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RESEARCH ARTICLE

Diversity and habitat preferences of benthic diatoms from South Bay (Livingston Island, Antarctica)

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Background and aims – Despite a long research history, knowledge of Antarctic marine benthic diatoms is fragmentary. This study reports on marine benthic diatoms from South Bay, Livingston Island, focusing on diatoms living on hard substrata, and species distribution across different coastal habitats.
Material and methods – Samples were collected from tidal pools (19), intertidal cobbles (9), artificial substrata installed at various depths (10), coastal rocks (2), and bottom sediments at depths > 20 m (2). Species identifications and community analyses were done using LM with additional information obtained using SEM. nMDS based on diatom abundance data was applied to display differences between the samples by habitat/substratum type and sampling month. The significance of the habitat/substratum type and sampling month on diatom communities was checked with PERMANOVA. Similarity/dissimilarity within and between sample groups and their contributing species were explored with SIMPER.
Key results – In total, 133 diatom taxa were recorded, of which 110 are benthic. A large number of taxa could not be certainly identified. Taxonomic remarks and ecology and distribution data for some rarely reported species with convoluted taxonomic and nomenclatural histories are given. One new combination is proposed. Diatom communities were influenced by the habitat/substratum type, but not by seasonality. Significant differences existed between communities in tidal pools and those on cobbles, artificial substrata, and sediments, and between those on sediments and artificial substrata. *Navicula* aff. *perminuta* dominated on cobbles and often on artificial substrata. Species forming mucilage tubes, tree-like colonies, and chains of cells embedded in mucilage were restricted to tidal pools.
Conclusion – Benthic diatom communities from South Bay are highly diverse and species show distinct distributions in the coastal habitats, but the scarce studies and often confusing nomenclature history of the taxa make their identification challenging, and potentially common species for the region remain unknown.

Keywords – Antarctica; diatoms; epilithon; habitats; marine benthos; species diversity; taxonomy.

INTRODUCTION

Diatoms (Bacillariophyceae) are likely one of the most studied groups of algae in Antarctica since the time they were first reported by Ehrenberg (1844) more than 150 years ago. Nevertheless, recent studies on the Antarctic non-marine diatom flora clearly showed that past reports were not entirely reliable, since many taxa were found to be previously "force-fitted" (Tyler 1996) to species from other regions, hence obscuring their identity and diversity (Zidarova et al. 2016 and references therein). Recently, with the application of a more "fine-grained taxonomy" (Vanormelingen et al. 2008), a large number of new diatom taxa were recognized and described, and the endemic origin of many Antarctic species, previously considered being cosmopolitan, was confirmed (Zidarova et al. 2016 and references therein). In contrast to the terrestrial and freshwater diatom flora, the Antarctic marine benthos (excluding sea ice diatoms) has received

