Polar Biology (2021) 44:421–431
https://doi.org/10.1007/s00300-021-02803-w

ORIGINAL PAPER

Transfer of the Antarctic diatom *Nitzschia barbieri* (Bacillariophyta) to the genus *Fragilariopsis* and emended descriptions of *F. barbieri* comb. nov. and *F. peragallii*

Adrián O. Cefarelli[1,2] · Martha E. Ferrario[3,4] · Maria Vernet[5] · Gabriela L. Campana[6,7] · Nina Lundholm[8]

Received: 31 March 2020 / Revised: 7 January 2021 / Accepted: 8 January 2021 / Published online: 7 February 2021

Abstract

Fragilariopsis is a marine diatom genus that has a critical ecological role in Antarctic waters due to its high abundance and ubiquity in plankton and sea ice. Several species of *Fragilariopsis* are used extensively in paleoceanography due to their good preservation in marine sediments. Detailed morphological studies on *Fragilariopsis* species from Antarctic water and ice samples were thus performed. Nevertheless, some species of this genus still remain poorly studied. Based on close morphological similarity between the valve structure of the Antarctic diatom *Nitzschia barbieri* and the genus *Fragilariopsis*, we propose transferring *N. barbieri* to *Fragilariopsis* as *Fragilariopsis barbieri* comb. nov. The description of the two rarely reported species, *F. barbieri* and *F. peragallii*, were emended. The girdle structure and the formation of doublets in *F. barbieri* and *F. peragallii* are described and illustrated for the first time. The analyses were carried out by light and electron microscopy and complete the morphological description of the fourteen known extant taxa of *Fragilariopsis* from Antarctica. Relative abundance of *Fragilariopsis* species from sea ice is also presented.

Keywords Diatom · *Fragilariopsis* · *Fragilariopsis barbieri* · *Fragilariopsis peragallii* · *Nitzschia* · Antarctica · Sea ice

Introduction

The diatom genus *Fragilariopsis* comprises planktonic and ice-associated species, which are all marine and mainly from polar waters (Round et al. 1990). *Fragilariopsis* species have a crucial ecological importance in Antarctic waters due to their high abundance and ubiquity in both plankton and sea ice (Round et al. 1990; Hegseth and von Quillfeldt 2002; Garibotti et al. 2003; Cefarelli et al. 2010; Rigual-Hernandez et al. 2019). Some species, such as *F. cylindrus*, *F. curta*, *F. kerguelensis*, are also frequently used as paleoenvironmental indicators due to good preservation in marine sediments (Leventer 1998; Gersonde and Zielinski 2000).

The genus *Fragilariopsis*, belonging to the family Bacillariaceae Ehrenberg, was established by Hustedt in Schmidt (1913) by separating *Fragilaria antarctica*

✉ Adrián O. Cefarelli
cefarelliadrian@gmail.com

1 Instituto de Desarrollo Costero, Universidad Nacional de la Patagonia San Juan Bosco (UNPSJB), Ruta Provincial 1, Km 4, 9005 Comodoro Rivadavia, Argentina

2 Centro de Investigaciones y Transferencia Golfo San Jorge, UNPSJB, Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Ruta Provincial 1, Km 4, 9005 Comodoro Rivadavia, Argentina

3 División Ficología, Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata, Paseo del Bosque s/n, 1900 La Plata, Argentina

4 CONICET, Godoy Cruz 2290, C1425FQB Ciudad Autónoma de Buenos Aires, Argentina

5 Integrative Oceanography Division, Scripps Institution of Oceanography, University of California San Diego, La Jolla, CA 92093-0218, USA

6 Departamento de Biología Costera, Instituto Antártico Argentino, Dirección Nacional del Antártico, 25 de Mayo 1143, 1650 San Martin, Argentina

7 Departamento de Ciencias Básicas, Universidad Nacional de Luján, Ruta 5 y Av. Constitución, 6700 Luján, Argentina

8 Natural History Museum of Denmark, University of Copenhagen, Øster Farimagsgade 5, 1353 Copenhagen K, Denmark

Castracane (=*Fragilariopsis kerguelensis* (O'Meara) Hustedt) from the genus *Fragilaria* Lyngbye. Afterward, several species were transferred to *Fragilariopsis* or described as new species of the genus, but the retention of the genus as a separate taxonomic entity was questioned (see Hasle 1965). In 1972, *Fragilariopsis* was reduced to a section of *Nitzschia* Hassall by Hasle (1972) based on the overlap in valve outline, stria structure, and the presence of a canal raphe, also present in *Nitzschia* and *Pseudo-nitzschia* Peragallo.

On the basis of morphological characters (valve shape, raphe structure, and stria structure) as well as the high diversity of *Nitzschia*, Round et al. (1990) considered *Fragilariopsis* as a natural group and suggested to reassign its generic status. Mann (1986) indicated the principal features of *Nitzschia* subgenus *Nitzschia* (based on the type *N. sigmoidea*): raphe raised on a keel, flaps of silica extending out from near the raphe (conopea) and poroids in the wall of the raphe canal. In contrast, the raphe in *Fragilariopsis* and *Pseudo-nitzschia* is not raised above the level of the valve, it is markedly eccentric and lacks conopea, and although both genera have a raphe canal, it lacks poroids in the outer raphe canal wall (Hasle 1993, 1994; Lundholm et al. 2002a; Lundholm and Hasle 2010). Based on the above-mentioned morphological differences, Hasle (1993, 1994) re-erected *Fragilariopsis* and *Pseudo-nitzschia* as separate genera distinct from *Nitzschia*, emended their diagnoses and made new combinations.

According to Hasle (1993), the frustules in *Fragilariopsis* are rectangular in girdle view, and broad and elliptical to linear-lanceolate and sometimes asymmetrical about the apical axis in valve view (transapical plane). Whereas in *Pseudo-nitzschia*, the frustules are strongly elongate, linear to lanceolate in girdle view, and mostly linear to lanceolate, sometimes asymmetrical about the transapical axis in valve view (apical plane). In addition, some *Pseudo-nitzschia* species have more complex poroid hymenes than found in *Fragilariopsis*. Finally, different types of colonies, ribbon-shaped in *Fragilariopsis* and stepped in *Pseudo-nitzschia*, differentiate the genera from each other.

Molecular analyses are in agreement with the morphological data revealing that *Fragilariopsis* and *Pseudo-nitzschia* are very closely related genera. In some analyses they appear as separate monophyletic genera, in other analyses a monophyletic *Fragilariopsis* clusters within a paraphyletic *Pseudo-nitzschia* (Lundholm et al. 2002a; Lim et al. 2018). *Nitzschia* does not make up a monophyletic clade, illustrating the need for a taxonomic revision of the genus (Lundholm et al. 2002a; Carballeira et al. 2017; Lim et al. 2018).

Nitzschia barbieri Peragallo was originally described by Van Heurck (1909) as *Nitzschia ostenfeldii* var. *minor* from sea ice in the west coast of the Antarctic Peninsula (65° 15.5′ S, 64° 30.0′ W). Peragallo (1921) established *N. barbieri* as a new species, different from *N. ostenfeldii* Heurck, because *N. barbieri* is shorter, has a smaller density of striae, and a higher density of fibulae (Peragallo 1921; Hasle 1965). Peragallo also established two new varieties smaller than *N. barbieri*: *N. barbieri* var. *minor,* with less evident pointed ends, and *N. barbieri* var. *latestriata,* with more rounded ends, a coarser striation and a lower density of striae and fibulae. Later, *N. barbieri* var. *latestriata* was by Hasle (1965) considered sufficiently distinct from *N. barbieri* to propose it as a separate species: *N. peragallii* Hasle [presently *Fragilariopsis peragallii* (Hasle) Cremer].

