc., Melville, NY, USA, and Diagnostic Instruments, Sterling Heights, MI, USA, respectively).

For morphological diatom identification, water aliquots fixed with acidic Lugol’s solution were cleaned of organic matter and mounted on permanent glass slides using Naphrax medium (Hasle and Fryxell 1970, Prygiel and Coste 2000). The slides were examined using a phase contrast and a differential interference contrast Leica DM 2500 light microscopes (Leica Microsystems GmbH, Wetzlar, Germany) equipped with digital cameras. In addition, cleaned material was prepared on stubs shadowed with gold-palladium for SEM, according to procedures outlined by Ferrario et al. (1995) and examined using a JSM-6360 LV (JEOL Ltd., Tokyo, Japan) located at the Museo de La Plata. Voucher material and permanent slides were deposited at the Diatom Collection (LPC), Herbarium of the División Científica Ficología, Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata, Argentina. Terminology follows Round et al. (1990) and Williams and Round (1987).

RESULTS

On the basis of our analyses, we propose an emendment to the original description of the genus *Thalassioneis* and the species *T. signyensis*. It includes new information about the plastids and colony formation as well as details of valve and cingulum ultrastructure. Our observations enhance the original description made by Round in Round et al. (1990).

Class Fragilariophyceae Round in Round et al. (1990).

Order Fragilariales Silva 1962 emend Round et al. (1990).