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far less attention. The major historical records for marine benthic diatoms in Antarctica date from the beginning of the 20th century, with the works of Van Heurck (1909), Peragallo (1921), Heiden & Kolbe (1928), through Mann (1937) and to Manguin (1957, 1960), Frenguelli & Orlando (1958), and Frenguelli (1960). Later, a number of different studies were done, including on the coastal marine sedimentary diatom assemblages (e.g. Tanimura 1992; Taylor et al. 1997; among others), the Holocene diatom flora from sediment cores (Cremer et al. 2003), and on surface sediments of saline lakes in East Antarctica (Roberts & McMinn 1999; Hodgson et al. 2001). The interest in marine benthic diatoms in Antarctica (sea ice diatoms excluded) steadily declined towards and during the 21st century. Klöser (1998) and Ligowski (2002) studied the marine benthic diatoms from different habitats (sediments, rocks, macrophytes, etc.) in near shore waters of King George Island, while Blazewicz-Paszkowycz & Ligowski (2002) reported on diatom species found in the guts of crustaceans from the same area. Several marine benthic diatom species were also reported from Kroner Lake on Deception Island (Izaguirre et al. 2006). In recent years, more attention was given to the marine epiphyton from both the Maritime and Continental Antarctic Region (Al-Handal & Wulff 2008b; Majewska et al. 2013, 2015, 2016). A number of papers dealt with taxonomy and morphology of particular species, with several new benthic taxa being described (e.g. Medlin 1990; Fernandes & de Souza-Mosimann 2001; Fernandes et al. 2007; Al-Handal et al. 2008, 2010, 2018, 2019; Almandoz et al. 2014; Ligowski et al. 2014) and the taxonomic identity of some species being revised (e.g. Williams 1988; Medlin 1990, 2019; Fernandes & Sar 2009; Romero 2011; Riaux-Gobin et al. 2019). Other papers dealt with a restudy of the morphology of selected species (Ferrario & Sar 1990; Fernandes & Procopiak 2003; Fernandes et al. 2014a). Despite all efforts in the last century, the identity of many marine benthic species in Antarctica remained far from known. In most recent floristic works, many of the encountered species remain unidentified or only identified with a high degree of uncertainty, indicating the need of further analyses and investigation (Majewska et al. 2013). More specifically, the diversity of the marine epilithon is poorly studied, compared to other ecological groups, with only a handful of recent papers on this group, for instance by Al-Handal & Wulff (2008a), who reported on diatoms from ceramic tiles and a rock in Potter Cove, King George Island (South Shetland Islands). Two other studies, although initially not aiming at epilithic diatom diversity, discussed the diatom species encountered during experiments on ceramic tiles (Daglio et al. 2018) and on plexiglass tiles and intertidal cobbles (Zidarova et al. 2020). Finally, epilithic diatoms from the intertidal zone of a glacier-influenced cove on King George Island were part of the study of Bae et al. (2021). Our knowledge of marine benthic diatom species ecology also remained highly fragmented. Al-Handal & Wulff (2008a) and Zidarova et al. (2020) compared diatoms on artificial substrata with those on natural substrata, but the specific habitat preferences of epilithic diatoms were only rarely addressed (e.g. in part in Klöser 1998).

The present paper reports on the marine benthic diatom flora from coastal waters near Livingston Island (South Shetland Islands, Maritime Antarctica), focusing mostly on the epilithon (with the exception of two samples from sediments) and species distribution across the sampled habitats and substrata. Nomenclatural remarks and notes on the ecology and geographical range of some rarely reported Antarctic species or species with a convoluted taxonomic history are also added. One new combination is proposed.

MATERIAL AND METHODS

Study area

Livingston Island is the second largest island of the South Shetland Islands, located ca 900 km south of the southernmost tip of South America and ca 130 km from the Antarctic Peninsula, and it has a typically maritime Antarctic climate with summer temperatures above freezing and high precipitation (Chipev & Veltchev 1996; Bañon et al. 2001). The South Bay is a large inlet on the southern side of the island, with a width of ca 12 km and entirely open to the south-southwest (fig. 1). The region experiences a mixed,

