

# Diatoms (Bacillariophyceae) associated with free-drifting Antarctic icebergs: taxonomy and distribution

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**Abstract** Free-drifting Antarctic icebergs can alter the phytoplankton in surrounding waters. In addition, diatom mats live attached to the submerged walls of the icebergs. In this study we describe a diverse diatom community associated with these mats and an atypical planktonic community in waters affected by icebergs. Samples were collected in the winter of 2008 and fall of 2009 from Antarctic icebergs and their adjacent waters, utilizing a remote operated vehicle and plankton nets, respectively, and subsequently analyzed using light and electron microscopy. *Thalassioneis signyensis*, dominant species growing on the icebergs' flanks, provided substrate for other diatoms, mainly *Synedropsis lata* var. *angustata*, *Synedropsis recta*, *Fragilaria* cf. *islandica* var. *adeliae*, *Attheya gausssii*, *Navicula* cf. *perminuta*, *Amphora* sp. and *Nitzschia* spp. New morphological characteristics are given for *S. lata* var. *angustata*, *S. recta* and *A. gausssii*. We report also *Biddulphia alternans* and *Coscinodiscus concinnus* for the first time in Antarctic waters. Similar to sea ice algae, the term sympagic is used to describe the habitat of these diatom communities. A particular planktonic community is also found close to icebergs, including diatoms known

to have a benthic, epiphytic, sympagic or freshwater habitat: *Amphora* sp., *B. alternans*, *Cocconeis* spp., *Delphineis minutissima*, *Licmophora gracilis*, *Luticola* cf. *australomutica*, *Ophephora* sp., *Pinnularia* spp., *Plagiogramma* sp., *Psammodictyon panduriforme* var. *minor*, *Pseudogomphonema kamtschaticum*, *Rhaphoneis amphiceros*, *S. recta* and *T. signyensis*. Our results support the hypothesis that species associated with icebergs exchange freely with plankton, ice shelves and sea ice, suggesting that icebergs can act as physical agents to transport and distribute organisms in between these habitats.

**Keywords** Diatom · Iceberg · Antarctica · Sympagic · Phytoplankton

## Introduction

Sea ice is known to play an important role in the ecology of the Southern Ocean. Beyond its influence on ocean physics, sea ice provides diverse habitats for countless organisms (Horner 1995; Knox 2007). Recent studies by Smith et al. (2007), Robison et al. (2011) and Ferrario et al. (2012) have also reported diatom communities living on submerged vertical walls of free-drifting Antarctic icebergs, as introduced previously by Whitaker (1977) for grounded icebergs. These diatoms are believed to feed the krill population in the vicinity (Robison et al. 2011). Due to the increasing frequency of icebergs in the Southern Ocean, in relation to the retreat and disappearance of ice shelves as a consequence of atmospheric warming, mainly over the Antarctic Peninsula (Vaughan and Doake 1996; Rott et al. 1998; Thompson and Solomon 2002), it is of particular interest to know the composition and dynamics of biological communities associated with or affected by icebergs.

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Mats and strands of colonial pennate diatoms (e.g., *Berkeleya rutilans*, *Fragilariopsis curta*, *F. cylindrus*, *Nitzschia stellata*), along with epiphytic pennate species, occur attached to the underside of the sea ice integrating a sub-ice community (Horner et al. 1988, 1992). Similarly, the pennate *Thalassioneis signyensis* was reported by Robison et al. (2011) and Ferrario et al. (2012) as the dominant diatom species associated with free-drifting icebergs.

*Thalassioneis signyensis* belongs to the monospecific genus established by Round et al. (1990), who based its description only on valve features, from sea ice samples collected near Signy Island. The analysis of living cells attached to sand grains or minerals removed from submerged flanks of several icebergs gave the possibility to enhance and emend its original description (Ferrario et al. 2012). Other diatoms have been sighted for the walls of free-floating Antarctic icebergs: *Biddulphia* aff. *punctata* and *Nitzschia* aff. *decepiens* (Smith et al. 2007) as well as *Nitzschia* sp. and *Synedropsis* sp. as epiphytes of *T. signyensis* (Robison et al. 2011). *Biddulphia punctata* had been previously observed as the predominant species growing on a small grounded iceberg (Whitaker 1977).

Different types of algal communities live in or in relation to different types of ice habitats. Likewise, various terms and criteria have been used to describe both the organisms that integrate these communities as well as their habitats (Horner et al. 1988, 1992; Garrison 1991). Particularly for the diatom *T. signyensis* associated with icebergs, Ferrario et al. (2012) used the term “sympagic” (=“with ice”), also proposed by Whitaker (1977).

Taking into account that the algal communities found associated with icebergs can contribute to the primary production in areas under icebergs influence, in addition to serving as food source and refuge for higher trophic levels (Smith et al. 2007; Robison et al. 2011), our purpose here is to complete the characterization of the diatom community sampled from the underwater surface of Antarctic icebergs. Additionally, we further discuss the origin of these organisms and the appropriate terminology to describe their habitat. Finally, we analyze taxonomy and abundance of diatoms found in waters surrounding icebergs, with a greater emphasis on those taxa uncommon to marine plankton.

## Materials and methods

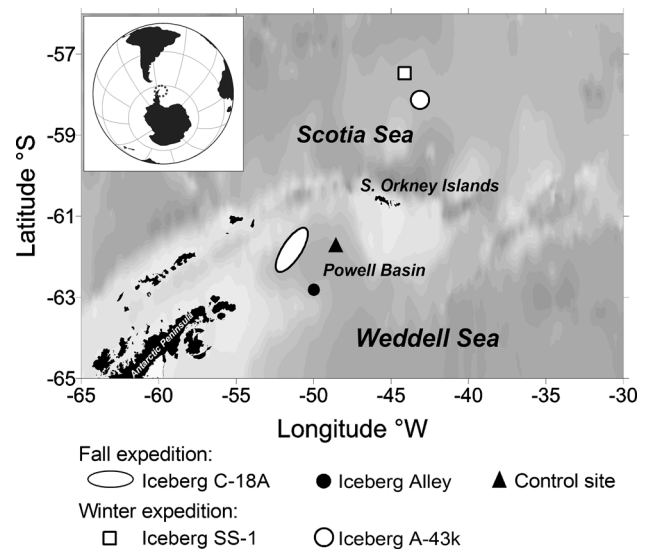
### Study sites and sampling

The present work was conducted 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.” Two Antarctic expeditions were carried out onboard the RVIB Nathaniel B. Palmer, one of them in the Scotia Sea (winter 2008, 7–25 June) and the other in the Powell Basin, northwestern Weddell Sea (late summer/fall 2009, 10 March–7 April) (Fig. 1). Prioritizing the seasonal chronology, first we describe the fall cruise and then the winter one.

### Fall expedition

Samples for the diatom mats were collected from a 35-km-long by 6-km-wide tabular iceberg, C-18A, localized at western Powell Basin, and from a smaller iceberg, IA-4, localized at southern Powell Basin in an area with numerous small icebergs (15 m to 2 km in largest dimension) labeled Iceberg Alley (Smith 2011). A remote operated vehicle (ROV-Phantom S2) was used for sampling. It was equipped with a CTD unit, video cameras and a suction sampler. Algal mats and particles attached to the icebergs’ flanks were removed with the nozzle of the sampler and pumped to a chamber system on the ROV (Hobson et al. 2011; Sherlock et al. 2011). Additionally, in waters near C-18A (0.3–1.0 km), far from the iceberg (16–18 km), in Iceberg Alley and in a control site 150 km east of C-18A, phytoplanktonic qualitative and quantitative samples were taken with a 20- $\mu$ m mesh net, from the ship’s seawater intake (9 m depth), and with Niskin bottles mounted in a circular rosette, from the surface (0–2.5 m depth), respectively (see Cefarelli et al. 2011 for more details).



**Fig. 1** Map showing the sampling areas. Fall expedition to the Powell Basin, northwestern Weddell Sea, between 61.37°–62.86°S and 48.44°–51.96°W. Winter expedition to the Scotia Sea, between 57.46°–58.24°S and 42.81°–44.12°W (base map courtesy of Hernan Isbert Perlender)

## Winter expedition

Phytoplanktonic qualitative and quantitative samples were collected in waters near (0.4–0.8 km) and far (16.5 km) from a 4.5-km-long tabular iceberg, SS-1, and near (0.2–0.4 km) and far (10.4 km) from a 38-km-long by 14-km-wide tabular iceberg, A-43k, both localized in the Scotia Sea. SS-1 was also examined with a ROV (Phoenix), but algal mats were not observed on the walls of this iceberg.

## Sample analysis

The collected material was preserved with acidic Lugol's solution. A preliminary analysis of fresh samples was done during cruises using a Nikon E800 light microscope (LM) equipped with a SPOT RT1 Slider digital camera. To identify organisms at the lowest possible taxonomical level, diatoms not cleaned and cleaned of organic matter (Hasle and Fryxell 1970; Prygiel and Coste 2000) and mounted on permanent glass slides with Naphrax medium (Ferrario et al. 1995) were examined using a phase contrast and a differential interference contrast Leica DM 2500 LM equipped with a Leica DFC420 digital camera. For more in-depth studies, the material, mounted on glass stubs and coated with gold–palladium according to Ferrario et al. (1995), was examined using a Jeol JSM-6360 LV scanning electron microscope (SEM). In order to describe certain taxonomic and ecological characteristics of the organisms, such as colony formation and epiphytism, many of the observations were done on whole cells, both at LM and at SEM. Permanent slides were deposited at the Herbarium of the División Ficología (LPC), Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata, La Plata, Argentina.