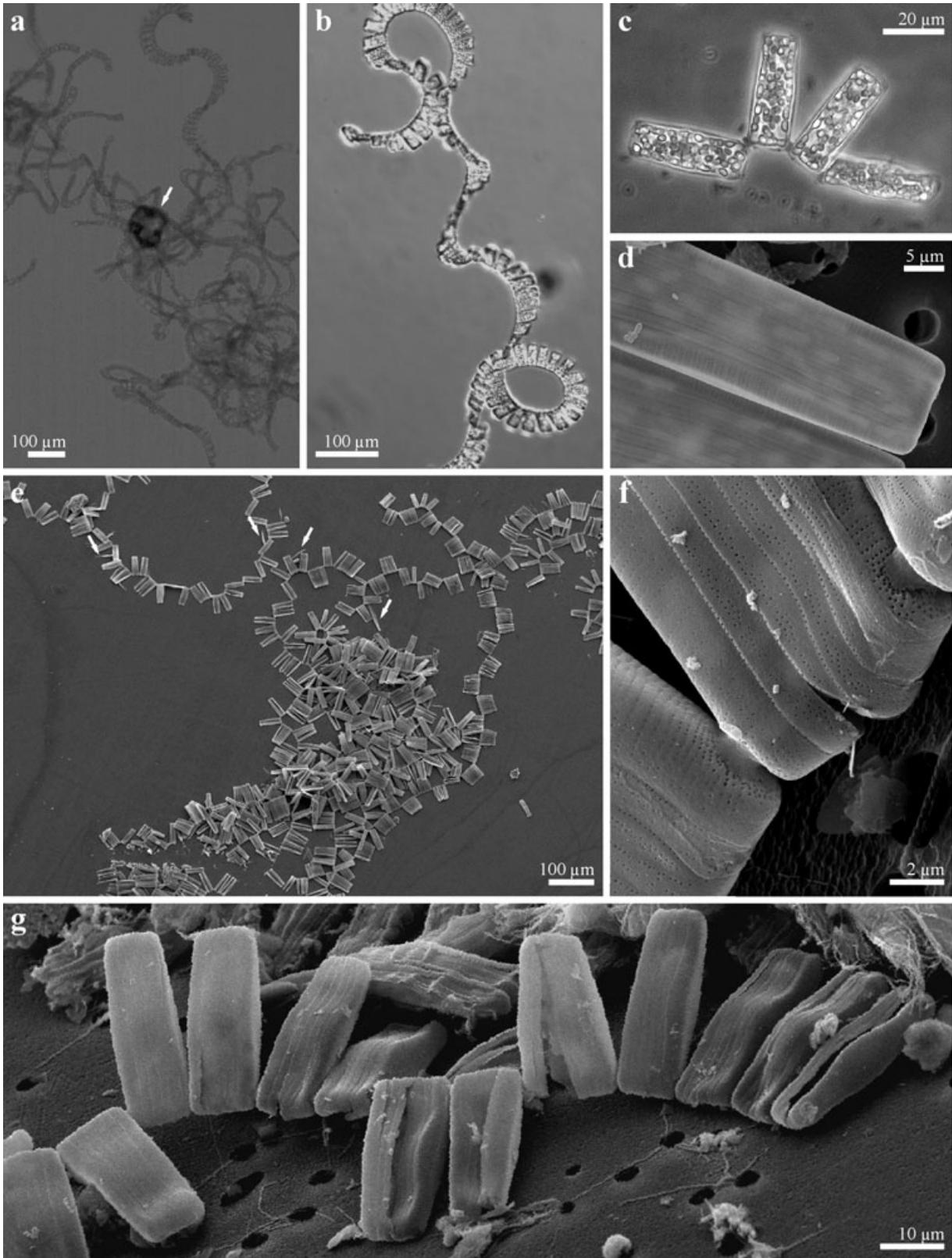


FIG. 2. *Thalassioneis signyensis*. General colony morphology and chloroplasts. (a, b) Cells from *T. signyensis* forming curved and twisted chains (by LM). Note how colonies are attached to a small mineral (arrow). (c) Living cells in girdle view showing numerous small plastids (by LM). (d) Part of frustules in girdle view showing numerous small plastids (by SEM). (e) Colonies of *T. signyensis* in general view. Note the presence of some epiphytic specimens, *Synedropsis* sp. indicated by arrows (by SEM). (f, g) *T. signyensis* cells joined to each other through mucilage pads at one of the valve ends (by SEM) (see detail in Fig. 2f).