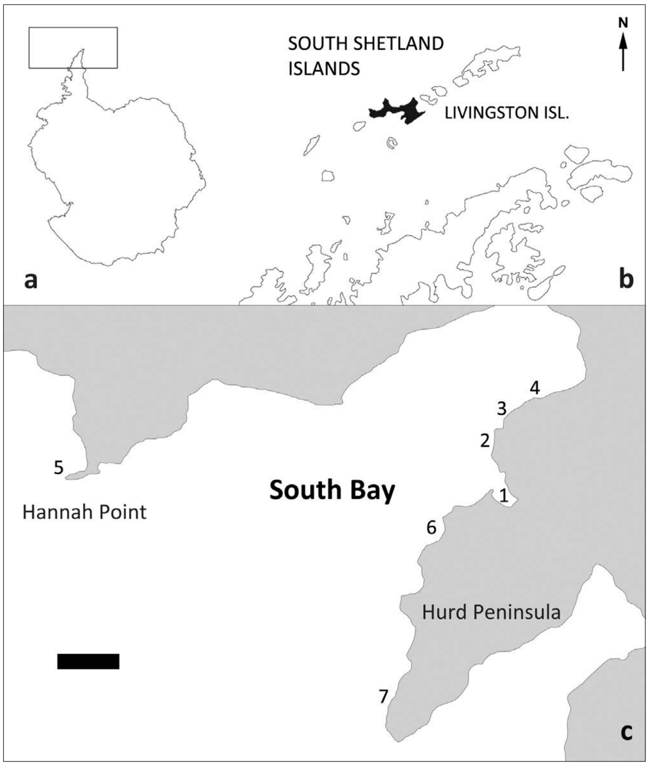

Figure 1 – Figure showing the relative positions of the South Shetland Islands to Antarctica (a), of Livingston Island to the archipelago (b), and a simplified map of South Bay (c) with the main locations of the sampling sites (1–7). 1 – Johnsons Dock, 2 – Mongolian (Reserve) Port, 3 – Playa Búlgara, 4 – eastern coast of South Bay, 5 – Hannah Point, 6 – Caleta Argentina, 7 – Sally Rocks. Scale bar = 2 km. Maps created with Adobe Illustrator® and Adobe Photoshop®, on the base of: (a) NASA, Public domain, via Wikimedia Commons (https://commons.wikimedia.org/wiki/File:Antarctica_satellite_globe.jpg), modified; (b), (c): © OpenStreetMap contributors (www.openstreetmap.org), via NOAA (https://charts.noaa.gov/InteractiveCatalog/nrnc.shtml), modified.

Table 1 – List of samples, sampled substrata and habitats with the measured environmental parameters (where available). For all samples from Johnsons Dock and Mongolian (Reserve) Port mean values are presented, based on repetitive measurements during the sampling seasons (min. n = 8, at depths 1, 3, and 6.5 m). For tidal pools and all localities, where only single measurements were possible, data from the exact sampling date are given.

Samples from artificial substrata

sample	date	location	substrate type	substrate exposure (days)	substrate depth (m)	Secchi depth (m)	pH	salinity (PSU)	conductivity (mS/cm)	O_2 (%)	O_2 (mg/L)
JD1	17 Dec. 2018	Johnsons Dock	plexiglass	22	1	1.4	8.2	31.4	49.6	102.9	12.7
J5B	17 Dec. 2018	Johnsons Dock	nylon rope	22	0.8						
JD3	24 Feb. 2020	Johnsons Dock	plexiglass	34	3	0.5	–	20.4	34.0	86.8	11.3
DNA3	17 Feb. 2020	Johnsons Dock	nylon rope	27	1.5						
DNA4	24 Feb. 2020	Johnsons Dock	polycarbonate	34	3						
JD6.5	24 Feb. 2020	Johnsons Dock	plexiglass	34	6.5	0.5	–	21.0	35.1	88.5	11.9
MP1	9 Jan. 2019	Mongolian (Reserve) Port	plexiglass	31	1	2.6	8.1	33.6	53.3	101.1	12.1
MP3	24 Feb. 2020	Mongolian (Reserve) Port	plexiglass	34	3	2.1	–	20.8	34.6	85.6	11.3
MP6.5	24 Feb. 2020	Mongolian (Reserve) Port	plexiglass	34	6.5	2.1	–	20.7	34.5	90.0	12.1
MB	20 Dec. 2018	Mongolian (Reserve) Port	nylon rope	12	0.8	2.6	8.1	33.6	53.3	101.1	12.0

Samples from natural substrata

sample	date	locality	habitat	pH	salinity (PSU)	conductivity (mS/cm)	O_2 (%)	O_2 (mg/L)	T (°C)
2D	22 Nov. 2018	Playa Búlgara	cobbles						
S3	27 Nov. 2018	coast of the South Bay	tidal pool	9.0	34.4	53.9	–	–	–
4D	27 Nov. 2018	coast of the South Bay	cobbles	8.1	33.9	54.0	103.6	12.9	–
S5	2 Dec. 2018	Johnsons Dock	cobbles	8.2	31.4	49.6	102.9	12.7	–
6D	8 Dec. 2018	coast of the South Bay	cobbles	8.1	33.6	53.4	101.5	12.4	–
S8	10 Dec. 2018	Playa Búlgara	cobbles	8.1	29.5	47.0	99.2	10.8	–
S10	13 Dec. 2018	Johnsons Dock	sediments	8.2	31.4	49.6	102.9	12.7	–
S11	16 Dec. 2018	Hannah Point	tidal pool	8.1	32.3	51.2	104.9	12.6	–
S13	16 Dec. 2018	Hannah Point	tidal pool	9.6	33.7	52.2	–	–	–
S14	16 Dec. 2018	Hannah Point	tidal pool	8.5	33.1	46.8	–	–	6.2
S15	20 Dec. 2018	Johnsons Dock	cobbles	8.2	31.4	49.6	102.9	12.7	–
MO	21 Dec. 2018	Mongolian (Reserve) Port	tidal pool	8.4	33.1	52.2	–	–	5.5