The two species, *N. barbieri* and *N. peragallii*, were not recognized as *Fragilariopsis* species by Hasle (1965, 1993) in spite of a valve structure similar to *Fragilariopsis* because they were only observed as single cells, never in ribbon-shaped colonies. They were, however, later included in the section *Fragilariopsis* by Hasle and Medlin (1990). Afterward *N. peragallii* was transferred to *Fragilariopsis* (Cremer et al. 2003), but without arguments for the transfer. Both species have an Antarctic distribution but have rarely been reported since their original description (Scott and Thomas 2005).

In the present study, we propose transferring *N. barbieri* to *Fragilariopsis* as *F. barbieri* comb. nov., based on morphological studies of phytoplankton and ice samples from Antarctica using light and electron microscopy. We compare the morphology of *F. barbieri* with similar *Fragilariopsis* species, and emend the previous descriptions of *F. peragallii* and *F. barbieri*. Finally, relative abundances of both taxa in sea ice are estimated.

Materials and methods

The present study was conducted in the framework of different Antarctic expeditions: (1) Expedition "ARGAU I" carried out onboard the icebreaker ARA Almirante Irizar along the Weddell Sea (February 2001). (2) Expedition "Iceberg II" carried out onboard the ARIB Nathaniel B. Palmer in the Scotia Sea (June 2008; Smith 2011). (3) Expedition "LMG 15-10" carried out on board the ARSV Laurence M. Gould in the Gerlache Strait and Andvord Bay on the Western Antarctic Peninsula (November–December 2015; Pan et al. 2019). (4) Expedition "CAV 2016/17" carried out at the Argentinean Carlini Station, Potter Cove, King George Island (summer 2017). See Table 1 and Fig. 1 for details of locations where taxa of interest for this study were found.

Phytoplankton net samples from ARGAU I and Iceberg II were taken with a 20-µm mesh net from the ship's seawater intake (9 m depth). Sea ice with brown coloration in Gerlache Strait was collected manually by scraping floating ice from a Zodiac (LMG 15-10). Pieces of glacier ice with brown coloration were sampled from coastal waters

Table 1 Details of Antarctic locations where *Fragilariopsis barbieri* and *F. peragallii* were found in the framework of different expeditions

Area	Expedition	Station	Sampling date	Latitude S	Longitude W	Species
Weddell Sea, plankton	ARGAU I	119	Feb. 23 2001	62° 34′	41° 21′	*F. barbieri, F. peragallii*
		135	Feb. 25 2001	71° 47′	31° 45′	*F. peragallii*
Scotia Sea, plankton	Iceberg II	27	Jun. 07 2008	57° 52′	44° 13′	*F. barbieri*
		100a	Jun. 17 2008	58° 10′	43° 26′	*F. peragallii*
Gerlache Strait, sea ice	LMG 15-10	24	Dec. 15 2015	64° 38′ 16″	62° 54′ 30″	*F. barbieri, F. peragallii*
Carlini Station, glacier ice	CAV 2016/17	CS	Jan. 27 2017	62° 14′ 17″	58° 40′ 14″	*F. barbieri*

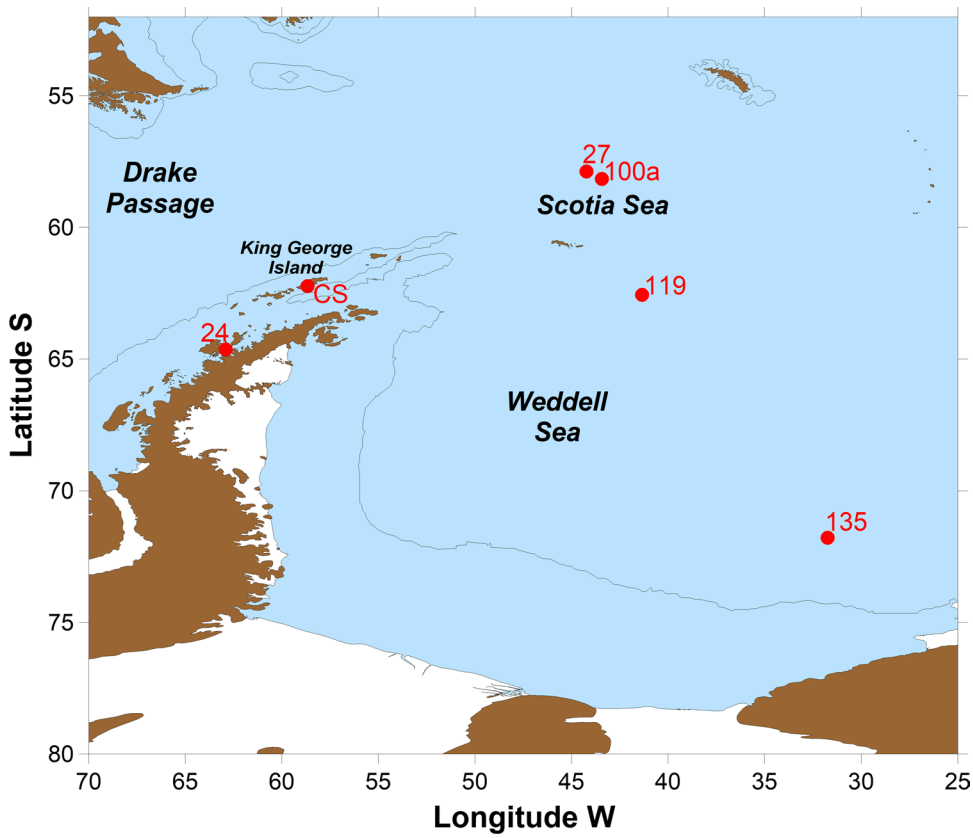

Fig. 1 Map showing Antarctic sampling locations where taxa of interest for this study were found

of Carlini Station (CAV 2016/17). After melting at room temperature, the resulting water was filtered through a 20-µm mesh net. All materials were preserved with Lugol's iodine solution.

The fixed material was washed with distilled water through centrifugation, cleaned with hydrogen peroxide at 90 °C, and washed and centrifuged again (Prygiel and Coste 2000). Both cleaned and non-cleaned materials were mounted on permanent glass slides with Naphrax (Ferrario et al. 1995) and examined using a phase contrast Leica DM 2500 light microscope (LM) equipped with a Leica DFC420 digital camera or a differential interference contrast Olympus BX51 LM equipped with an Olympus DP71 digital camera. Aliquots of rinsed and non-rinsed materials were mounted on stubs, coated with gold–palladium (Ferrario et al. 1995) and examined with a Jeol JSM-6360LV scanning electron microscope (SEM) of the Museo de La Plata, La Plata, Argentina or with a Jeol JSM-6460LV SEM of Aluar Aluminio Argentino SAIC, Puerto Madryn, Argentina. Untreated samples from CAV 2016/17 were examined at the Carlini Station's lab with an Olympus BX53F LM equipped with an Olympus DP21 digital camera. Permanent slides have been stored at the Herbarium of the División Ficología (LPC), Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata, La Plata, Argentina.