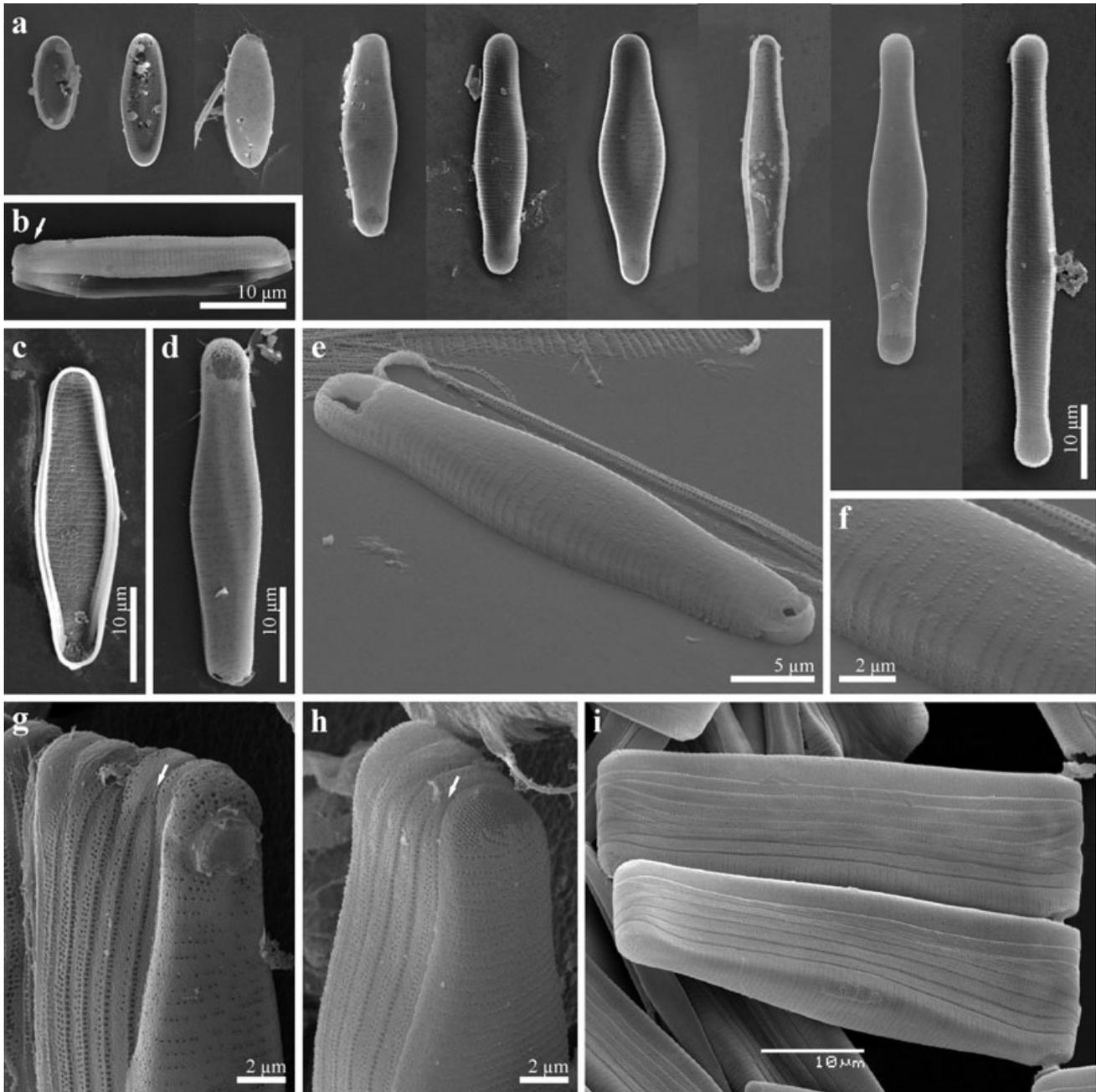


FIG. 3. Frustule shape and size within *T. signyensis* population including details of frustule ultrastructure (by SEM). (a) This is an average of the valve shape of a typical population of *T. signyensis* cells. (b) External valve view showing the flat surface and the sinking of one of the apical pore fields (arrow). (c, d) Internal and external valve view showing uniseriate striae arranged in opposite and/or alternate rows in the same valve. (e) Areolae occluded externally with a delicate velum and continuing onto valve mantle. (f) Detail of the areolae. (g) Part of frustules in external view showing the apical pore field situated on the valve surface. (h) Same as (g) with the apical pore field situated on the valve mantle. (i) Frustules in girdle view showing the thecae with three to four open copulae. Each copula has two or three irregular rows of poroids (in g, h note the open bands, arrows).

Family Fragilariaceae Kützing (1844).

Generitype: *Thalassioneis* Round in Round et al. (1990), amend M. E. Ferrario, A. O. Cefarelli et M. Vernet.

Description: Cells are joined to each other by one of its ends through prominent mucilage pads (Fig. 2, f and g), forming long chains in a 2–4

frustule alternating pattern, generally curved and twisted (Fig. 2, a, b, and e). The plastids are numerous, small, discoids, distributed throughout the whole cell; they can be observed in water mounts (Fig. 2, c and d). The valve is variable in shape and size, linear to lanceolate with central inflation, and apices rostrate to capitate in the larger specimens