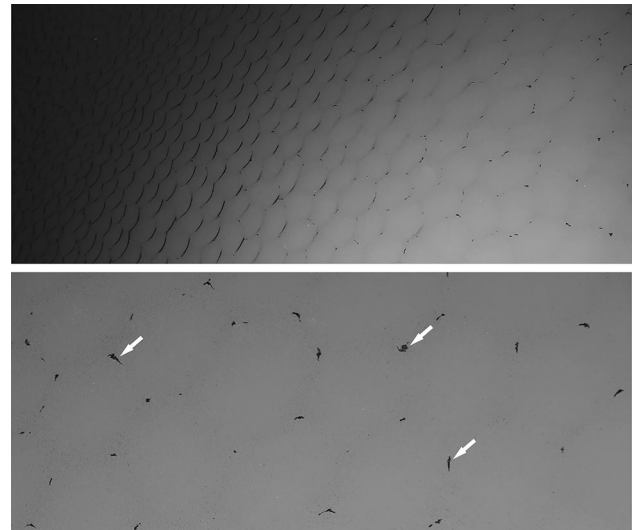
To estimate cell abundance, quantitative samples were examined at 400 $\times$  magnification with an Iroscope SI-PH inverted microscope (Utermöhl 1958). Previously, 100 ml of each sample had settled for 48 h in sedimentation chambers. At least 300 individuals were counted in random fields, and the results were expressed as number of cells per liter of water.

To estimate the relative abundance of the diatom species, at least 500 valves present in the permanent slides prepared from the net samples were counted at 1000 $\times$  magnification using LM and oil immersion, and the results were expressed as percentages.

## Results and discussion

### Physical properties of icebergs and their surrounding waters

Icebergs included in this study were studied in waters of the northwestern Weddell Sea, characterized by Antarctic



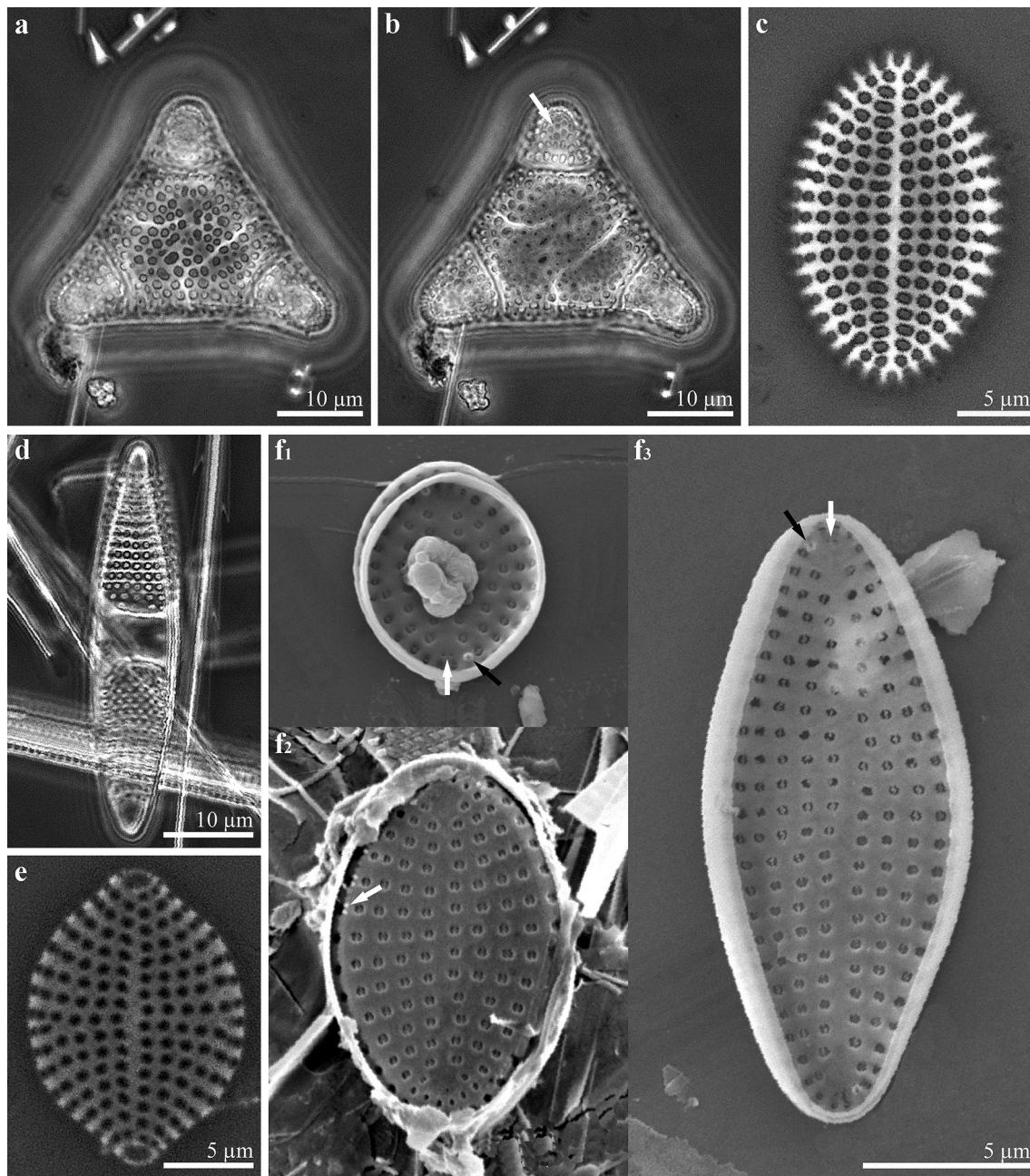
**Fig. 2** Submerged vertical wall of iceberg C-18A showing diatom mats attached to the edges of concavities present on the ice surface (indicated by white arrows) (photographs collected with the ROV, courtesy of Bruce Robison, Rob Sherlock and Ken Smith)

Surface Water and Winter Water (Stephenson et al. 2011), and in waters of the Scotia Sea. In situ surface water temperatures varied from  $-0.94$  to  $0.54$  °C and salinities of 33.698–34.148 in fall and from  $-1.60$  to  $0.00$  °C and salinities of 33.946–34.713 in winter. Free-drifting icebergs found in these waters had submerged walls showing countless concavities approximately 6–8 cm in diameter and 1–2 cm deep (Fig. 2). The edges of these concavities formed slightly elevated ridges (Robison et al. 2011).

### Diatoms in waters around icebergs, with special emphasis on those taxa usually not planktonic

#### Diatoms during the fall expedition

Diatoms were the numerically dominant taxonomic group of phytoplankton in surface waters in the four sampled areas during fall ( $n = 14$ ,  $\bar{x} = 652,307 \pm 496,200$  cells  $l^{-1}$ ), being *Fragilariopsis nana* (Steemann Nielsen) Paasche the more abundant taxon (see Cefarelli et al. 2011 for details). In this study, we concentrate on taxa usually not planktonic that occurred in waters with possible iceberg influence: near C-18A, far C-18A and Iceberg Alley (Stephenson et al. 2011; Vernet et al. 2011; Helly et al. 2015). *Licmophora gracilis* (Ehrenberg) Grunow and *Synedropsis recta* Hasle, Medlin and Syvertsen were found near C-18A; *Biddulphia alternans* (Bailey) Van Heurck (Fig. 3a, b), *Cocconeis* sp. (Fig. 3c), *Plagiogramma* sp. (Fig. 3d) and *Rhaphoneis amphiceros* (Ehrenberg) Ehrenberg (Fig. 3e) were in far C-18A; *Pinnularia* sp. occurred in Iceberg Alley; *Thalassioneis signyensis* Round emend



**Fig. 3** **a, b** ML Valve of *Biddulphia alternans* in two different focal planes. Note the pseudocellate elevations (indicated by the *arrow*) with inner costae at the base, the areolation pattern and the *curved lines* in the valve central region. **c** ML Valve of *Cocconeis* sp. **d** ML Valve of *Plagiogramma* sp. showing a thick fascia. **e** ML Valve of *Rhaphoneis amphicerus*. **f** SEM Specimens of *Delphineis minutissima*

showing morphometric variability. Note in **f<sub>1</sub>** and **f<sub>3</sub>** the presence of two tiny pores (indicated with *white arrows*) and one labiate process (indicated with *black arrows*) at each valve end. Note in **f<sub>2</sub>** the presence of external minute granules on the valve face/mantle junction (indicated with *white arrow*)

Ferrario, Cefarelli et Vernet was found near C-18A and in Iceberg Alley, while *Delphineis minutissima* (Hustedt) Simonsen (Fig. 3f) occurred both near and far C-18A as well as in Iceberg Alley. Percentages of these diatoms, obtained as relative abundance only, are indicated in Table 1. In addition, two benthic taxa usually not marine

were found at the control site: two valves from *Cocconeis* sp. and one valve from *Pinnularia borealis* Ehrenberg.