The species *F. barbieri* and *F. peragallii* occurred very rarely in most samples. During preliminary microscope observations on water mounts *F. barbieri* and *F. peragallii* occurred relatively frequently in a sea ice sample from Gerlache Strait. In order to be able to estimate the relative

abundance of *F. barbieri* and *F. peragallii* with other *Fragilariopsis* species also present, permanent slides were prepared from this sample and a total of 1872 valves of *Fragilariopsis* were counted and identified at 1000X magnification using LM and oil immersion, and the results were expressed as percentages.

Results

Detailed morphological analyses of *N. barbieri* and *F. peragallii* specimens allowed us to make a complete description of both species (see below) establishing similarities and differences between allied taxa. On the basis of these analyses, we propose transferring *N. barbieri* to *Fragilariopsis* as *Fragilariopsis barbieri* comb. nov. In addition, we provide an emended description of *F. barbieri* and *F. peragallii*.

Emended description of *Fragilariopsis barbieri* (Peragallo) Cefarelli, Ferrario & Lundholm comb. nov. (Figs. 2, 3)

Basionym: *Nitzschia barbieri* Peragallo (1921).

Synonym: *Nitzschia ostenfeldii* var. *minor* Heurck (1909) (See Fig. 7a).

Type locality: Sea ice (65° 15.5′ S, 64° 30.0′ W).

The cells are solitary or joined in doublets, valve against valve (Fig. 2a, b). The frustules are rectangular in girdle view, height c. 5 µm. The valve outline is linear and isopolar, with pointed ends (Fig. 2c–f). The valve length is 45.5–100.5 µm, width 8.0–13.5 µm, and the average length-to-width ratio is 6.9 ($n = 31$, Table 2, Fig. 6). The transapical striae are straight, sometimes slightly oblique in diverging directions (Fig. 2c), and towards the ends they become curved (Figs. 2, 3). Each stria contains one (occasionally two) rows of poroids clearly visible in LM (Fig. 2c–f), sometimes with incomplete or irregular rows in parts of the valve face (Figs. 2b, 3a–e). The fibulae sometimes occur at a slightly lower density than the striae. The stria density is 9–12 in 10 µm, fibula density 9–11 in 10 µm, and poroid density 15–26 in 10 µm (Table 2). A raphe slit is at the edge between valve face and valve mantle, slightly displaced towards the mantle (Fig. 3e–g). The valve mantle is unperforated and relatively low, height c. 1 µm. The cingulum consists of a valvocopula (width 1.65 µm, $n = 4$) with one irregular row of small poroids close to the advalvar edge, and a second unperforated and narrower copula (width 1.20 µm, $n = 4$) (Fig. 3e–g).

Distribution

Fragilariopsis barbieri was hard to find in all studied net samples. It was recorded at station 119, Weddell Sea, at a

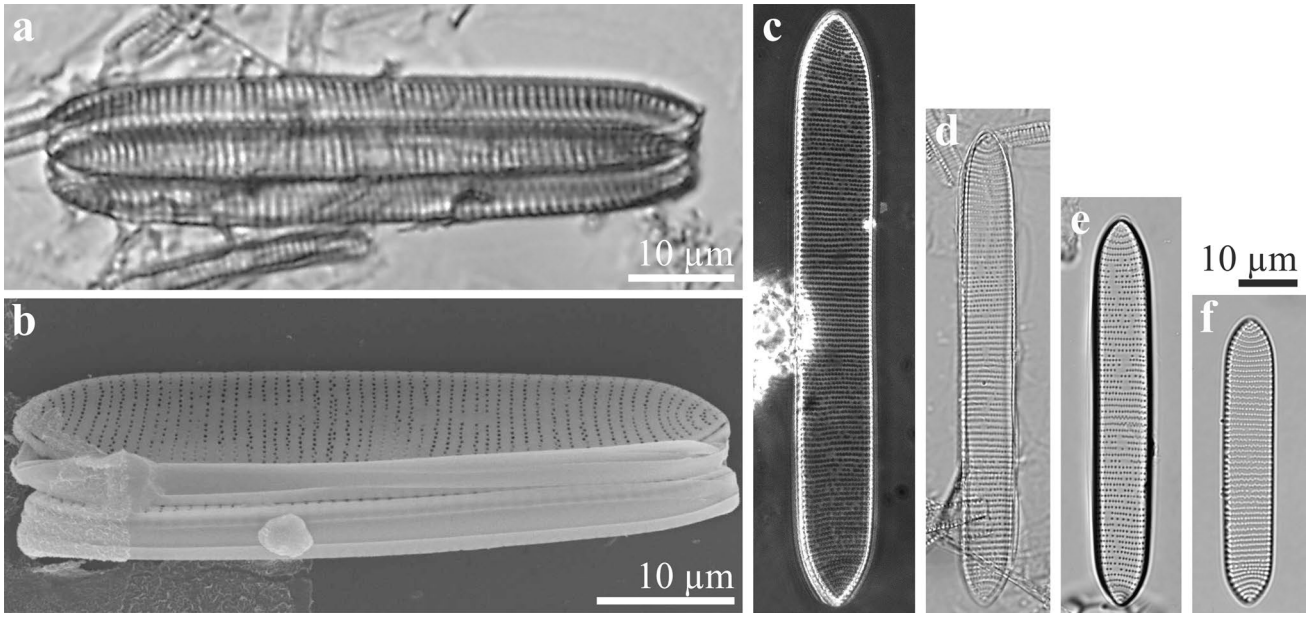

Fig. 2 **a–f** *Fragilariopsis barbieri*. **a** LM Cells united in doublet. **b** SEM Doublet of cells in valve and girdle view showing the pattern of striae, valvocopulae, and copulae. Note some incomplete uniseriate striae and others with two also incomplete rows of poroids. **c–f** LM Specimens including different sizes. Note the pattern of striae, with striae slightly oblique in different directions on each side of the middle part of the valve, especially in c