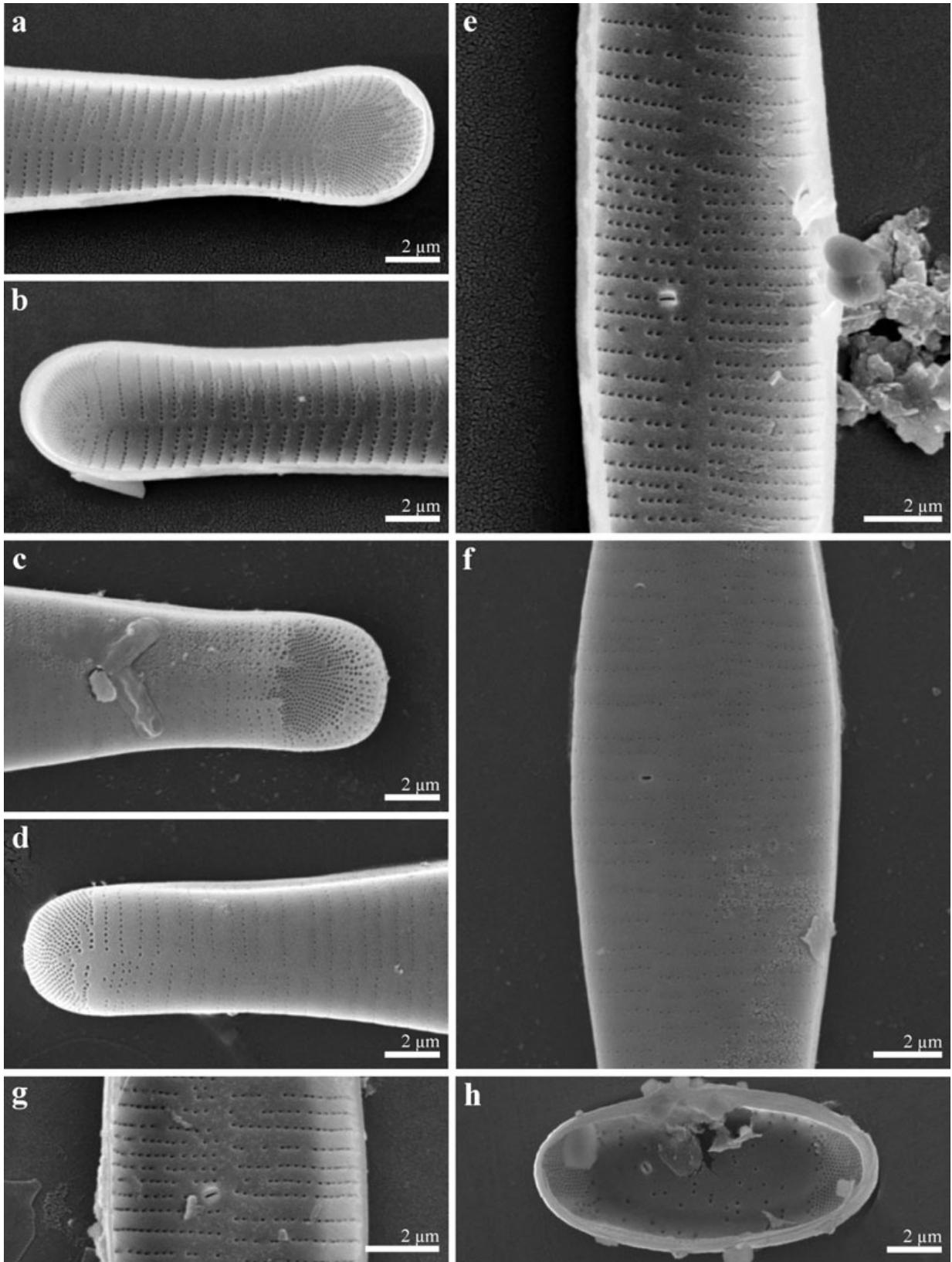


FIG. 4. Valve views, details of the rimoportula, and the apical pore fields in *T. signyensis* (by SEM). (a, b) Ends of the same valve showing the pore fields located on the interior valvar surface and the mantle, respectively. (c, d) Same as in (a, b), but the apical pore fields in external view. (e, f) Internal and external valve view showing rimoportula opening, oriented transapically. (g, h) Internal valve view showing rimoportula oriented obliquely.

(Fig. 3a). In the smaller ones, the valves are oval with widely rounded apices (Figs. 3a and 4h). The valve surface is flat having uniseriate striae, usually irregular, arranged in opposite and/or alternate rows on the same valve, perpendicular to a narrow sternum, sometimes only a trace of a sternum (Fig. 4, f and h). The striae are composed of areolae, which are almost circular (4–5 in 1 μm), occluded externally with a delicate domed velum, and continuing onto a deep valve mantle (Fig. 3, e and f). The velum is usually removed by acid treatment. The apical pore fields are large and demarcated by several longitudinal rows of small round pores arranged linearly, usually in an oblique way with respect to the apical axis and sometimes accompanied by a few scattered irregularly (Fig. 4, a–d). These pore fields are situated one within a surface depression on the valve face (Fig. 3, b and g), which is not a true ocellulimbus, but is still a unique feature within this genus, and the other one positioned on the mantle, sometimes extending from the apex mantle onto the valve face (Fig. 4, a–d). The former, which is on the valve face, plays a role in uniting contiguous cells within the colony (Fig. 2f). The exact position of the apical polar fields on the valve face is variable. In cleaned material, the apical pore fields are evident in LM, although difficult to recognize. The cingulum is composed of three to four open bands (Fig. 3, g–i). The valvocopula appears with two or three irregular rows of poroids arranged one in advalvar position and the rest in the middle position. The other copulae are structurally similar in width and arrangement, with three to five irregular rows of poroids, one of them in an advalvar position (Fig. 3, g–i). A single central rimoportula is situated on the valve face, with transapical orientation, or slightly oblique to the sternum (Fig. 4, e–h). It is closer to one pole (Figs. 3, a and c; 4h).

Thalassioneis signyensis Round in Round et al. (1990) amend M. E. Ferrario, A. O. Cefarelli et M. Vernet.

Holotype: BM 81503.

Type material: Signy Island, Antarctica.

Description: As the genus is monospecific the characteristics of the species are those mentioned for the genus. The apical axis varied from 12.5 to 60 μm , the transapical axis from 5 to 9.5 μm , and the perivalvar axis from 8.5 to 20.5 μm . There are 11–21 striae in 10 μm usually increasing toward the ends to 12–28 striae in 10 μm , discernible with LM in clean material (phase contrast, oil immersion).

Distribution: *T. signyensis* has been reported in sea ice from Antarctica, frequent in samples from Signy Island (Round in Round et al. 1990). In our study, we found *T. signyensis* as the dominant species attached to small minerals included in the vertical faces of Antarctic icebergs (Fig. 2a), always submerged. The species formed mats; their distribution reached a maximum between 20 and 92 m, below

the depth of wave action and down to a depth of 1% surface irradiance (Robison et al. 2011). The species was abundant in austral summer (icebergs A-52 and W-86 sampled in December 2005 near Elephant Island, Antarctic Peninsula, Smith et al. 2007) and fall (iceberg C-18a and other smaller ones, IA-4, in Powell Basin, northwest Weddell Sea in March–April 2009). In situ water temperatures varied from -1.19°C to 0.04°C and salinities of 33.796–34.487.