Table 1 (continued) – List of samples, sampled substrata and habitats with the measured environmental parameters (where available). For all samples from Johnsons Dock and Mongolian (Reserve) Port mean values are presented, based on repetitive measurements during the sampling seasons (min. n = 8, at depths 1, 3, and 6.5 m). For tidal pools and all localities, where only single measurements were possible, data from the exact sampling date are given.

Samples from natural substrata									
sample	**date**	**locality**	**habitat**	**pH**	**salinity (PSU)**	**conductivity (mS/cm)**	**O_2 (%)**	**O_2 (mg/L)**	**T (°C)**
EBS1	23 Jan. 2020	Johnsons Dock	sediments						–
LT1	25 Jan. 2020	coast of the South Bay	tidal pool		18.3	30.4	–	–	7.0
LT2	25 Jan. 2020	coast of the South Bay	tidal pool		20.3	33.7	105.0	13.5	5.6
LT3	28 Jan. 2020	coast of the South Bay	tidal pool		20.4	33.3	112.0	12.6	8.0
LT4	2 Feb. 2020	Caleta Argentina	tidal pool		18.0	30.0	147.0	18.3	4.6
LT5	2 Feb. 2020	Caleta Argentina	tidal pool		16.3	27.5	195.0	20.4	4.8
LT6	2 Feb. 2020	Caleta Argentina	tidal pool		21.1	35.2	88.0	11.5	2.8
LT7	3 Feb. 2020	Mongolian (Reserve) Port	tidal pool		20.7	33.2	92.0	11.4	3.4
LT8	3 Feb. 2020	Mongolian (Reserve) Port	tidal pool		17.7	29.9	123.0	15.3	5.4
LT9	4 Feb. 2020	Hannah Point	tidal pool		17.6	29.5	111.0	11.6	10.1
LT10	4 Feb. 2020	Hannah Point	tidal pool		6.5	11.47	126.0	11.6	18.8
LT11	9 Feb. 2020	Mongolian (Reserve) Port	tidal pool		–	–	–	–	–
NE1	8 Feb. 2020	Playa Búlgara	cobbles		12.0	20.7	73.0	8.0	3.0
NE2	8 Feb. 2020	Johnsons Dock	cobbles		20.4	33.9	67.0	8.6	2.9
NE3	9 Feb. 2020	Mongolian (Reserve) Port	cobbles	8.1	33.6	53.3	101.1	12.1	
NE4	9 Feb. 2020	Mongolian (Reserve) Port	large rock						
DNA1	17 Feb. 2020	Sally Rocks	large rock		–	–	–	–	–
DNA2	17 Feb. 2020	Caleta Argentina	tidal pool		–	–	–	–	–
DNA5	24 Feb. 2020	Mongolian (Reserve) Port	tidal pool		–	–	–	–	–
DNA6	25 Feb. 2020	coast of the South Bay	tidal pool		–	–	–	–	–

mainly semi-diurnal tidal regime, with daily inequality in the two tidal cycles, which may influence both the salinity and water temperature (Vidal et al. 2011). Tides are associated with tidal currents, with maximum tidal amplitude (spring tide) near Livingston Island of about 2 m (López et al. 1994).