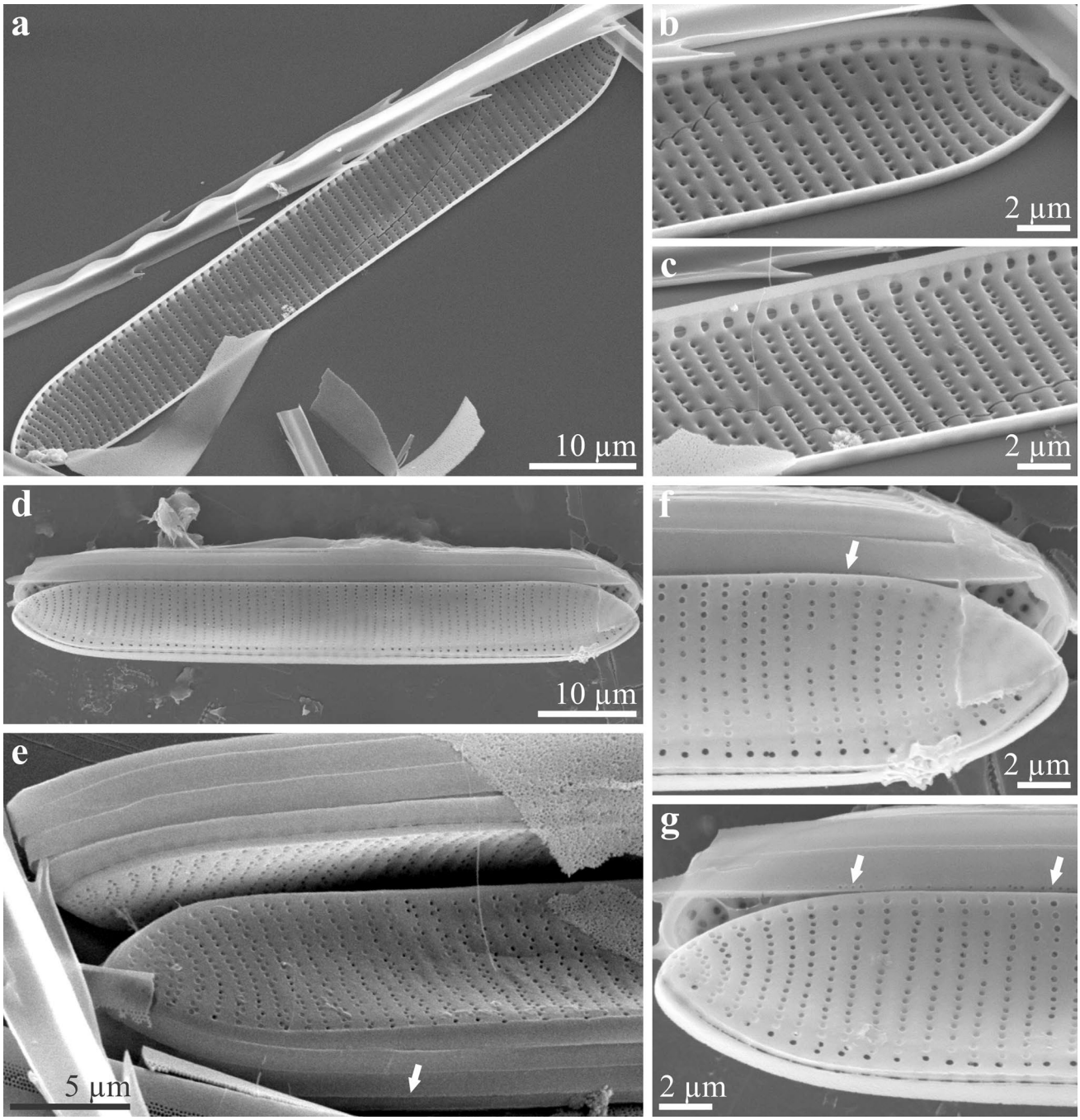

Fig. 3 **a–f** SEM *Fragilariopsis barbieri*. **a** Internal view of valve showing patterns of striae and fibulae. Note some incomplete uniseriate striae. **b** End of the same valve with striae becoming curved. **c** Middle part of the same valve showing fibulae and raphe canal in detail. **d** Open frustule with a lower density of fibulae than striae. **e** Part of two frustules in valve and girdle view presumably united before. The upper apparently without perforations on the copulae and the lower with incipient perforations (arrow) on the advalvar edge of the valvocopula. Note the position of the raphe displaced towards the mantle. **f**, **g** Ends of the same frustule as d showing details of the valvocopula with one irregular row of small poroids (arrows) and unperforated copula. Note the raphe situated between valve face and mantle

water temperature of − 1.2 °C and a salinity of 33.2, and at station 27, Scotia Sea, at a temperature of − 0.5 °C and a salinity of 34.7. An empty frustule was also found in glacier ice in the coastal waters of Carlini Station (Table 1, Fig. 1).

Although it could not be quantified, *F. barbieri* occurred in relatively high abundance in a sea ice sample collected in Gerlache Strait, western Antarctic Peninsula, at station 24 (Table 1, Fig. 1), where several other *Fragilariopsis* species

Table 2 Morphometric data for *Fragilariopsis barbieri*, *F. peragallii*, and allied taxa

Taxa	Length (µm)	Width (µm)	Length-to-width ratio	Transapical striae in 10 µm	Fibulae in 10 µm	Poroids in 10 µm
F. barbieri ($n=31$, present study)	**45.5**–100.5 (65.8 ± 16)	8.0–13.5 (9.5 ± 1.4)	6.9 ± 1.3	**9–12**	9–11	15–**26**
F. barbieri as *N. ostenfeldii* var. *minor* (Van Heurck 1909), reproduced in Fig. 7a	ca. 100	10	–	10	10	–
F. barbieri as *N. barbieri* (Peragallo 1921)	75–100	–	–	10	10	–
F. barbieri as *N. barbieri* (Hasle 1965)	49–118	8–14	–	10–11	8–11	ca. 15*
N. ostenfeldii (Van Heurck 1909), reproduced in Fig. 7b	160	ca. 10.5	–	11	ca. 5.5	–
N. barbieri var. *minor* (Peragallo 1921), reproduced in Fig. 7c	30–70	–	–	9	9	–
F. peragallii ($n=21$, present study)	32.5–67.5 (50 ± 8.4)	7.0–8.0 (7.5 ± 0.3)	6.8 ± 1.1	**6.5–9.5**	8–9	**15–20**
F. peragallii as *N. barbieri* var. *latestriata* (Peragallo 1921), reproduced in Fig. 7d	50–60	–	–	8	8	–
F. peragallii as *N. peragallii* (Hasle 1965)	32–90	7–8	–	7–9	7–9	ca. 16*
F. rhombica ($n=32$, Cefarelli et al. 2010)	8.5–48.5 (24 ± 9.4)	7–12 (10 ± 1.5)	2.4 ± 0.8	9–16	9–16	22–32
F. rhombica (Hasle 1965)	8–53	7–13	–	8–16	8–16	22–26
F. separanda ($n=14$, Cefarelli et al. 2010)	10–36 (19 ± 8.2)	5.5–12.5 (9.5 ± 2.5)	1.9 ± 0.5	10–14	10–14	12–20
F. separanda (Hasle 1965)	10–33	8–13	–	10–14	10–14	12–15
F. linearis (Hasle 1965)	40–72	7–9	–	7.5–9	7.5–9	ca. 25

Average ± standard deviation in parenthesis. Numbers in bold represent new ranges of data for *F. barbieri* and *F. peragallii*

*From Scott and Thomas (2005)

Table 3 *Fragilariopsis* spp. relative abundance (as %) from a sea ice sample at station 24 in Gerlache Strait

Fragilariopsis species	Relative abundance (%)
F. barbieri	0.11
F. curta	14.32
F. cylindrus	66.03
F. kerguelensis	3.10
F. nana	12.07
F. obliquecostata	0.21
F. peragallii	0.27
F. rhombica	0.96
F. ritscheri	1.28
F. separanda	0.21
F. vanheurckii	1.44

also occurred in high abundances. The relative abundance of *F. barbieri* of total *Fragilariopsis* species was, however, only 0.11%, with *F. cylindrus* as the dominant species (Table 3).

Fragilariopsis peragallii (Hasle) Cremer emend Cefarelli, Ferrario & Lundholm (Figs. 4, 5)

Basionym: *Nitzschia peragallii* Hasle (1965).

Synonym: *Nitzschia barbieri* var. *latestriata* Peragallo (1921) (See Fig. 7d).

Type locality: Argentine Islands, West Antarctic Peninsula.