DISCUSSION AND CONCLUSIONS

The analysis carried out in this study shows that *Thalassioneis* is characterized mainly by its ability to form colonies, for having small and numerous discoid plastids, for the position of the apical fields (one on the valve and other on the mantle), and for possessing a cingulum with open bands. New data, not reported in the description and pictures of the type material (Round in Round et al. 1990, pp. 386–7 and 677, figs. a–i), justify the emendment of the genus.

The genus *Thalassioneis* was originally conceived as a sea-ice araphid diatom (Round et al. 1990). Araphid pennate diatoms sensu Round et al. (1990, p. 651) are characterized by possessing a sternum and a pennate arrangement of striae.

Although *Thalassioneis* belongs to the family Fragilariaceae, within the araphid diatoms with a pennate arrangement of the striae, in this study, we observed that some specimens differ in relation to the presence of a sternum, which is a character difficult to differentiate even if present (Fig. 4, f and h). Similar sternum development is present in Plagiogrammaceae, which was removed from the araphid pennates to the centric order Triceratales (Round et al. 1990). On the other hand, using molecular and morphological analysis, Kooistra et al. (2004) advocate the return of the Plagiogrammaceae to the pennate diatoms. Thus, we believe that this information calls into question the use of the sternum as a diagnostic character for the circumscription of the Fragilariaceae family.

In the present work, we propose that the presence and position of the rimoportula, the structure of the apical pore fields and the cingulum can be used as diagnostic characters to distinguish *Thalassioneis* from other similar araphid genera. Furthermore, we propose that morphometric and morphological data, such as valvar size and shape, should not be considered relevant characters. In our material, *T. signyensis* shows a high degree of variability in valvar contour, from linear forms with rostrate rounded ends with or without a central expansion to oval forms with rounded ends (Fig. 3a), characteristics that overlap with most of the related genera (Table 1). Similarly, the type of striae, relatively uniform, uniseriate, with one row of rounded poroids, is not adequate for identification purposes. The one exception would be *Ulnaria*

TABLE 1. Comparison between morphological and ecological characteristics of *Thalassioneis* and similar genera.

Genera	<i>Brandinid</i> ^a	<i>Creamid</i> ^b	<i>Fossilid</i> ^c	<i>Fragilarid</i> ^d	<i>Rimoneis</i> ^e	<i>Synedropsis</i> ^f	<i>Thalassioneis</i> ^g	<i>Ulnaria</i> ^h
Chloroplasts	Two	n/d	Two	Two	n/d	Two, rarely one	Numerous	Two
Cells	Solitary	Usually stellate or ribbon-shaped colonies	Ribbon-shaped colonies	Usually ribbon-shaped colonies	Ribbon-shaped colonies	Solitary, stellate, rarely in ribbons colonies	Usually curved and twisted colonies	Usually stellate or ribbon-shaped colonies
Bands	Open, one row of poroids	n/d	Open, one to four rows of poroids	Open, one row of poroids	Open, without poroids	Open, one row of poroids	Open, two to four rows of poroids	Close, one row (valvocopula) or two rows (in the copulae of some species) of poroids
Rimoportulae	Two on the valve face	Two, one at each end on valve face/mantle junction	One on the valve mantle	One on the valve face	Absent	One on the valve face	One on the valve face	Two on the valve face
Apical fields	Ocellulimbus	On the valve mantle. One row of five to seven rectangular openings	Two rows of elongate pores on the mantle	Ocellulimbus	Apical slit fields, two longitudinal slits per valve apex	Apical slit fields, two to eight longitudinal slits on the mantle	Apical pore fields (not true ocellulimbus), one on the mantle, another extended onto part of the valve face within a surface depression	Ocellulimbus
Striae	Uniseriate	Uniseriate	Uniseriate	Uniseriate	Uniseriate	Uniseriate	Uniseriate, widely separated	Uni- or biserate in the same valve
Distribution	Antarctic	Antarctic	Arctic	Cosmopolitan	Tropical and subtropical	Arctic and Antarctic, tropical regions (Brazil-Gulf of Mexico)	Antarctic, endemic northwest Weddell Sea?	Cosmopolitan
Habitat	Sea ice, epilithon	Fossil	Marine planktonic	Freshwater, except <i>F. striatula</i>	Freshwater and brackish water	Sea ice and brackish water, common epiphytic	Sea ice, epilithon	Freshwater
Spines	Not present	Not present	Not present	Present	Present	Not present	Not present	May or may not be present

n/d, no data. ^aFernandez et al. (2007). ^bOlney et al. (2009). ^cHasle et al. (1996); von Quillfeldt (2001). ^dWilliams and Round (1987); Silva and Hasle (2006). ^eGarcia (2010). ^fHasle et al. (1994); Prasad and Livingston (2005). ^gRound et al. (1990); present study. ^hTuji (2009); Morales (2003).