Sampling

Samples (n = 42) were collected from late November 2018 till early January 2019 and in January–February 2020 in several coastal localities of South Bay: Playa Búlgara, the eastern coast of South Bay, Mongolian (Reserve) Port area, Johnsons Dock, Caleta Argentina, Sally Rocks area, and Hannah Point (fig. 1). Of these, Johnsons Dock is a small glacier-influenced cove with typically "milky" water due to high glacier meltwater input (Agustí & Duarte 2000), while Caleta Argentina, and especially Hannah point, are influenced by ornithogenic nutrient input from the bird colonies, present on the shores (Metcheva et al. 2004; Barbosa et al. 2012). Samples, listed in table 1, were taken from several different habitats and types of substrata:

1. Tidal pools – These are smaller or larger pools on or between large rocks in the intertidal zone, formed during low tide on the coastal rocks, but flooded by sea water during high tide. Such habitats are common for the area and were found at Caleta Argentina, Playa Búlgara, and almost along the entire eastern coast near the Bulgarian base, as well as at the Mongolian (Reserve) Port and Hannah Point. Diatom samples (n = 19) were taken from either the sides or the rocky/stony bottom of the pools during low tide. One sample included the thick brownish layer on the coarse sandy bottom of a large pool behind coastal rocks (sample LT5).

2. Cobbles/small boulders in the intertidal zone – These samples (n = 9) contain the biofilm collected from several stones at each site. Sampling was done during spring low tide, assuring that the sampled cobbles are always submerged under water, even at the lowest tide. Biofilm from the intertidal cobbles was taken from several localities, including Johnsons Dock, the Mongolian (Reserve) Port, and Playa Búlgara in 2020, all having stony shores. For the purposes of the study, 6 additional samples obtained from cobbles in 2018–2019, previously used in the study by Zidarova et al. (2020), are also included in the dataset.

3. Large coastal rocks – Two samples were collected from two localities (Sally Rocks and the Mongolian (Reserve) Port) in 2020, including the thick brownish biofilm present on large rocks under the splashes of the waves during low tide.

4. Bottom sediment samples – Sediment sampling was not intended, but 2 samples taken from inside Johnsons Dock in both 2018 and 2020, at depths of > 20 m, are included in the study as well.

5. Artificial substrata – A total of 10 samples were obtained from two localities (Johnsons Dock and the Mongolian (Reserve) Port) in 2018–2019 and 2020. The artificial substrata used in this study were roughly hand-sanded plexiglass tiles (6 samples, total sampled area per sample 75 cm^2); one sample was taken from the polycarbonate plates, holding the substrata, and 3 other samples were obtained from the three stranded nylon anchor ropes, holding the plates. Substrata were submerged into the water column at three different depths (1 m, 3 m, and 6.5 m). The diatom biofilm from the substrata was collected after they had been exposed for at least 3 weeks, except for the samples from the nylon ropes, which were taken randomly – on day 12, 22, and 27 of their exposure (table 1). For the purposes of this study, 2 samples that were used in the analyses of Zidarova et al. (2020) are also included here (i.e. samples from plexiglass tiles collected in 2018–2019 at a depth of 1 m). More information regarding the hard artificial substrata arrangement and sampling can be found in Zidarova et al. (2020).

All samples from hard substrata were collected by removing the diatom biofilm using a toothbrush, while those from the bottom of Johnsons Dock were taken by a grab. The sample from the coarse-sandy bottom of one large tidal pool was taken by a pipette. All samples were fixed in 3% formaldehyde in situ.

Several main parameters of the sea water were measured (table 1) using a handheld WTW3410 multimeter; however, pH was not measured in 2020, while measurements of water temperature of tidal pools were not intended in 2018. For the localities where the artificial substrata were placed (Johnsons Dock and Mongolian (Reserve) Port), mean values of the parameters are given (table 1), based on repetitive measurements during the period of their exposure (min. n = 8 for each locality and each depth in 2020), while for 2018, mean values are taken from Zidarova et al. (2020). For samples from other localities, where we were unfortunately unable to obtain repetitive data, reported values are based on single measurements.