The cells are solitary or united in doublets (Fig. 4a, b). The frustules are rectangular in girdle view, height c. 5 µm. The valve outline is linear and isopolar, with more or less pointed ends (Fig. 4c–g). The valve length is 32.5–67.5 µm, width 7.0–8.0 µm, and the average length-to-width ratio is 6.8 ($n=21$, Table 2, Fig. 6). The striae are straight, except toward the ends where they become curved (Figs. 4c–g,

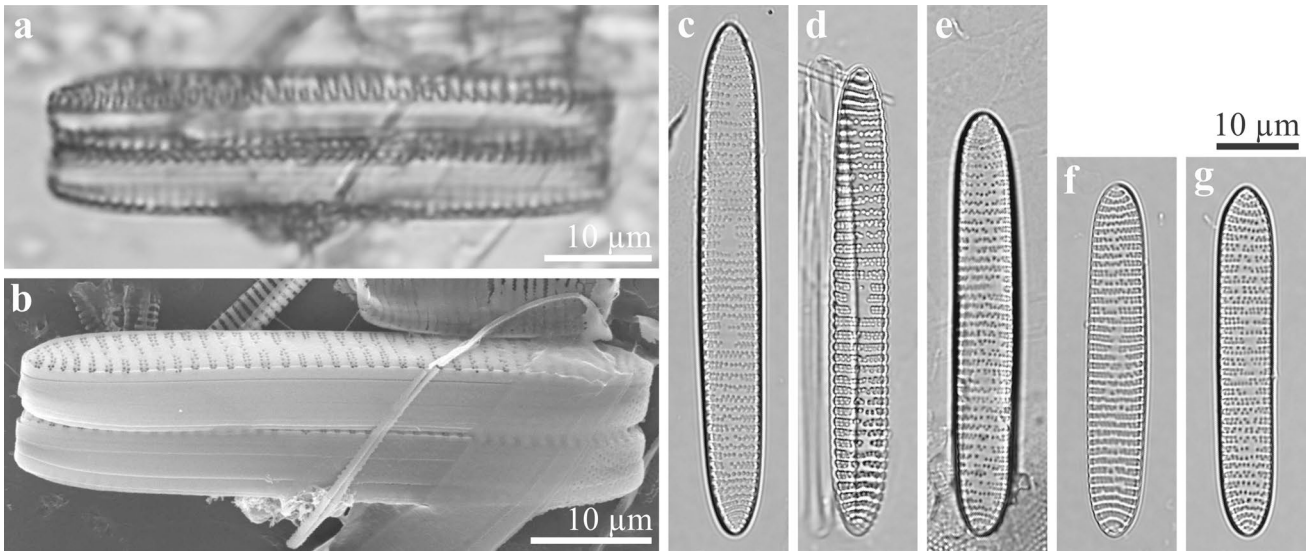

Fig. 4 **a–g** *Fragilariopsis peragallii*. **a** LM Cells united by the whole valve face forming doublets. **b** SEM Cells forming doublets. **c–g** LM Different valves showing different outlines and sizes. **f** Valve with less evident pointed ends

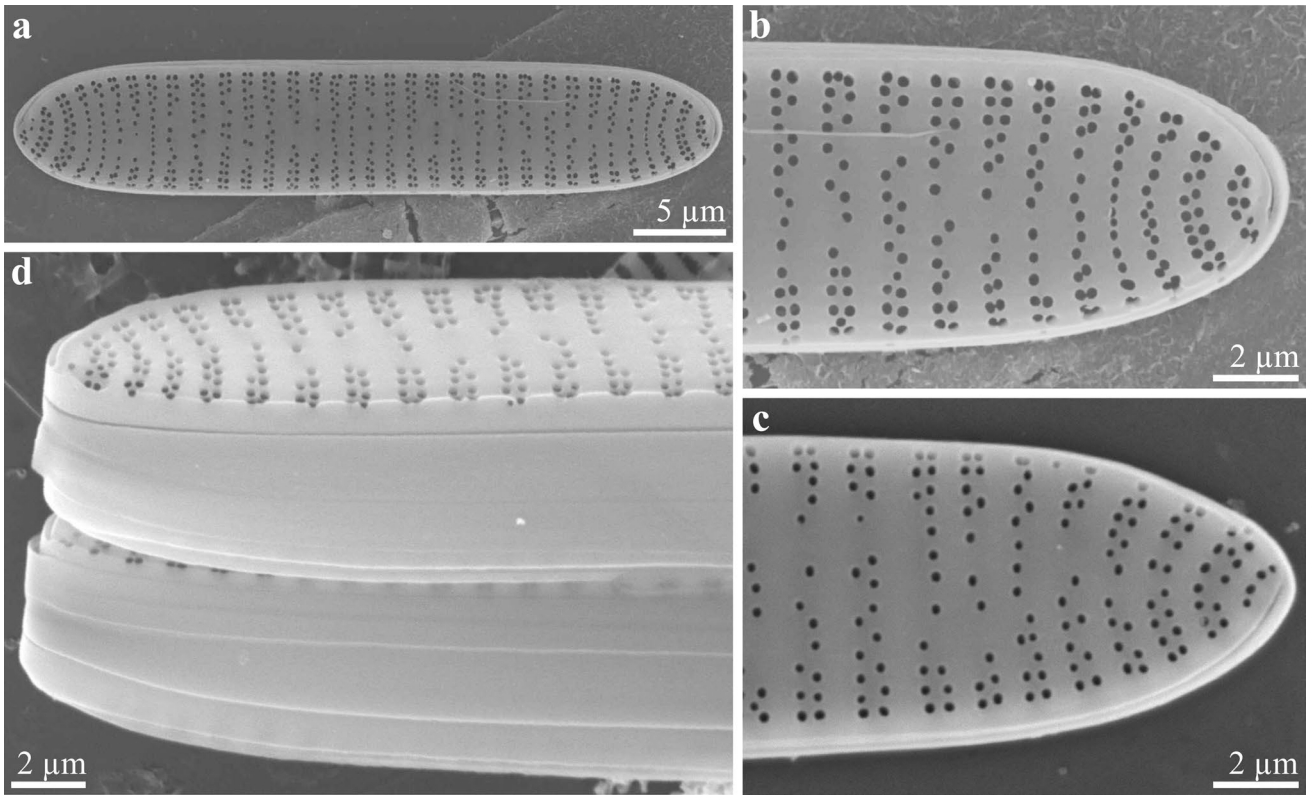

Fig. 5 **a–d** SEM *Fragilariopsis peragallii*. **a** Valve in external view showing pattern of striae. Note several incomplete biseriate striae and others with an incipient third row of poroids close to the valve edge. **b** End of the same valve showing details of striae becoming curved. **c** Part of other valve with more pointed end. Note the raphe situated between valve face and mantle. **d** Part of two joined frustules in valve and girdle view showing unperforated valvocopulae and copulae