**Remarks:** The genera *Delphineis* and *Rhaphoneis* belong to the family Rhaphoneidaceae, which includes diatoms from shallow coastal waters over sandy shores and mudflats,

**Table 1** Relative abundance of diatom taxa usually not planktonic (as %) collected from surface waters with a net during the fall

Taxa	Area			
	Iceberg Alley	Near C-18A	Far C-18A	Control site
<i>Biddulphia alternans</i>			0.13	
<i>Cocconeis</i> spp.			0.13	+
<i>Delphineis minutissima</i>	0.25	0.08	0.37	
<i>Licmophora gracilis</i>		0.16		
<i>Pinnularia borealis</i>				+
<i>Pinnularia</i> sp.	0.25			
<i>Plagiogramma</i> sp.			0.13	
<i>Rhaphoneis amphicerus</i>			0.13	
<i>Synedropsis recta</i>		0.16		
<i>Thalassioneis signyensis</i>	0.25	0.16		

+, Below detection limit

often occurring attached to sand grains, on other diatoms, or integrating the plankton when they are resuspended by turbulent waters (Hasle and Syvertsen 1997; Sar et al. 2007). *Delphineis minutissima* was considered by Ferrario et al. (2003) as a tycho-planktonic organism from marine coastal waters of Buenos Aires, Argentina. In turn, Witkowski et al. (2000) presented it as a marine species of widespread distribution in the littoral, probably cosmopolitan. Similarly, *R. amphicerus* has been described as a coastal cosmopolitan species (Hasle and Syvertsen 1997; Witkowski et al. 2000).

Other taxa found in the plankton, such as *L. gracilis* and *Cocconeis* spp., are considered epiphytic and/or benthic forms. They were reported by Al-Handal and Wulff (2008a, b) in Potter Cove as epiphytes of macroalgae and on shallow sediments. *Biddulphia alternans*, species equally cited as epiphyte of macroalgae (Hoban 1983; Witkowski et al. 2000) or as tycho-planktonic along shore (Kraberg et al. 2010), could be identified by the presence of pseudocellate elevations in the three valve corners, internally delimited by well-developed costae, and by the presence of a tripartite curved line in the center of the valve (Hoban op. cit.); both structures were visible with LM (Fig. 3a, b). Our record of *B. alternans* is new for the Antarctic region.

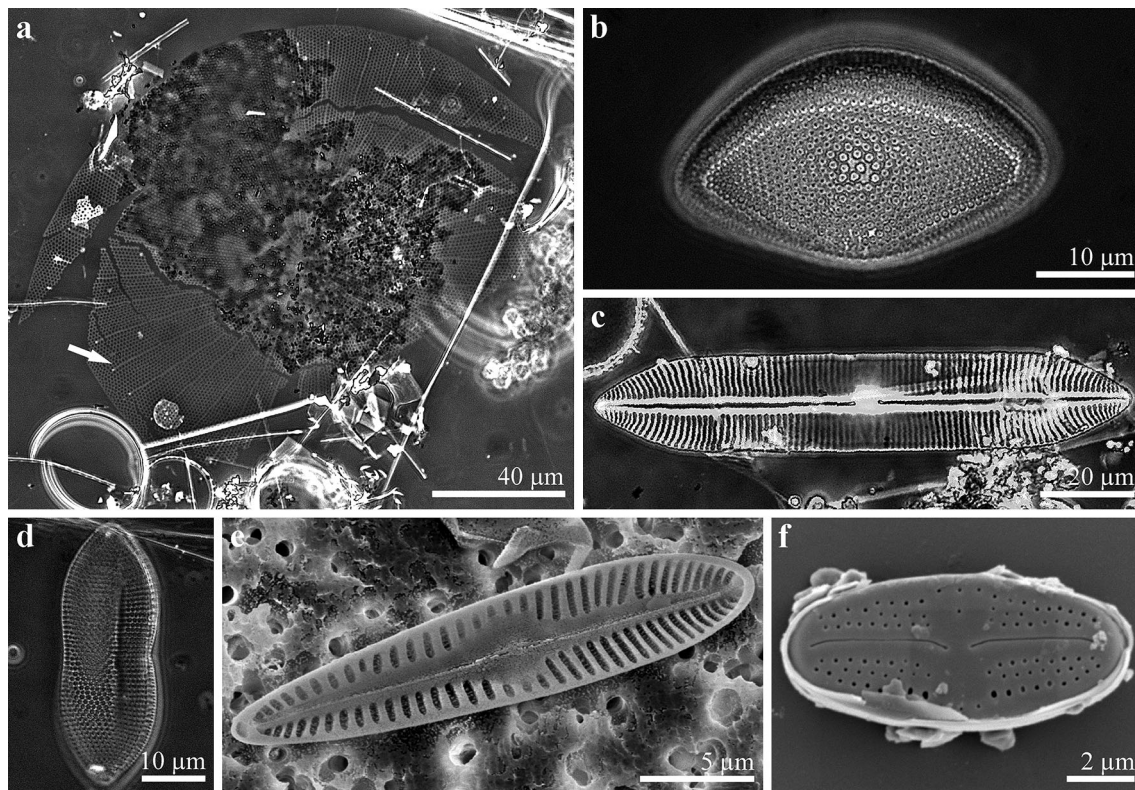
*Synedropsis recta* and *T. signyensis*, abundant on the icebergs' walls, also occurred in plankton. The presence of unexpected species in the plankton surrounding icebergs (Table 1) supports the hypothesis proposed by Schwarz and Schodlok (2009) and Robison et al. (2011) who first suggested icebergs as agents of dispersion. Although sea ice could be considered another source, our study of free-drifting icebergs was carried out far from the sea ice edge.

#### Diatoms during the winter expedition

Phytoplankton presented low density during the winter ( $n = 10$ ,  $\bar{x} = 69,869 \pm 31,840$  cells  $l^{-1}$ ), as expected for

this time of the year. Different from the fall community, unidentified small flagellated and coccoid cells dominated in surface waters. Diatoms were on average 3454 cells  $l^{-1}$ , less abundant than flagellated/coccoid and dinoflagellate cells. The numerically dominant diatoms were *Corethron pennatum* (Grunow) Ostenfeld and *Haslea* sp. Among the rare marine species for Antarctica, it is worth mentioning *Coscinodiscus concinnus* Smith (Fig. 4a) and *Hemidiscus cuneiformis* Wallich (Fig. 4b), both occurring near A-43k. On the other hand, among the species usually not found in plankton samples, *T. signyensis* and *Amphora* sp. were found near SS-1; *Pinnularia quadratarea* var. *bicuneata* Heiden (Fig. 4c), *Psammodictyon panduriforme* var. *minor* (Gregory) Haworth and Kelly (Fig. 4d), *Pseudogomphonema kamtschaticum* (Grunow) Medlin (Fig. 4e) and *R. amphicerus* were observed in samples far from SS-1; *Luticola* cf. *australomutica* (Fig. 4f) near A-43k; *Opephora* sp. far A-43k; *Cocconeis* sp. both near and far SS-1 as well as near A-43k; and *D. minutissima* in the four sampled areas. Percentages of these taxa, obtained by relative abundance estimation, are indicated in Table 2. With the exception of *D. minutissima*, all other species are present at very low percentages, similar to what was observed in the fall.

**Remarks:** In the case of uncommon diatoms for Antarctica, *C. concinnus* could be positively identified by us, representing the first mention of the species in Antarctic waters. According to Kraberg et al. (2010), this taxon can be found either in oceanic or in coastal areas, mainly in cold waters. Moreover, *H. cuneiformis*, which occurred also near A-43k, is predominantly a species of warm water regions, albeit with wide distribution in all oceans (Simonsen 1974; Hasle and Syvertsen 1997). It was cited by Hargraves (1968) for subantarctic waters at a temperature of 5.7 °C, considering his finding as a fortuitous event. More recently, Scott and Thomas (2005) describe and illustrate this



**Fig. 4** **a** ML Part of valve of *Coscinodiscus concinnus* with remains of organic matter. Note distinct hyaline lines from the marginal labiate processes toward the valve center (indicated with the arrow). **b** ML Specimen of *Hemidiscus cuneiformis*. **c** ML Valve of

*Pinnularia quadratarea* var. *bicuneata*. **d** ML Specimen of *Psammodictyon panduriforme* var. *minor*. **e** SEM Valve of *Pseudogomphonema kamschaticum* in internal view. **f** SEM Frustule of *Luticola* cf. *australomutica* in external view

**Table 2** Relative abundance of diatom taxa usually not planktonic (as %) collected from surface waters with a net during the winter

Taxa	Area			
	Near SS-1	Far SS-1	Near A-43k	Far A-43k
<i>Amphora</i> sp.	0.15			
<i>Cocconeis</i> spp.	0.15	0.17	0.17	
<i>Coscinodiscus concinnus</i>			0.17	
<i>Delphineis minutissima</i>	0.75	3.48	1.36	0.20
<i>Luticola</i> cf. <i>australomutica</i>			0.17	
<i>Hemidiscus cuneiformis</i>			0.17	
<i>Opephora</i> sp.				0.20
<i>Pinnularia quadratarea</i> var. <i>bicuneata</i>		0.17		
<i>Psammodictyon panduriforme</i> var. <i>minor</i>		0.17		
<i>Pseudogomphonema kamschaticum</i>		0.17		
<i>Rhaphoneis ampiceros</i>		0.17		
<i>Thalassioneis signyensis</i>	0.15			

species from coastal waters of East Antarctica. Only one specimen was recorded in our study, which showed a smaller size than documented before (apical axis 37  $\mu\text{m}$  and transapical axis 22  $\mu\text{m}$  vs. 40–288  $\mu\text{m}$  by 30–158  $\mu\text{m}$ , respectively).