(Table 1) that has uniseriate and/or biseriate striae in the same valve (figs. 43 and 44 in Morales 2003, Tuji 2009).

Although plastid morphology has not been described in detail in all taxa, most of the species in related genera differ from *Thalassioneis* in having two parietal plates placed along the inside of the valve (Table 1). These results support Prasad and Livingston (2005) who proposed that plastid properties, such as number, form, and position inside the cell, are not enough to separate groups into different genera within the araphid diatoms. Some genera such as *Licmophora* (Honeywill 1998) and *Fragilariforma* (Williams and Round 1987, 1988) have small discoid plastids similar to *Thalassioneis*. In contrast, Edlund et al. (2006) argued that after falling into disfavor in the mid-20th century, protoplast organization is being used with increasing frequency in systematic studies.

If we compare *Thalassioneis* with similar genera, *Brandinia*, *Creania*, *Fossula*, *Fragilaria*, *Rimoneis*, *Synedropsis*, and *Ulnaria* (Table 1), we find that the rimoportula, the apical pore fields and the cingulum seem to be the most stable characters to differentiate them. In contrast to *Thalassioneis*, *Brandinia* has two rimoportulae on the valve face, one at each end and a distinctive ocellulimbus on the mantle. Both genera have open bands, with one row of poroids in *Brandinia* and more than one in *Thalassioneis*. Furthermore, they are restricted to marine habitats in the Antarctic area. In relation to the fossil genus *Creania*, recently described from Antarctic sediments as a sea-ice indicator (Olney et al. 2009), the differences are given not only by the presence of two rimoportulae per valve, located at each end and positioned at opposite sides with respect to the apical axis but also by the type of apical fields made up of 5–7 short rectangular openings.

Another similar genus, described from marine Arctic waters is *Fossula* (Hasle et al. 1996), which, although having only one rimoportula per valve, lies on the mantle. On the other hand, each apical field is formed only by two rows of elongated pores. The cingulum is composed of open bands as in *Thalassioneis*. Although the genus *Fragilaria*, like *Thalassioneis*, has only one rimoportula on the valve face and their bands are open, *Fragilaria* differs by having a well-defined ocellulimbus on the valvar mantle and the presence of spines. In addition, it is a cosmopolitan genus (including polar regions) mainly found in freshwater habitats. However, as indicated by Silva and Hasle (2006), the Williams and Round (1987) revision treated *Fragilaria* as a freshwater genus exclusively without commenting on the marine species *Fragilaria striatula*. Silva and Hasle (op. cit.) suggested accommodating *F. striatula* within the *Grammonema* genus, and treated it as monospecific. *Thalassioneis* differs from *Rimoneis* by the presence of a rimoportula, by the absence of spines and the type

of the apical field which in *Rimoneis* has two longitudinal slits per valve apex. With respect to its distribution, *Rimoneis* has been so far found in freshwater environments and brackish water in tropical and subtropical regions. The main difference between *Thalassioneis* and *Synedropsis* is the well-defined apical slit fields instead of apical pore fields as in *Thalassioneis*. Both genera have a single rimoportula, but in the case of *Synedropsis*, it is located on the apex. Moreover, although they also have perforated open bands, in *Synedropsis* the poroids are located in one row, whereas in *Thalassioneis*, they are in more than one row. In relation to distribution, the latter seems to be restricted to Antarctic waters, while *Synedropsis* has been found in Antarctic, Arctic, and tropical waters. The most obvious differences occur when comparing *Thalassioneis* with *Ulnaria*. The latter genus has two rimoportulae per valve, an ocellulimbus, closed bands, and spines that may or may not be present. In relation to habitat, this genus has been restricted to freshwater, with cosmopolitan distribution.

The frequency of *T. signyensis* in sea-ice samples around Signy Island in the South Orkneys Islands (Round op. cit.) and the abundance registered in this study from the submerged vertical faces of icebergs suggest that it is a common ice species in the Weddell Sea area. It has been suggested that *T. signyensis* could be inoculated onto an iceberg's or ice shelf's vertical sides while they are in contact with sea ice during austral winter within the Weddell Sea gyre (Robison et al. 2011). If we consider this species' habitat within a global context, *T. signyensis* could be termed a sympagic species, meaning "with ice," which includes both its sea ice and the glacier ice habitats (Horner et al. 1992). On the other hand, if we consider that the mats were found living attached to small minerals (rocky substrate), as occurred in this study, *T. signyensis* could also be considered an epilithic species. As *T. signyensis* has only been reported in the northwest Weddell Sea and South Orkney Islands (Round et al. 1990, this study), and not elsewhere in the Weddell Sea or other Antarctic waters (Garrison and Buck 1985, Horner 1985b, Medlin and Priddle 1990, Hasle and Syvertsen 1997, Scott and Thomas 2005), it may be endemic to this region.