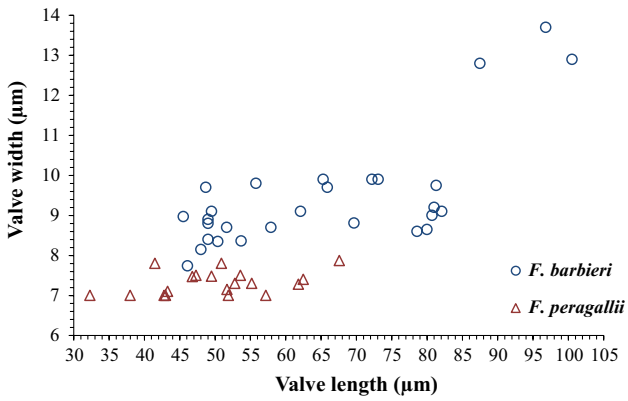

Fig. 6 Valve width (µm) as a function of valve length (µm) for *Fragilariopsis barbieri* and *F. peragallii*

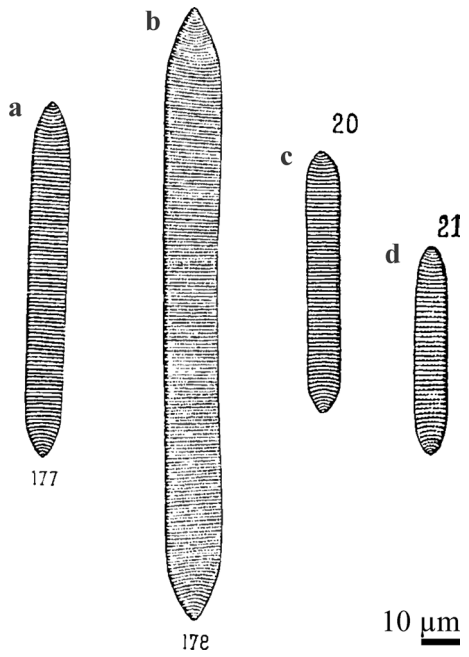

Fig. 7 Reproductions of original drawings of **a** *Nitzschia ostenfeldii* var. *minor* (Van Heurck 1909, Fig. 177), **b** *N. ostenfeldii* (Van Heurck 1909, Fig. 178), **c** *N. barbieri* var. *minor* (Peragallo 1921, Fig. 20), and **d** *N. barbieri* var. *latestriata* (Peragallo 1921, Fig. 21)

5a–c). Each stria contains two rows of poroids clearly visible using LM (Fig. 4c–g). The striae are frequently incomplete or reduced to only one row of poroids in parts of the valve face (Fig. 5a–c). In some specimens, a third incipient row of poroids can occur close to the valve edge (Fig. 5a, d). The fibulae sometimes occur at a slightly higher density than the striae. The stria density is 6.5–9.5 in 10 µm, fibula density 8–9 in 10 µm, and poroid density 15–20 in 10 µm (Table 2). A raphe slit is seen at the edge between valve face and valve mantle, slightly displaced towards the mantle (Fig. 5b–d). The valve mantle is unperforated and relatively low, height c. 1 µm (Fig. 5d). The cingulum consists of a valvocopula (width c. 2 µm) and a narrower copula (width c. 1.4 µm), both unperforated (Fig. 5d).

Distribution

Fragilariopsis peragallii was hard to find in net samples. It was recorded at stations 119 and 135, Weddell Sea, at water temperatures of − 1.2 and − 1.3 °C, and salinities of 33.2 and 33.3, respectively, and at station 100a, Scotia Sea, at a temperature of − 0.7 °C and a salinity of 34.1 (Table 1, Fig. 1).

Fragilariopsis peragallii occurred in relatively high abundance in a sea ice sample at station 24 in Gerlache Strait (Table 1, Fig. 1), with a relative abundance of only 0.27% of total *Fragilariopsis* species (Table 3).

Discussion

Transferring *Nitzschia barbieri* to *Fragilariopsis* and comments on *F. peragallii*

Like all *Fragilariopsis* species, and unlike most *Nitzschia* species, *F. barbieri* has a raphe canal which is not raised above the level of the valve face and lacks poroids in the wall of the raphe canal. Furthermore, the raphe system in *F. barbieri* is extremely eccentric and lacks a conopea, in contrast to *Nitzschia* subgenus *Nitzschia* and in accordance with *Fragilariopsis* (Hasle 1993; Hasle and Syvertsen 1997; Lundholm et al. 2002a).

Fragilariopsis barbieri has striae with one row of poroids like most *Nitzschia* species. Until the present study, *F. separanda* was the only other species of *Fragilariopsis* with uniseriate striae (Hasle and Syvertsen 1997; Lundholm et al. 2002a). But both *F. barbieri* and *F. separanda* have striae which sometimes have an additional incomplete row of poroids (Cefarelli et al. 2010; present study).

The fact that the valve structure of *F. barbieri* and *F. peragallii* is similar to *Fragilariopsis* species was noted already by Hasle (1965, 1972) and Medlin and Sims (1993). The lack of the colony-formation characteristic of *Fragilariopsis* was, however, used as argument against transferring the two taxa to *Fragilariopsis*. Colony formation as a character to delimit the genera *Nitzschia*, *Pseudo-nitzschia*, and *Fragilariopsis* has been questioned first by Hasle (1972) and later by Lundholm et al. (2002a). First, because some *Pseudo-nitzschia* species, like *P. americana*, mainly occur as single cells. This species was for a long time described as a *Nitzschia* species until it was cultured and sequenced and found to produce colonies in culture and cluster with *Pseudo-nitzschia* in phylogenetic analyses

(Lundholm et al. 2002b). Second, because colony formation is known to change with growth phase, and hence the cells sometimes appear as single cells (mainly at the stationary phase), sometimes in colonies (mainly in the exponential phase). The type of colony formation is, however, included in the diagnosis of *Fragilariopsis* and *Pseudo-nitzschia* (Hasle 1993, 1994). Both *F. barbieri* and *F. peragallii* were in the present study found in nature as solitary cells and for the first time also as doublets, as often seen in other *Fragilariopsis* species, e.g., *F. cylindrus, F. nana*, and *F. pseudonana* (Quillfeldt 2004; Scott and Thomas 2005; Cefarelli et al. 2010, 2011). We never saw ribbon-shaped colonies including more than two cells (the doublets), but we suggest that if cells are brought into culture, ribbon-shaped colony formation will be seen, similar to what has been seen, for e.g., *P. americana* and other species as mentioned above. Due to the fact that we found doublets, not proper ribbon-shaped colonies, we focused on frustule structure as the main argument for transferring *N. barbieri* to the genus *Fragilariopsis*.

Fragilariopsis peragallii was transferred to *Fragilariopsis* by Cremer in Cremer et al. (2003) without arguments for the transfer. Our analyses as well as those carried out by Hasle (1965, 1972) and Cefarelli et al. (2010) support the assertion that *F. peragallii* has the same valve structure as other *Fragilariopsis* species. We are, however, not convinced that the valves shown by Cremer et al. (2003) are *F. peragallii*. They resemble small specimens of *F. obliquecostata* as shown in Cefarelli et al. (2010) and Beszteri et al. (2018), with slightly oblique striae and rounded ends, in contrast to *F. peragallii*. A more detailed morphological study will be necessary to confirm or reject this assertion.