For taxa usually not planktonic, *Luticola* is a fresh or slightly brackish water genus, most common in soils or

subaerial habitats and in estuaries (Round et al. 1990), being considered one of the dominant diatom genera in terrestrial habitats of the Antarctic (Van de Vijver and Mataloni 2008; Van de Vijver et al. 2011). The specimen found by us could not be definitively determined, but it resembles *L. australomutica* Van de Vijver, which was described as a new species from soil samples of Deception

Island, South Shetland Islands (Van de Vijver and Mataloni op. cit.). Our specimen has a larger size and lower density of striae than the available description for this species. *Pinnularia*, in turn, is mainly an epipelagic and freshwater genus (Round et al. 1990). The Arctic marine species of *Pinnularia* are characterized as periphytic, common in bottom sea ice (Poulin 1990). For Antarctica, different varieties of *P. quadratarea* are also cited (Frenguelli and Orlando 1958; Poulin 1990; Kellogg and Kellogg 2002; Scott and Thomas 2005; Al-Handal and Wulff 2008b), and according to Antoniadou et al. (2008) the *P. quadratarea* species complex is represented by a small number of taxonomic forms that can tolerate high salinity levels. *Pinnularia quadratarea* var. *bicuneata* was established by Heiden in Heiden and Kolbe (1928) from material collected during the German South Polar Expedition 1901–1903. As far as we know, our study is the first to identify this variety after its original description.

*Pseudogomphonema kamtschaticum*, usually not planktonic, has been reported in Antarctica as epiphyte of macroalgae or at the underside of sea ice (Scott and Thomas 2005). *Psammodictyon panduriforme* var. *minor* has also been found by Ferrario and Ferreyra (1987) in water samples around the South Orkney Islands and identified as a rare species for Antarctic waters. According to Round et al. (1990), *Psammodictyon* is an epipelagic marine genus, widespread on sandy substrata. Finally, *Opephora*, upon which it was not possible to conduct identification to specific level, is another epiphytic or most commonly epipsammic taxon, present in marine and/or brackish environments (Round et al. 1990; Sabbe and Vyverman 1995). It is noteworthy that several taxa currently included

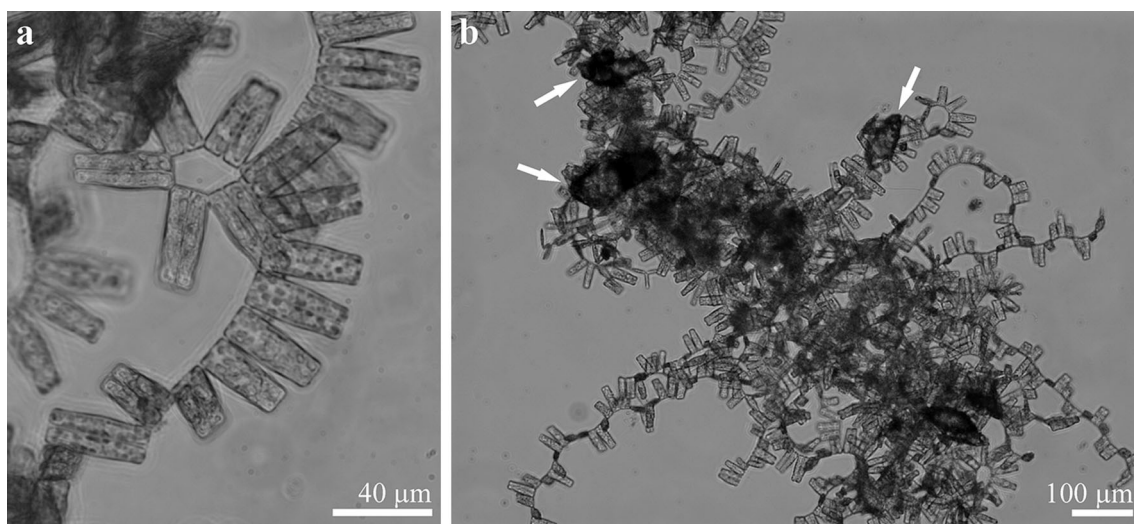
in the genus *Opephora* should be transferred to other allied or new genera on the basis of SEM studies (Morales 2002).

#### *Diatoms growing on the icebergs' flanks*

During the fall expedition, diatom mats and tufts were found on the flanks of the examined icebergs. The mats were observed on the edges of the ice concavities (Fig. 2), at depths between 20 and 145 m, more abundant between 20 and 55 m (Robison et al. 2011). These mats included several species of diatoms described here.

The diatom community was dominated by *T. signyensis*. It appeared in long chains, forming dense strands attached to small minerals embedded in ice (Fig. 5a, b). The diatoms initially identified as *Biddulphia* aff. *punctata* and *Nitzschia* aff. *decepiens* by light microscopy (Smith et al. 2007) were later conclusively identified as *T. signyensis* by Ferrario et al. (2012) using scanning electron microscopy. This species shows a large range of cell shapes and sizes, with the apical axis varying from 12.5 to 60.0  $\mu\text{m}$  and the transapical axis from 5.0 to 9.5  $\mu\text{m}$  (Ferrario et al. op. cit.). According to Robison et al. (2011), the chlorophyll *a* content is 10.66 pg per cell, or 24.25 ng per tuft of *T. signyensis*. In fall, with an estimated 100 tufts per  $\text{m}^2$ , the authors calculated a primary production of 7.7–1306  $\mu\text{g C m}^{-2} \text{day}^{-1}$ .

In association with *T. signyensis* colonies, other diatoms were found in lesser abundance (Table 3): *Synedropsis lata* var. *angustata* Hasle, Medlin and Syvertsen, *S. recta*, *Fragilaria* cf. *islandica* var. *adeliae*, *Attheya gaussii* (Heiden) Crawford, *Navicula* cf. *perminuta*, *Amphora* sp. and *Nitzschia* spp. Colonial and epiphytic species were common, suggesting that these life forms are advantageous to grow and develop



**Fig. 5** *Thalassioneis signyensis*. **a** ML Cells in curved and twisted chains. **b** ML Dense strands of cells attached to mineral particles (indicated by arrows)

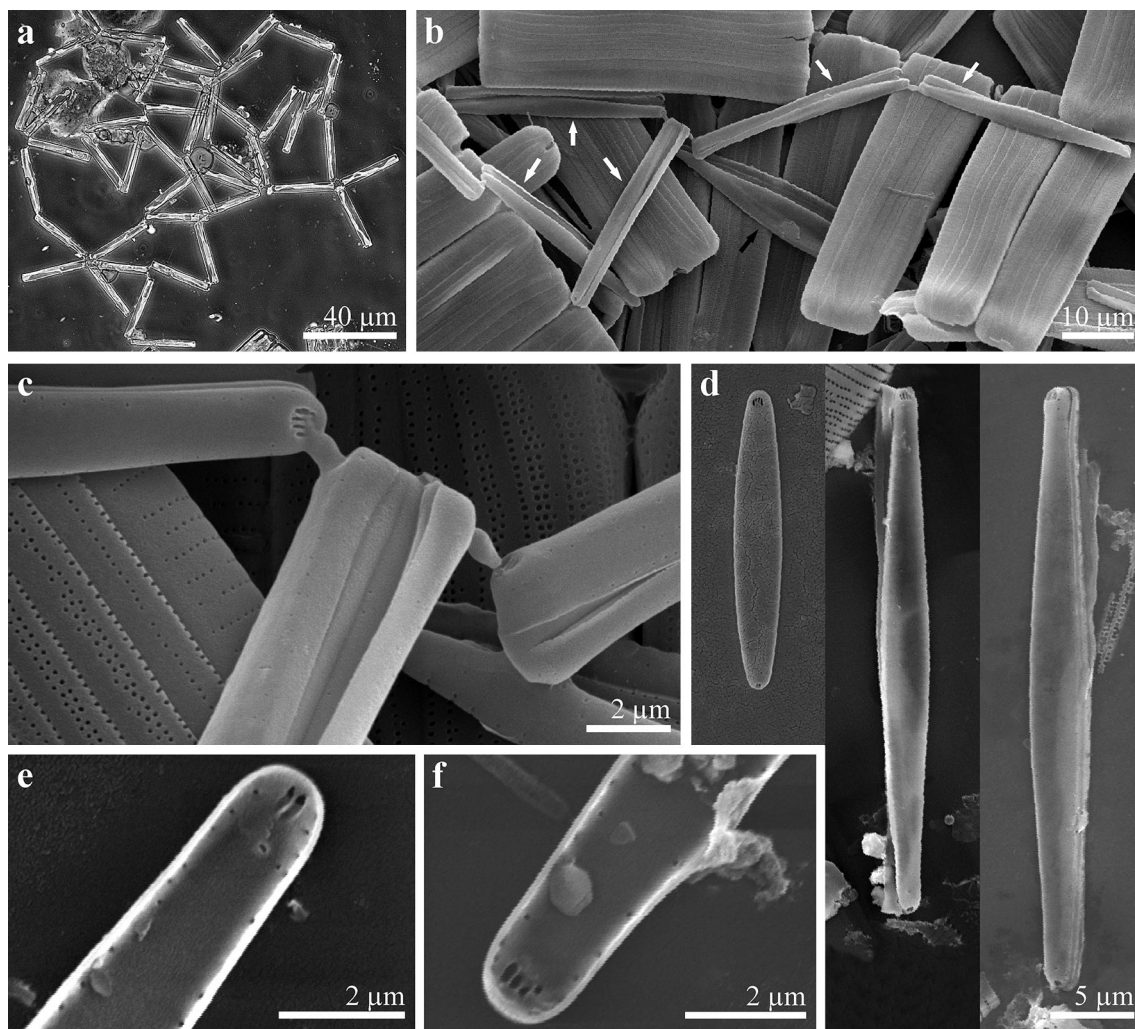
**Table 3** Relative abundance of diatom taxa (as %) collected with ROV from C-18A and IA-4 flanks during the fall

