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 *Ulnaria*, 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

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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 transapically 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 ~61°S and 63°S and 50°W and 54°W (3–28 December 2005 and 10 March–7 April 2009) on board the ARSV *Laurence 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 µm net attached to the ROV’s front or we pumped the water with the particles and filtered them through a 300 µm 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 onboard 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 emendation 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).

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).
Family Fragilariaceae Kützing (1844).


**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. 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).
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 aivalvar 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).


**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 pervalvar 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 Triceratiales (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.

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

Although plasti d 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, proplast 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 area. It has been suggested that T. signyensis could be 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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