Similar taxa

According to Hargraves (1968), the morphological differences between *F. barbieri* and *F. peragallii* were insufficient to separate the two species because several specimens had morphological characteristics of both taxa. But the present analysis, including several specimens of each species, has shown that the two species make up clearly separate, although closely related taxa. *F. barbieri* has wider valves than *F. peragallii* (Fig. 6), more pointed ends, and a higher density of striae and fibulae (Table 2). In addition, *F. barbieri* has one row of poroids per stria, whereas *F. peragallii* has two rows, and *F. barbieri* has a valvocopula with a row of small poroids (Fig. 3e–g), while *F. peragallii* apparently has copulae lacking poroids (Fig. 5d). Despite the fact that Hasle (1965) questioned the number of rows of poroids per stria as having taxonomic importance because it varies even within a single valve, we consider this character useful to distinguish *F. barbieri* from *F. peragallii* (and e.g., also *F. rhombica* and *F. separanda*, Cefarelli et al. 2010), when used in combination with other characters. Even though it is possible to find variable or irregular patterns of rows of poroids in both species, this phenomenon occurs only in some parts of the valve face. It is still relatively easy to assign a general number of rows of poroids to each valve.

When comparing *F. barbieri* and *F. peragallii* with morphologically similar Antarctic *Fragilariopsis* species, Scott and Thomas (2005) noted the similarity among *F. barbieri* (as *N. barbieri*), *F. rhombica* and *F. separanda.* The valve outline of *F. rhombica* and *F. separanda* is elliptical to broadly lanceolate, isopolar, and with pointed ends; the larger valves with straight and parallel margins in the middle part (Cefarelli et al. 2010). On the contrary, valves of *F. barbieri* and *F. peragallii* never have an elliptical shape and more importantly have a higher length-to-width ratio (Table 2). The length of the apical axis in *F. barbieri* and *F. peragallii* reaches double or triple those of *F. rhombica* and *F. separanda,* respectively (Table 2); nevertheless, valve length is not always considered a robust differentiating character for diatoms due to the size reduction during vegetative cell divisions in diatoms (Beszteri et al. 2018). In the case of *F. barbieri* and *F. separanda*, both species have one row of poroids in the striae. They differ from each other by having very different, not overlapping, ranges of valve length. Similarly, *F. peragallii* and *F. rhombica* both have biseriate striae, and they differ from each other by *F. peragallii* having a lower density of poroids (Table 2), and lacking poroids on the copulae while *F. rhombica* has poroids on valvocopula (Cefarelli et al. 2010). Regarding habitat, *F. barbieri* and *F. peragallii* are characterized as sea ice species while *F. rhombica* and *F. separanda* are planktonic (Hasle and Medlin 1990; Hasle and Syvertsen 1997).

Based on morphometric data, *F. barbieri* and *F. peragallii* could also be confused with *F. linearis* due to the overlap of morphometric data (Table 2). Although *F. linearis* was not analyzed in the present study, it is described as a solitary species by Scott and Thomas (2005), isopolar, with almost straight parallel valve margins and biseriate striae. Unlike *F. barbieri* and *F. peragallii, F. linearis* has obtusely rounded ends and striae that become nearly parallel to the apical axis at the ends (Hasle 1965). Particularly *F. peragallii*, which has biseriate striae and less evident pointed ends, can also be distinguished from *F. linearis* by having a lower density of poroids.

Although the *N. ostenfeldii*-type material is not available for comparison (pers. comm. Dr. Bánk Beszteri, Alfred Wegener Institute, Germany, and Dr. Bart Van de Vijver, Botanic Garden Meise, Belgium), the original description tells that the species is larger (160 µm) than *F. barbieri*, has a slightly concave valve margin on the distal side, and has twice as many striae as fibulae (Van Heurck 1909, p. 21, pI. III, Fig. 178, reproduced in Fig. 7b) (Table 2). Concerning Peragallo's variety *N. barbieri* var. *minor,* the type material could not be found (pers. comm. Dr. Bánk Beszteri and Dr.

Bart Van de Vijver) and Peragallo's illustration is the only material available (Peragallo 1921, p. 66, pI. III, Fig. 20, reproduced in Fig. 7c). Our *F. barbieri* specimens resemble *N. barbieri* var. *minor* with respect to the valve outline, and partly coincide in stria and fibula density, but our specimens were never seen with such short valve length as mentioned for the variety (30 µm) (Table 2). Both *N. ostenfeldii* and *N. barbieri* var. *minor* have never been reported since their original descriptions, in 1909 and 1921, respectively.

Conclusion

Based on the close morphological similarity between the valve structure of *Nitzschia barbieri* and the genus *Fragilariopsis,* we suggest to transfer *N. barbieri* to *Fragilariopsis* as *Fragilariopsis barbieri* comb. nov. and emend its description. We recognize the transfer of *F. peragallii* to *Fragilariopsis* by Cremer in Cremer et al. (2003) and emend the description. The two taxa are morphologically closely related species, but with sufficient differential characters to be distinguished. The present study is the first to describe and illustrate the girdle structure of *F. barbieri* and *F. peragallii* as well as the first to show the formation of doublets in the two taxa.

We consider *F. barbieri* and *F. peragallii* as rare Antarctic species; a conclusion we base on the few previous records and own limited findings, also compared with other *Fragilariopsis* species. The taxa seem to be more frequent in sea ice than in plankton.

The present study completes the morphological description of the fourteen presently known extant species of *Fragilariopsis* from Antarctica, helping future species identifications of a genus of huge ecological significance in the region, frequently used in paleoceanographic studies.

Acknowledgements We thank Ms. Patricia Sarmiento and Mr. Mauricio Luquet for their excellent technical assistance with SEM work in the EM Service, Museo de La Plata, Argentina, and in Aluar Aluminio Argentino SAIC, Argentina, respectively. We thank MSc Luc Ector for providing pertinent bibliographic references for this work. We also thank the logistical support of Carlini Station, Instituto Antártico Argentino/Dirección Nacional del Antártico during the summer Antarctic expedition CAV 2016/17 and the financial support by ANPCyT-DNA (PICTO 2010-0116 and PICT 2017-2691). MV acknowledges support from the US National Science Foundation Fjord Eco project (PLR -1443705), the students and co-Principal Investigators involved in the sampling, the captain and crew of R/V Lawrence M. Gould and RVIB Nathaniel B. Palmer and United States Antarctic Program contractors.

Author contributions AC, NL, and MF conceived and designed research. AC, NL, and MV wrote the manuscript. AC, NL, and MF analyzed the morphologic characters of the diatoms taxa. AC, MV, and GC conducted field and laboratory work.

Funding This study was carried out within the frame of different projects: Project "Cooperation Program between France and ARGentina for the study of the AUstral Atlantic Ocean" (expedition "ARGAU I"); Project "Free-drifting Icebergs as Proliferating Dispersion Sites of Iron Enrichment, Organic Carbon Production and Export in the Southern Ocean" (expedition "Iceberg II"); Project "Fjord ecosystem structure and function on the West Antarctic Peninsula—Hotspots of productivity and biodiversity?" (expedition "LMG 15-10"); Project "Effects of global change on marine benthic algal communities at Potter Cove (South Shetland, Antarctica)" (expedition "CAV 2016/17"); and Project "Benthic primary producers in the coastal Antarctic ecosystem: consequences of climate change" (expedition "CAV 2016/17").

Compliance with ethical standards

Conflicts of interest The authors declare that they have no conflict of interest.

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

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.