Taxa	Icebergs' flanks
<i>Amphora</i> sp.	1.19
<i>Attheya gaussii</i>	1.43
<i>Navicula</i> cf. <i>perminuta</i>	5.35
<i>Nitzschia medioconstricta</i>	0.36
<i>Synedropsis lata</i> var. <i>angustata</i>	1.78
<i>Synedropsis recta</i>	7.97
<i>Thalassioneis signyensis</i>	81.68
Non identified Pennate	0.24

tufts on the icebergs' walls. These taxa, sighted for the first time for icebergs' diatom communities, are described below.

*Synedropsis lata* var. *angustata* Hasle, Medlin and Syvertsen

The cells are joined to each other through mucilaginous material at one of the valve ends forming zig-zag and fan-like colonies (Fig. 6a–c). The valve shape is narrowly elliptical, with a slight dilation in the central part and slight constrictions close to the rounded ends (Fig. 6d). The striae, uniseriate, are only evident at the valve margins and mantle, whereas the sternum occupies almost the entire valve face,



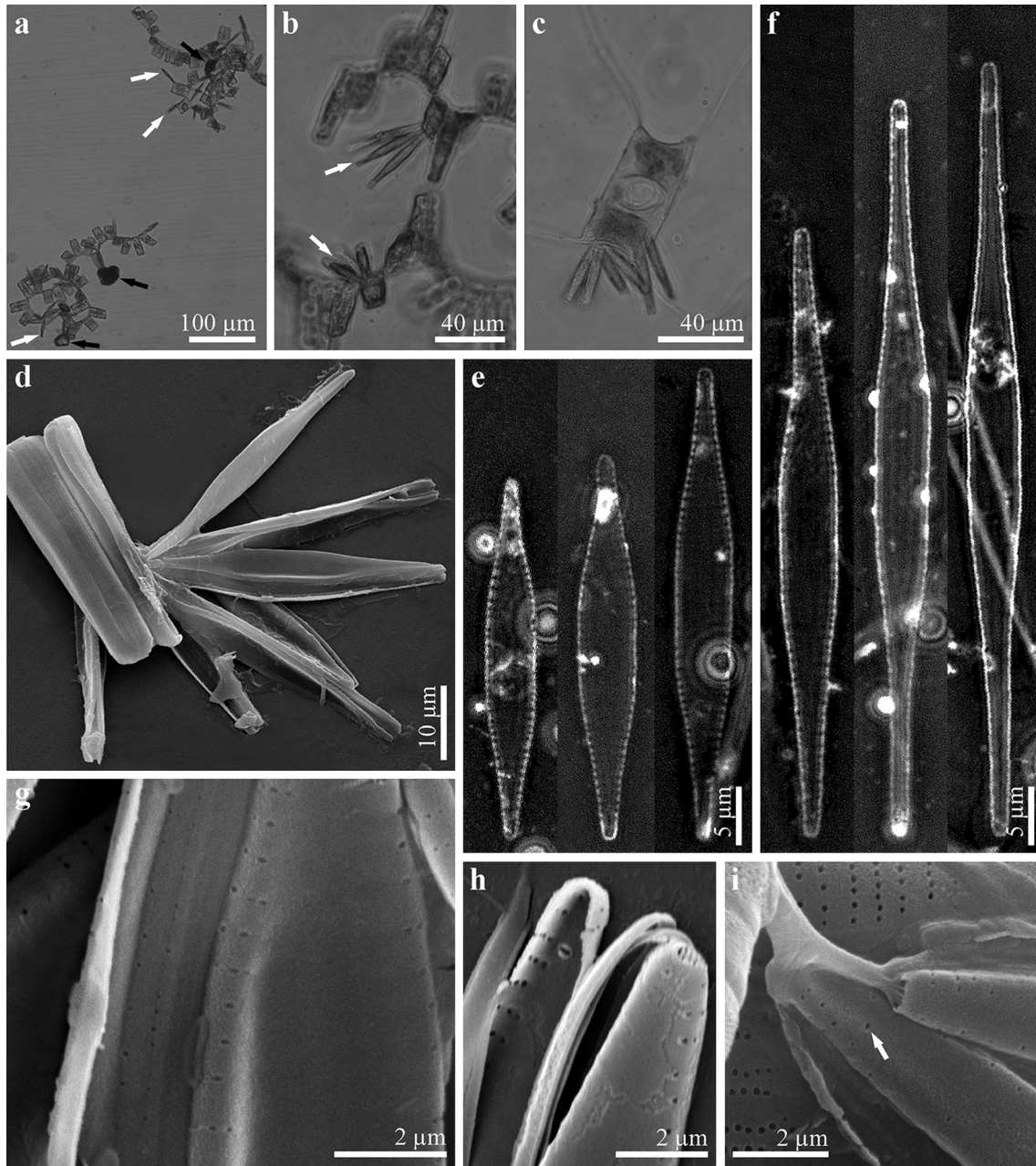
**Fig. 6** *Synedropsis lata* var. *angustata*. **a** ML Cells in zig-zag and fan-like colonies. **b** SEM Cells forming colonies in between *Thalassioneis signyensis* strands (indicated with white arrows). Note the presence of a frustule of *Synedropsis recta* (indicated with a black arrow). **c** SEM Details of the valve ends with higher number of slits joined to each other through mucilaginous material. Note details of

valve and girdle views. **d** SEM Specimens exemplifying different shapes and sizes. **e** SEM Valve end in internal view showing the labiate process and the apical field with lower number of slits. **f** SEM Valve end in internal view showing the apical field with higher number of slits



acquiring a poorly structured appearance (Fig. 6c–f). A single labiate process is situated two or three striae from one of the ends, with perpendicular or slightly oblique orientation with respect to the apical axis (Fig. 6e). The apical fields (slit fields) have an unequal number of slits at each end of the valve: two slits at the end with a labiate process,

which are displaced toward the apex mantle, and four or five slits at the end without the process, which are situated on the valve face (Fig. 6d–f). These latter play a role in uniting contiguous cells within the colony (Fig. 6c). The cingulum is composed by at least two open bands, perforated by one row of irregularly spaced poroids (Fig. 6c).



**Fig. 7** *Synedropsis recta*. **a** ML Single cells (indicated with *white arrows*) epiphytes on colonies of *Thalassioneis signyensis* attached to small minerals (indicated with *black arrows*). **b** ML Pin-cushion-shaped colonies (indicated with *white arrows*) on *T. signyensis*. **c** ML Same as in (**b**), but on *Atheya gaussii*. Note the coiled horns between the sibling valves of *A. gaussii*. **d** SEM Same as in (**b**). **e** ML Specimens showing different sizes. **f** ML Specimens showing a more elongated valve, ends more tapered and larger apical axis than the

original description of the species. These specimens were considered *S. recta*. **g** SEM Detail of frustule in valve and girdle view. **h** SEM Valve ends in internal and external view showing the labiate process and the apical slit field. **i** SEM Part of the epiphytic cells on *T. signyensis* showing the process opening (indicated with the arrow) and the apical slit field releasing mucilaginous material to adhere to the cells

Morphometric data: the apical axis is 18.0–35.5  $\mu\text{m}$  ( $\bar{x}$  = 30.0  $\mu\text{m}$ ); the transapical axis is 2.1–2.9  $\mu\text{m}$  ( $\bar{x}$  = 2.6  $\mu\text{m}$ ); and the transapical striae count 16–20 in 10  $\mu\text{m}$ .

*Synedropsis lata* var. *angustata* grows in between *T. signyensis* strands, not attached to anything.

#### *Synedropsis recta* Hasle, Medlin and Syvertsen

The cells are solitary or united at the ends forming pin-cushion-shaped colonies with two to six cells, in both cases attached to *T. signyensis* or *A. gaussii* (Fig. 7a–d). The valves are linear-lanceolate with straight margins in the middle part and rostrate or subcapitate ends. The striae, uniseriate, are evident principally at the valve margins and mantle (Fig. 7e, g). The sternum occupies most of the valve face. A single labiate process is situated on the second, third or exceptionally on the fourth stria from one of the ends, perpendicular or slightly oblique to the apical axis (Fig. 7h, i). The apical fields have five or six slits at both ends (Fig. 7h, i). The cingulum is composed by at least three open bands, perforated by one row of poroids arranged in advalvar position. The valvocopula, most of the time, appears with less evident perforations (Fig. 7g).