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- Al-Handal, A. Y. & Wulff, A. 2008. Marine benthic diatoms from Potter Cove, King George Island, Antarctica. *Bot. Mar.* 51:51–68.
- De Sève, M. A. & Dunbar, M. J. 1990. Structure and composition of ice algal assemblages of St. Lawrence, Magdalen Islands area. *Can. J. Fish. Aquat. Sci.* 47:780–8.
- Edlund, M. B., Brant, L. A., Levkov, Z. & Nakov, T. 2006. An emended description of *Decussata* (Patrick) Lange-Bertalot & Metzeltin that includes protoplast organization and detailed valve and cingulum ultrastructure. *Diatom Res.* 21:269–80.
- Fernandes, L. F. & Prokopiak, L. K. 2003. Observations on valve structures of *Navicula directa* (Wm. Smith) Ralfs in Pritchard and *Navicula glaciei* V. Heurck from rocky substrates in Antarctic Peninsula. *Hoehnea* 30:1–10.
- Fernandes, L. F., Prokopiak, L. K. & Portinho, D. 2007. *Brandinia mosimanniae* gen. nov. et sp. nov., a new marine epilithic diatom from the Antarctic coasts. *Diatom Res.* 22:45–56.
- Ferrario, M. E., Sar, E. A. & Sala, S. E. 1995. Metodología básica para el estudio del fitoplancton con especial referencia a las diatomeas. In Alveal, K., Ferrario, M. E., Oliveira, E. C. & Sar, E. A. [Eds.] *Manual de métodos ficológicos*. Universidad de Concepción, Concepción, Chile, pp. 1–23.
- García, M. 2010. A new diatom: *Rimoneis* M. García (Fragilariaceae, Bacillariophyceae): a new hyaline araphid genus based on observations of frustules from Southern Brazil. *Diatom* 26:1–9.
- Garrison, D. L. 1991. Antarctic sea ice biota. *Am. Zool.* 31:17–33.
- Garrison, D. L. & Buck, K. R. 1985. Sea-ice algal communities in the Weddell Sea: species composition in ice and plankton assemblages. In Gray, J. S. & Christiansen, M. E. [Eds.] *Marine Biology of Polar Regions and Effects of Stress on Marine Organisms*. John Wiley, New York, pp. 103–22.
- Garrison, D. L., Buck, K. R. & Fryxell, G. A. 1987. Algal ice edge assemblages in Antarctic pack ice and in ice-edge plankton. *J. Phycol.* 23:564–72.
- Hasle, G. R. & Fryxell, G. A. 1970. Diatoms: cleaning and mounting for light and electron microscopy. *Trans. Am. Microsc. Soc.* 89:468–74.
- Hasle, G. R., Medlin, L. K. & Syvertsen, E. E. 1994. *Synedropsis* gen. nov., a genus of araphid diatoms associated with sea ice. *Phycologia* 33:248–70.
- Hasle, G. R. & Syvertsen, E. E. 1997. Marine diatoms. In Tomas, C. R. [Ed.] *Identifying Marine Phytoplankton*. Academic Press, San Diego, California, pp. 5–385.
- Hasle, G. R., Syvertsen, E. E. & von Quillfeldt, C. H. 1996. *Fossula arctica* gen. nov., spec. nov., a marine Arctic araphid diatom. *Diatom Res.* 11:261–72.
- Honeywill, C. 1998. A study of British *Licmophora* species and a discussion of its morphological features. *Diatom Res.* 13:221–71.
- Horner, R. A. 1985a. Ecology of sea ice microalgae. In Horner, R. A. [Ed.] *Sea Ice Biota*. CRC Press, Boca Raton, Florida, pp. 1–19.
- Horner, R. A. 1985b. Algal species reported from sea ice. In Horner, R. A. [Ed.] *Sea Ice Biota*. CRC Press, Boca Raton, Florida, pp. 191–203.
- Horner, R. A., Ackley, S. F., Dieckmann, G. S., Gulliksen, B., Hoshiai, T., Legendre, L., Melnikov, I. A., Reeburgh, W. S., Spindler, M. & Sullivan, C. W. 1992. Ecology of the sea ice biota. I. Habitat, terminology, and methodology. *Polar Biol.* 12:417–27.
- Knox, G. A. 2007. *Biology of the Southern Ocean*. CRC Press, Boca Raton, Florida, 621 pp.
- Kooistra, W. H. C. F., Forlani, G., Sterrenburg, F. A. S. & De Stefano, M. 2004. Molecular phylogeny and morphology of the marine diatom *Talaroneis posidoniae* gen. et sp. nov. (Bacillariophyta) advocate the return of the Plagiogrammaeaceae to the pennate diatoms. *Phycologia* 43:58–67.