References

Beszteri B, Allen C, Almandoz GO, Armand L, Barcena MÁ, Cantzler H, Crosta X, Esper O, Jordan RW, Kauer G, Klaas C, Kloster M, Leventer A, Pike J, Rigual Hernández AS (2018) Quantitative comparison of taxa and taxon concepts in the diatom genus *Fragilariopsis*: a case study on using slide scanning, multiexpert image annotation, and image analysis in taxonomy. J Phycol 54:703–719

Carballeira R, Trobajo R, Leira M, Benito X, Sato S, Mann DG (2017) A combined morphological and molecular approach to *Nitzschia varelae* sp. nov., with discussion of symmetry in Bacillariaceae. Eur J Phycol 52:342–359

Cefarelli AO, Vernet M, Ferrario ME (2011) Phytoplankton composition and abundance in relation to free-floating Antarctic icebergs. Deep-Sea Res II 58:1436–1450

Cefarelli AO, Ferrario ME, Almandoz GO, Atencio AG, Akselman R, Vernet M (2010) Diversity of the diatom genus *Fragilariopsis* in the Argentine Sea and Antarctic waters: morphology, distribution and abundance. Polar Biol 33:1463–1484

Cremer H, Roberts D, McMinn A, Gore D, Melles M (2003) The Holocene diatom flora of marine bays in the Windmill Islands, East Antarctica. Bot Mar 46:82–106

Ferrario ME, Sar EA, Sala SE (1995) Metodología básica para el estudio del fitoplancton con especial referencia a las diatomeas. In: Alveal K, Ferrario ME, Oliveira EC, Sar EA (eds) Manual de métodos ficológicos. Univ Concepción, A Pinto Edit, Chile, pp 1–23

Garibotti IA, Vernet M, Ferrario ME, Smith RC, Ross RM, Quetin LB (2003) Phytoplankton spatial distribution patterns along the western Antarctic Peninsula (Southern Ocean). Mar Ecol Progr Ser 261:21–39

Gersonde R, Zielinski U (2000) The reconstruction of late Quaternary Antarctic sea-ice distribution—the use of diatoms as a proxy for sea-ice. Palaeogr Palaeoclim Palaeoecol 162:263–286

Hargraves PE (1968) Species composition and distribution of net plankton diatoms in the Pacific Sector of the Antarctic Ocean. Ph.D. thesis, School of Marine Science, College of William and Mary, Virginia

Hasle GR (1965) *Nitzschia* and *Fragilariopsis* species studied in the light and electron microscopes. Part III. The genus *Fragilariopsis*. Skr Norske Vidensk-Akad I Mat-Nat Kl NS 21:1–49

Hasle GR (1972) *Fragilariopsis* Hustedt as a section of the genus *Nitzschia* Hassall. Nov Hed Beih 39:111–119

Hasle GR (1993) Nomenclatural notes on marine planktonic diatoms. The family Bacillariaceae. Nov Hed Beih 106:315–321

Hasle GR (1994) *Pseudo-nitzschia* as a genus distinct from *Nitzschia* (Bacillariophyceae). J Phycol 30:1036–1039

Hasle GR, Medlin LK (1990) Family Bacillariaceae: the genus *Nitzschia* section *Fragilariopsis*. In: Medlin LK, Priddle J (eds) Polar marine diatoms. British Antarctic Survey, National Environmental Research Council, Cambridge, pp 181–196

Hasle GR, Syvertsen EE (1997) Marine diatoms. In: Tomas CR (ed) Identifying marine phytoplankton. Academic Press, San Diego, pp 5–385

Hegseth EN, Von Quillfeldt CH (2002) Low phytoplankton biomass and ice algal blooms in the Weddell Sea during the ice-filled summer of 1997. Antarct Sci 14:231–243

Leventer A (1998) The fate of Antarctic ''sea ice diatoms'' and their use as paleoenvironmental indicators. In: Lizotte MP, Arrigo KR (eds) Antarctic sea ice biological processes, interactions and variability. American Geophysical Union. Antarct Res Series 73:121–137

Lim HC, Tan SN, Teng ST, Lundholm N, Orive E, David H, Quijano-Scheggia S, Leong SCY, Wolf M, Bates SS, Lim PT, Leaw CP (2018) Phylogeny and species delineation in the marine diatom *Pseudo-nitzschia* (Bacillariophyta) using cox1, LSU, and ITS2 rRNA genes: a perspective in character evolution. J Phycol 54:234–248

Lundholm N, Hasle GR (2010) *Fragilariopsis* (Bacillariophyceae) of the Northern Hemisphere—morphology, taxonomy, phylogeny and distribution, with a description of *F. pacifica* sp. nov. Phycologia 49:438–460

Lundholm N, Daugbjerg N, Moestrup Ø (2002a) Phylogeny of the Bacillariaceae with emphasis on the genus Pseudo-nitzschia (Bacillariophyceae) based on partial LSU rDNA. Eur J Phycol 37:115–134

Lundholm N, Hasle GR, Fryxell GA, Hargraves P (2002b) Morphology, phylogeny and taxonomy of species within the *Pseudo-nitzschia americana*-complex (Bacillariophyceae), with description of two new species. Phycologia 41:480–497

Mann DG (1986) *Nitzschia* subgenus *Nitzschia* (Notes for a monograph of the Bacillariaceae, 2). In: Ricard M (ed) Proceedings of the eighth international diatom symposium. Koeltz Scientific Books, Köenigstein. pp 215–226

Medlin LK, Sims PA (1993) The transfer of *Pseudoeunotia doliolus* to *Fragilariopsis*. Nov Hed Beih 106:323–334

Pan BJ, Vernet M, Reynolds RA, Mitchell BG (2019) The optical and biological properties of glacial meltwater in an Antarctic fjord. PLoS ONE 14:e0211107

Peragallo M (1921) Deuxième Expédition Antarctique Française 1908–1910 Commandée par le Dr. Jean Charcot. Botanique. Diatomées d'eau douce et diatomées d'eau salée. Masson, Paris, pp 1–98

Prygiel J, Coste M (2000) Guide méthodologique pour la mise en ouvre de l'Indice Biologique Diatomées. Agences de l'Eau, Ministère de l'Aménagement du Territoire et de l'Environnement, Direction de l'Eau & CEMAGREF, Bordeaux

Rigual-Hernandez AS, Pilskaln CH, Cortina A, Abrantes F, Armand LK (2019) Diatom species fluxes in the seasonally ice-covered Antarctic Zone: new data from offshore Prydz Bay and comparison with other regions from the eastern Antarctic and western Pacific sectors of the Southern Ocean. Deep-Sea Res II 161:92–104

Round FE, Crawford RM, Mann DG (1990) The diatoms, biology and morphology of the genera. Cambridge University Press, Cambridge

Schmidt A (1913) *Atlas der Diatomaceenkunde.* Pl. 299, figs 9–14. Reisland OR, Leipzig

Scott FJ, Thomas DP (2005) Diatoms. In: Scott FJ, Marchant HJ (eds) Antarctic marine protists. Australian Biological Resources Study, Canberra, pp 13–201

Smith KL Jr (2011) Free-drifting icebergs in the Southern Ocean: an overview. Deep-Sea Res II 58:1277–1284

Van Heurck H (1909) Diatomées. In: Expédition antarctique belge. Résultates du voyage du S.Y. Belgica 1897–1899. Buschmann, Antwerp

Von Quillfeldt CH (2004) The diatom *Fragilariopsis cylindrus* and its potential as an indicator species for cold water rather than for sea ice. Vie Milieu 54:137–143