Morphometric data: the apical axis is 19.5–51.5  $\mu\text{m}$  ( $\bar{x}$  = 35.0  $\mu\text{m}$ ); the transapical axis is 3.4–5.0  $\mu\text{m}$  ( $\bar{x}$  = 4.4  $\mu\text{m}$ ); and the transapical striae count 12–17 in 10  $\mu\text{m}$ .

Another morphotype, also identified as *S. recta* (Fig. 7f), showed a more elongated valve shape, tapering toward the ends, and sometimes with longer apical axis (50–66  $\mu\text{m}$ ) than the original description of the species (17–48  $\mu\text{m}$ ).

**Remarks:** The genus *Synedropsis*, belonging to the araphid pennate diatom group, is principally characterized by having apical fields composed of longitudinal slits. It is a relatively new and little known genus, established in 1994 by Hasle, Medlin and Syvertsen from sea ice-associated polar syndroid diatoms; one species has been described for the Arctic and five for the Antarctic. In the past, the *Synedropsis* taxa have probably been recorded as either *Fragilaria* or *Synedra* spp. or overlooked. These two genera, however, have a well-defined ocellulimbus at each apex instead of apical slit fields as in *Synedropsis*. Furthermore, unlike the other related genera, *Synedropsis* presents a high variability in the shape and size of the sternum, which may occupy nearly the entire valve face (Hasle et al. 1994).

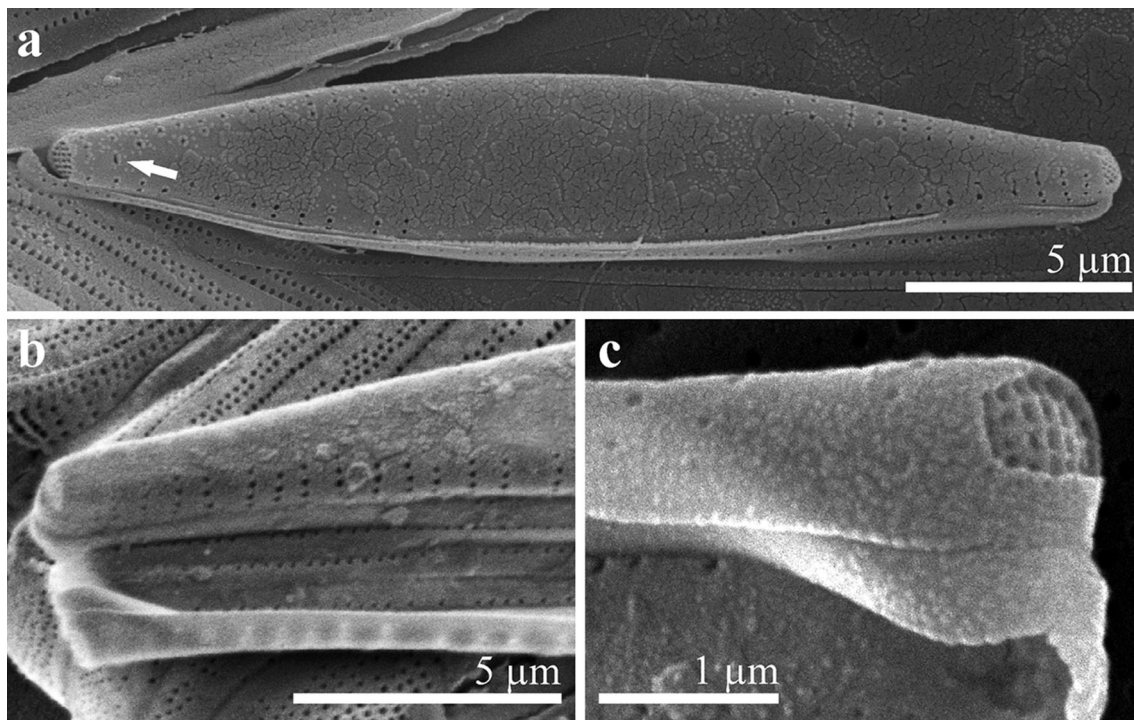
*Synedropsis lata* differs from the other species of the genus by the unequal number of slits at each end. The present study represents the first electron microscopy description of *S. lata* var. *angustata* in girdle view and the first report of colony formation for the species. Some of our analyzed specimens also presented smaller size regarding the one observed by Hasle et al. (1994).

The straight margins of the middle part of the valve and the subcapitate ends are the most evident characters that make possible to differentiate *S. recta* from other *Synedropsis* species (Hasle et al. 1994). *Synedropsis recta* is considered colonial because a few cells were observed united at the ends (Hasle et al. op. cit.). We documented this species as colonial and as epiphyte on diatoms associated with icebergs. On the other hand, and similar to observations reported by Al-Handal and Wulff (2008a), striae density of our analyzed specimens was higher than the one presented in the original description of the species (12–17 striae in 10  $\mu\text{m}$  in our material, 11–14 striae in 10  $\mu\text{m}$  in Hasle et al. 1994).

The more elongated specimens of *S. recta* observed in our material (Fig. 7f) are reminiscent of *Synedropsis laevis* (Heiden) Hasle, Medlin and Syvertsen; however, they show straight valvar margins in the middle of the valve. For this reason, they are included with *S. recta* until more information is available.

Considering the ecology and distribution of the genus, with the exception of *Synedropsis roundii* Torgan, Menezes and Melo, described from a tropical brackish coastal lagoon in southeastern Brazil (Melo et al. 2003), and *Synedropsis karsteteri* Prasad, described from brackish waters in northeastern Gulf of Mexico (Prasad and Livingston 2005), *Synedropsis* basically is a marine genus with polar distribution. *Synedropsis hyperborea* (Grunow) Hasle, Medlin and Syvertsen is the unique Arctic species, which can be found in the plankton, on ice or as epiphyte on the ice-associated *Melosira arctica* Dickie. The remaining five species of the genus [*Synedropsis fragilis* (Manguin) Hasle, Syvertsen and Medlin, *Synedropsis hyperboreoides* Hasle, Syvertsen and Medlin, *S. laevis*, *S. lata* Hasle, Medlin and Syvertsen, *S. recta*] are Antarctic, mainly occurring in diatom communities at the bottom of sea ice (Hasle et al. 1994; Hasle and Syvertsen 1997). *Synedropsis fragilis* and *S. hyperboreoides* were also found as epiphytes of large benthic and sea ice diatoms (Hasle et al. 1994; Scott and Thomas 2005). *Synedropsis recta*, in particular, was reported as rare on macroalgal rhodophytes in the sublittoral zone of Potter Cove, King George Island (Al-Handal and Wulff 2008a), and on calcareous bryozoans and hydroids associated with these same macroalgae in coastal waters of Terra Nova Bay, Ross Sea (Majewska et al. 2013). Additionally, *S. hyperboreoides* and *S. recta* can occur in the plankton close to the ice (Hasle and Syvertsen 1997). In our study, *S. recta* was also observed as a rare species in waters near C-18A during fall.

It is worth mentioning that the type material of *S. lata* comes from the grounded iceberg sampled by Whitaker (1977) at Signy Island, South Orkney Islands, similar to the present description.



**Fig. 8** *Fragilaria* cf. *islandica* var. *adeliae*. **a** SEM Valve in external view showing the labiate process opening (indicated with an *arrow*) and the apical pore fields. **b** SEM Part of frustule in valve and girdle view. **c** SEM Apical pore field situated on the apex mantle

### *Fragilaria* Lyngbye

Single cells of the genus *Fragilaria*, identified as *F.* cf. *islandica* var. *adeliae*, were found during the SEM analyses. The valves are linear-lanceolate with rostrate or subcapitate ends (Fig. 8a). A wide sternum occupies a large part of the valve face. Uniseriate striae are evidenced principally at the valve margins, extending to the valve face/mantle junction. A single labiate process is located at one valve end (Fig. 8a, b). The apical pore fields (ocellulimbus) composed of larger areolae are present on the mantle of each apex (Fig. 8a, c). The cingulum consists of three bands perforated by one row of poroids arranged in advalvar position. The valvocopula has the perforations irregularly distributed (Fig. 8b).

Morphometric data: the apical axis is 23.5–37.0 µm; the transapical axis is 3.7–4.5 µm; and the transapical striae count 14–18 in 10 µm.