- Kützing, F. T. 1844. *Die Kieselschaligen Bacillarien order Diatomaceen*. Köhne, Nordhausen, Germany, 152 pp.
- Lundholm, N. & Hasle, G. R. 2008. Are *Fragilariopsis cylindrus* and *Fragilariopsis nana* bipolar diatoms? – Morphological and molecular analyses of two sympatric species. *Nova Hedwigia Beih.* 133:231–50.
- Medlin, L. K. & Priddle, J. 1990. *Polar Marine Diatoms*. British Antarctic Survey, Natural Environment Research Council, Cambridge, UK, 214 pp.
- Morales, E. A. 2003. *Fragilaria pennsylvanica*, a new diatom (Bacillariophyceae) species from North America, with comments on the taxonomy of the genus *Synedra* Ehrenberg. *Proc. Acad. Nat. Sci. Phila.* 153:155–66.
- Olney, M. P., Bohaty, S. M., Harwood, D. M. & Scherer, R. P. 2009. *Creania lacyae* gen. nov. et sp. nov. and *Synedropsis cheethamii* sp. nov., fossil indicators of Antarctic sea ice? *Diatom Res.* 24:357–75.
- Palmisano, A. C. & Garrison, D. L. 1993. Microorganisms in Antarctic sea ice. In Friedmann, E. I. [Ed.] *Antarctic Microbiology*. Wiley-Liss, New York, pp. 167–218.
- Poulin, M. 1990. Family Naviculaceae: Arctic species. In Medlin, L. K. & Priddle, J. [Eds.] *Polar Marine Diatoms*. British Antarctic Survey, Natural Environment Research Council, Cambridge, UK, pp. 137–48.
- Prasad, A. K. S. K. & Livingston, R. J. 2005. Fine structure and taxonomy of *Synedropsis karsteteri* sp. nov. (Fragilariaceae, Bacillariophyta), a bloom-forming, brackish-water, planktonic, araphid diatom from Perdido Bay, northeastern Gulf of Mexico. *Diatom Res.* 20:145–62.
- Prygiel, J. & Coste, M. 2000. *Guide Méthodologique pour la mise en oeuvre de L'Indice Biologique Diatomées*. Agences de l'Eau, Ministère de l'Aménagement du Territoire et de l'Environnement, Direction de l'Eau, Bordeaux, France, 134 pp.
- von Quillfeldt, C. H. 2001. Identification of some easily confused common diatom species in Arctic spring blooms. *Bot. Mar.* 44:375–89.
- Roberts, D., Craven, M., Cai, M., Allison, I. & Nash, G. 2007. Protists in the marine ice of the Amery Ice Shelf, East Antarctica. *Polar Biol.* 30:143–53.
- Robison, B. H., Vernet, M. & Smith, K. L. Jr 2011. Algal communities attached to free-drifting, Antarctic icebergs. *Deep-Sea Res. Part II Top. Stud. Oceanogr.* 58:1451–6.
- Round, F. E., Crawford, R. M. & Mann, D. G. 1990. *The Diatoms, Biology and Morphology of the Genera*. Cambridge University Press, Cambridge, 747 pp.
- Scott, F. J. & Thomas, D. P. 2005. Diatoms. In Scott, F. J. & Marchant, H. J. [Eds.] *Antarctic Marine Protists*. Australian Biological Resources Study, Canberra, pp. 13–201.
- Silva, P. C. 1962. Classification of algae. In Lewin, R. A. [Ed.] *Physiology and Biochemistry of Algae*. Academic Press, New York, pp. 827–37.
- Silva, P. C. & Hasle, G. R. 2006. Taxonomic and nomenclatural history of *Fragilaria* (Bacillariophyceae). *Taxon* 51:200–2.
- Smith Jr, K. L., Robison, B. H., Helly, J. J., Kaufmann, R. S., Ruhl, H. A., Shaw, T. J., Twining, B. S. & Vernet, M. 2007. Free-drifting icebergs: hot spots of chemical and biological enrichment in the Weddell Sea. *Science* 317:478–82.
- Tuji, A. 2009. The transfer of two Japanese *Synedra* species (Bacillariophyceae) to the genus *Ulnaria*. *Bull. Natl. Mus. Nat. Sci. Ser. B* 35:11–6.
- Williams, D. M. & Round, F. E. 1987. Revision of the genus *Fragilaria*. *Diatom Res.* 2:267–88.
- Williams, D. M. & Round, F. E. 1988. *Fragilariforma*, nom. nov., a generic name for *Neofragilaria* Williams & Round. *Diatom Res.* 3:265–7.