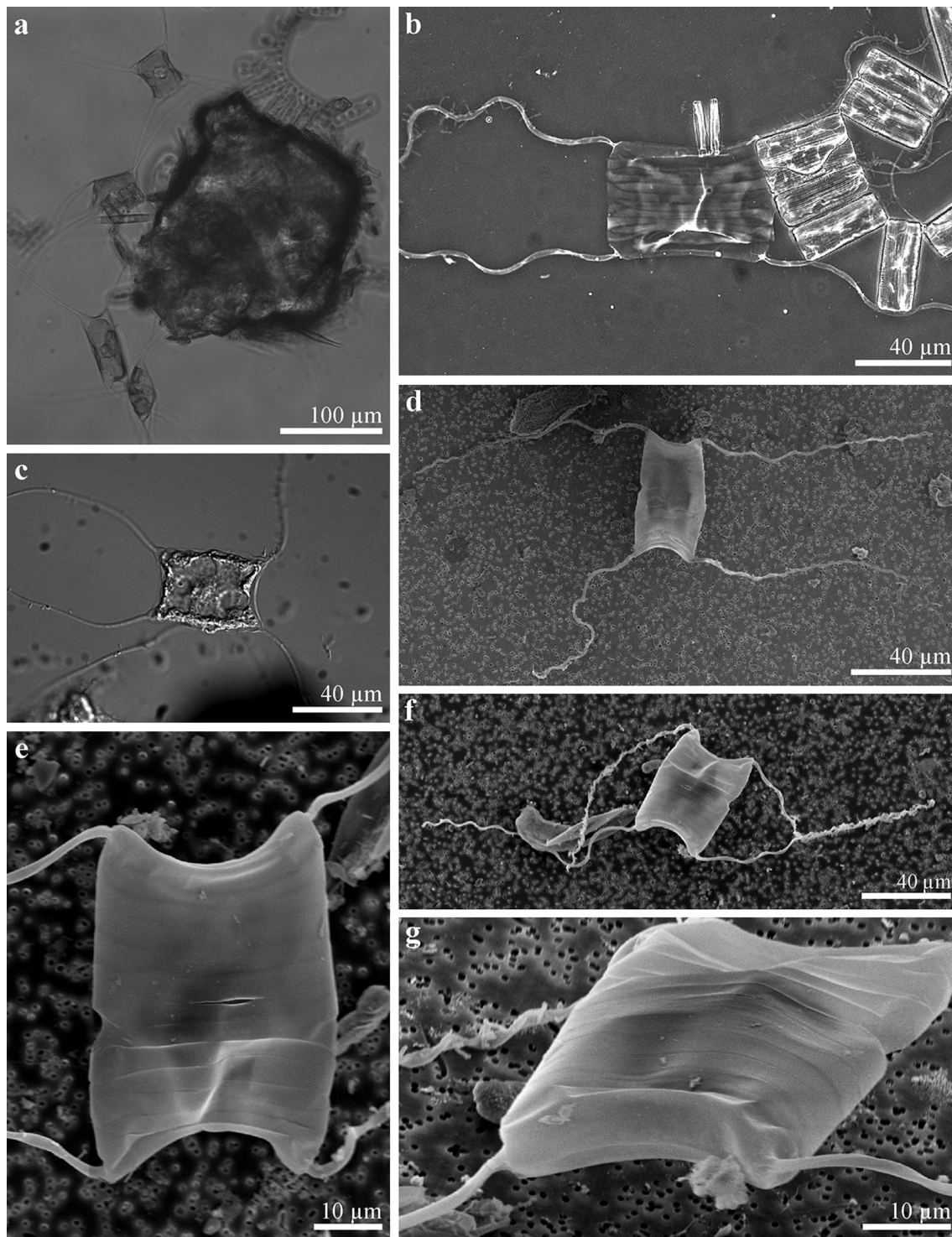
**Remarks:** *Fragilaria* is an araphid pennate diatom. Different new genera have been established on the basis of some taxa originally ascribed to *Fragilaria* (Williams and Round 1987). Usually, the species of *Fragilaria* form ribbon-like colonies, although some of them can be observed as single cells, as in our material. Unlike *Synedropsis* spp., the species in this genus present spines at the valve face/mantle junction and apical pore fields at the valve ends. In their study, Williams and Round (op. cit.) did not include any marine species, considering, for example, *Fragilaria*

*striatula* Lyngbye (identified as marine) as not belonging to *Fragilaria* sensu stricto. Round et al. (1990) also restricted the definition of *Fragilaria* to freshwater species, suggesting that marine diatoms previously classed as *Fragilaria* should be placed in other taxa. *Fragilaria islandica* Grunow is another marine species, which has been reported for the Antarctic region (Scott and Thomas 2005). Specifically, *Fragilaria islandica* var. *adeliae* Manguin was established in 1960 from Terre Adélie (southeastern Antarctica) and described as a form probably littoral (Manguin 1960). This species was also found in rocky sea bottom under fast ice, East Antarctica (Hasle et al. 1994), forming ribbon-like colonies (Scott and Thomas 2005; G. Campana, Instituto Antártico Argentino, pers. comm.).

In agreement with Hasle et al. (1994)'s observations, examined with LM *F.* cf. *islandica* var. *adeliae* is similar to *S. recta*, except in the middle part of the valves, having *F. islandica* var. *adeliae* convex margins.

### *Attheya gaussii* (Heiden) Crawford

*Attheya gaussii* was observed in association with *T. signyensis* colonies and also attached directly to small mineral particles (Fig. 9a, b). Several cells, two to six, shared the same substrate, but never forming true colonies (Fig. 9a). A single plate-like plastid slightly constricted

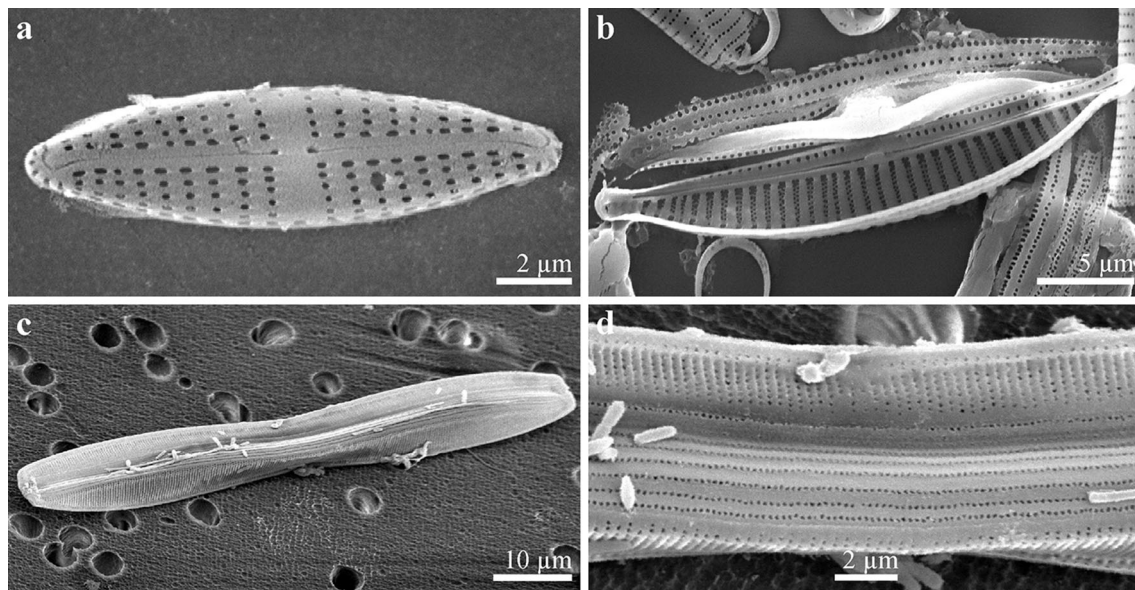


**Fig. 9** *Attheya gaussii*. **a** ML Several cells attached to a mineral particle. **b** ML Cell with *Synedropsis recta* epiphytes and connected to a *Thalassioneis signyensis* colony. **c** ML Cell showing a single plate-like plastid folded toward the edges. **d–f** SEM Frustules in

girdle view showing numerous bands and long horns. **g** SEM A frustule showing the valve surface, the insertion of horns and numerous bands

near the nucleus occupies most of the cell in girdle view and it is folded on the valve margins (Fig. 9c). The frustules are quadrangular to rectangular in girdle view, with

ten to twelve unperforated bands (Fig. 9b, d–f). The perivalvar axis is well developed and only exceptionally shorter than the apical axis (Fig. 9b). The valve surface



**Fig. 10** **a** SEM Valve of *Navicula* cf. *perminuta* in external view. **b** SEM Valve of *Amphora* sp. in internal view. **c** SEM Frustule of *Nitzschia medioconstricta* with remarkable constriction in its middle

part. **d** SEM Same frustule of *N. medioconstricta* in girdle view showing details of striation of the mantle, numerous bands, eccentric raphe system and central nodule

is concave, with long horns arising from the ends forming angles approximately at  $45^\circ$  to the valve margins (Fig. 9c–g).

Morphometric data: the perivalvar axis is 28.5–66.0  $\mu\text{m}$  ( $\bar{x}$  = 43.5  $\mu\text{m}$ ) and the apical axis is 23.5–66.0  $\mu\text{m}$  ( $\bar{x}$  = 36.0  $\mu\text{m}$ ).

**Remarks:** *Attheya gausssii* was initially described as *Chaetoceros gausssii* by Heiden in Heiden and Kolbe (1928). Further studies demonstrated differences between both genera, mainly in the seta and band structures. The setae of *Chaetoceros* are perforated tubes composed of a precise latticework of siliceous strips, with tips completely closed at maturity, while the horns of *Attheya* consist of a series of circular or spiral strips of silica supported by other longitudinal strips. Moreover, *Chaetoceros* usually has the girdle composed of half bands, while *Attheya*'s girdle is composed of full open bands. It is worth mentioning that at least in the case of *Attheya flexuosa* Gardner and *Attheya longicornis* Crawford and Gardner, the valvocopula is closed (Evensen and Hasle 1975; Crawford et al. 1994, 2000). Another feature of the genus *Attheya* occurs during cell division, when the new horns are coiled or folded between the new sibling valves. This particularity could be verified in our study as shown in Fig. 7c. Due to these characters, Crawford et al. (2000) transferred *C. gausssii* to the genus *Attheya*. Scott and Thomas (2005), however, still consider this taxon as *C. gausssii*. Independent of cell division, Crawford et al. (op. cit.) noted that the horns coil up if the turgor of cytoplasmic contents is lost. Therefore,

excessive curl or twist in the horns observed in non-fresh specimens is attributed to this process (Fig. 9f).

Our analysis expanded the ranges of length of the perivalvar and apical axes given for the transfer of this taxon; likewise, Heiden presented higher values in the original description.

A common ecological characteristic of the genus *Attheya* is its benthic lifestyle, occurring on substratum such as sand grains, sea ice or other diatoms; its habit also distinguishes this genus from *Chaetoceros*, characterized as a planktonic taxon (Crawford et al. 1994). While *A. gausssii* was only found within a polynya and in waters close to sea ice (Crawford et al. 2000), the authors also infer a possible benthic habit for this species, without excluding a planktonic one (sensu Reynolds 1984).

This study presents the first evidence of the species associated with other diatoms and/or attached to small minerals embedded in glacier ice, confirming its sympagic habit.

#### *Navicula* Bory

A single species of the genus *Navicula*, identified as *N. cf. perminuta*, was found during the ML and SEM analyses of diatom mats. The valve shape is lanceolate with obtusely rounded ends. The central area is rectangular and is demarcated by the middle striae pair, which are reduced to only one or two lineolae. Terminal raphe fissures are deflected toward the same side and shaped like a hook (Fig. 10a).

Morphometric data: the apical axis is 12.0–18.0  $\mu\text{m}$  and the transapical axis is 3.5–3.8  $\mu\text{m}$ . The striae are slightly radiate and count 16–17 in 10  $\mu\text{m}$ .

**Remarks:** After the circumscription of *Navicula* sensu stricto (Cox 1979), the genus includes around 250–300 mainly freshwater species, many of them adapted to brackish environments (Lange-Bertalot 2001). There is a small number of marine *Navicula* species; from those, the solitary forms found in plankton are usually considered to be resuspended from the bottom or detached from a substrate (Hasle and Syvertsen 1997). *Navicula perminuta* Grunow, particularly, has been indicated as a cosmopolitan taxon, common in brackish zones of rivers and along the coast of the northern hemisphere (Lange-Bertalot 2001); however, its taxonomic entity is rather confusing. Before SEM studies carried out by Busse and Snoeijs (2002), the descriptions were only based on LM observations, with poor details of the valve structure. According to Al-Handal and Wulff (2008b), better studies of the type material are necessary to establish the correct identity of this taxon. It has been adjudicated to different Antarctic environments (Kellogg and Kellogg 2002). In particular, Al-Handal and Wulff (2008a, b) reported *N. cf. perminuta* in Potter Cove from benthic marine communities and as epiphyte of marine macroalgae. In agreement with these authors, we prefer to denominate our analyzed specimens as *N. cf. perminuta*, until a better description of the type material becomes available.

#### *Amphora Ehrenberg ex Kützing*

A few specimens of the genus *Amphora* were observed during the SEM examination of diatom mats, not being possible their identification to specific level due to the paucity of material (Fig. 10b).

Morphometric data: the apical axis is 29.0–34.0  $\mu\text{m}$  and the transapical axis is 4.3–4.7  $\mu\text{m}$ . The dorsal striae are biseriolate and radiate (12–13 in 10  $\mu\text{m}$ ), counting with 40–47 areolae in 10  $\mu\text{m}$ .

**Remarks:** *Amphora* is a heterogeneous genus present in marine, brackish and fresh waters, either as epiphytic, epilithic or epipelagic organisms (Round et al. 1990; Sala et al. 2007). It has been registered in diverse Antarctic regions including sea ice (Scott and Thomas 2005). For example, in Potter Cove and Terra Nova Bay, different *Amphora* species occurred in benthic communities, in sediments, on macroalgae or on the sessile epiphytic fauna (Al-Handal and Wulff 2008a, b; Majewska et al. 2013).

#### *Nitzschia Hassall*

Several solitary specimens of the genus *Nitzschia* were observed in the diatom mats, being only possible the identification to specific level of *Nitzschia medioconstricta* Hustedt. The valve shape is linear-lanceolate, notably constricted in the middle part. The ends are subcapitate, becoming truncate in girdle view. The raphe system is eccentric and is interrupted by a central nodule. The cingulum is composed of numerous perforated bands (Fig. 10c, d).

Morphometric data: the apical axis is ca. 80  $\mu\text{m}$ . The uniseriate striae count 28–30 in 10  $\mu\text{m}$  and the fibulae 9–10 in 10  $\mu\text{m}$ .

**Remarks:** The genus *Nitzschia* includes both marine and fresh water species, solitary and colonial. Those species associated with sea ice have been mostly reported for the Arctic, with only a few for Antarctica (Medlin and Hasle 1990; Scott and Thomas 2005). As far as we know, *N. medioconstricta* was only cited and illustrated by Scott and Thomas (2005) since its original description in 1958. We show in detail the ultrastructure of the bands and report this taxon for the first time for a sympagic environment.

### Concluding remarks

We present for the first time a complete description of diatoms found on the walls of free-floating Antarctic icebergs. The study provides new and relevant diagnostic characters, both taxonomic and ecological, for *S. lata* var. *angustata*, *S. recta* and *A. gausssii*. *Biddulphia alternans* and *C. concinnus* are recorded for the first time in Antarctic waters.

The mats growing on the icebergs' flanks, previously considered unialgal, showed a diverse diatom community upon further investigation. Colonial species grow entangled with *T. signyensis* strands, such as *S. lata* var. *angustata* or as epiphytes, such as *S. recta*. Species like *A. gausssii* could attach itself to minerals, similar to *T. signyensis*. Other species are from a diversity of environments. The predominance of colonial and epiphytic species suggests these life forms are of advantage when growing dense tufts on the iceberg's flanks.

When considering the diversity of habitats of the species described in this study, the question arises on the origin and fate of diatoms found both attached and in the plankton. Different mechanisms have been suggested for sea ice species (Horner et al. 1992; Spindler 1994; Arrigo et al. 2010) but only one explanation has been proposed for

diatoms associated with icebergs (Robison et al. 2011). These authors hypothesized that the colonization of icebergs' flanks by *T. signyensis*, originally described as a sea ice species (Round et al. 1990), could originate from the time icebergs were surrounded by sea ice in their trajectory around the Weddell Gyre (Stuart and Long 2011). *Thalassioneis signyensis* could also grow directly on the ice shelves where icebergs originate (Robison et al. op. cit.). After calving, icebergs could carry and distribute the associated diatoms during their travels over different water masses.

Although difficult to test, we envision an exchange of diatom species between diverse habitats to explain the diversity observed in the icebergs' tuft community and in the phytoplankton community in waters affected by icebergs. Coastal diatoms growing in the benthos, periphyton, ice shelves, sea ice and plankton could become associated with, or become released from, a substrate due to turbulence, with subsequent attachment to glacier ice. Icebergs become then physical agents that transport organisms to oceanic waters (Schwarz and Schodlok 2009; Robison et al. 2011). This hypothesis is supported by the presence of *T. signyensis* and *S. recta* both on icebergs' flanks and in waters under icebergs influence. The origin of the other species, usually not planktonic, observed in the vicinity of icebergs, is more difficult to ascertain. We suggest they are also released to surrounding waters during ablation, together with mineral particles collected by the glaciers and maintained in the ice shelves. Kellogg and Kellogg (1987) provide evidence of a mixed sedimentary flora, both marine and continental and of different age, on the ice surface of the McMurdo Ice Shelf, which is almost entirely of marine origin, exemplifying the diversity of algae associated with ice shelves.

Different terminology, such as epontic, cryophilic and sympagic, has been used to refer to sea ice organisms and habitats (Whitaker 1977; Horner et al. 1988, 1992). Horner et al. (1992) suggested using sympagic as the most encompassing term that includes the different types of organisms living in or associated with sea ice. No specific terminology exists so far in relation to organisms living closely associated with icebergs. Nevertheless, Whitaker (1977) also considered as sympagic habitat the underwater ice of a small grounded iceberg (ice foot, shelf area and vertical walls), where growth of diatoms was observed, without entering into any other consideration on the origin of the ice, if marine or glacier. Specifically for the colonial diatom *T. signyensis* found on icebergs, Ferrario et al. (2012) applied also the term sympagic, in a global context, combined with the term epilithic, as this species is attached to small minerals (rocky substrate) embedded in the icebergs' ice. In this study we extend the classification of sympagic to include all species growing in the diatom community that live in close association with icebergs.

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#### Compliance with ethical standards

**Conflict of interest** The authors declare that they have no conflict of interest.

**Research involving human participants and/or animals** This article does not contain any studies with human participants or animals performed by any of the authors.

**Informed consent** Additional informed consent was obtained from all individual participants for whom identifying information is included in this article.

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