Sample preparation, microscopic analyses, and identification

For microscopic analyses, samples were treated following the method in Hasle & Fryxell (1970). A small amount of the cleaned material was air-dried on cover slips and mounted in Naphrax®. Light microscopy (LM) observations for taxa identifications were performed using an Olympus BX51 microscope at 1000 × magnification, equipped with Differential Interference Contrast (Nomarski) optics and Olympus digital imaging system. For taxonomic purposes, the following works were used: Hasle et al. (1994), Witkowski et al. (2000, 2010), Scott & Thomas (2005), Al-Handal & Wulff (2008a, 2008b), Al-Handal et al. (2008, 2010, 2018), Levkov (2009), Cefarelli et al. (2010), Romero (2011), Almandoz et al. (2014), Fernandes et al. (2014a), Ligowski et al. (2014), and Zidarova et al. (2016). Older Antarctic literature, such as Van Heurck (1909), Peragallo (1921), Mann (1937), Manguin (1957), Frenguelli & Orlando (1958), Frenguelli (1960), as well as Simonsen (1992), who studied the types of Heiden in Heiden & Kolbe (1928), was likewise consulted. After the identity of the species was clarified, in order to assess the diatom community structure in each sample, at least 400 valves were identified and enumerated on each slide. These latter analyses were performed using an Amplival Carl Zeiss Jena microscope at 1000 × magnification. For SEM, a small part of the sample was filtered through a Teknokroma® nylon filter with a pore diameter of 0.2 µm. After air-drying, small pieces of the filters were affixed to aluminum stubs and sputter-coated with gold. Observations were done at 8 kV with a Phillips 515 SEM.

Data analyses

Non-parametric multidimensional scaling (nMDS) was used to display the differences in diatom communities, originating from the different habitats/substratum types and different sampling months. The entire set of samples and all species with their abundances square-root transformed were included. Two-way PERMANOVA with the habitat/substratum type (rock, cobble, tidal pool, sediment, and artificial substrata) and the month of sample collection added as two fixed factors was performed, in order to explore whether significant differences are present between the different sample groups in relation to any of these factors and their interaction. Finally, similarity percentage analysis (SIMPER) was applied to identify the taxa contributing the most to the observed similarity within each sample group (= habitat/substratum type) and dissimilarity between the groups. All analyses were performed using Primer v.7 with PERMANOVA+ (Anderson et al. 2015; Clarke & Gorley 2015).

RESULTS

Diatom species composition, diversity, and abundance

A complete list of all recorded species with their presence and abundances in the studied habitat/substratum types is presented in table 2. In total, 133 taxa (including species, varieties, and forms) have been recorded. Of these, 20 taxa are known to be planktonic (marked with * in table 2). These were mostly found in the bottom sediment samples, and had rare occurrences: 15 of the planktonic taxa were recorded in one sample, outside the counts or with abundances of < 1%. Other three taxa are non-marine (*Luticola muticopsis*, *Nitzschia homburgiensis*, and *N. vandeputteana*). The marine benthic species constituted the majority of the recorded taxa (110 species; almost all depicted on figs 3–10). Of these, 52 taxa could only be indentified up to genus level, whereas the generic affinity of five others could not be resolved. Most of the genera (28 out of 34, excluding the planktonic ones and the non-marine *Luticola*) were represented by 1–3 species, while the highest diversity was found within four genera: *Cocconeis* (21 taxa), *Navicula* (16), *Nitzschia* (10, excluding *N. homburgiensis* and *N. vandeputteana*), and *Amphora* sensu lato (9). Most of the species in these genera, and especially all species in the genus *Cocconeis*, were found either in very low numbers, or in a small number of samples, or both (table 2). Many of the benthic species had low abundances in the samples. Approximately 23% of the taxa (25 out of 110 benthic species) were found with abundances of less than 1%. Another 30% of the taxa (33 taxa) were recorded only outside the counts. A few taxa were regularly observed, present in more than half of the samples, and in high abundances, such as *Achnanthes bongrainii*, *Brandinia charcotii* comb. nov., *Fragilaria* aff. *striatula*, and *Pseudogomphonema kamtschaticum*. Two taxa, often in high numbers, were present in all 42 samples: *Navicula* aff. *perminuta* (fig. 9C, P) and *N. glaciei* (fig. 9H). With regard to the different groups of samples by habitat/substratum type, the highest diversity was found in the two bottom sediment samples (92 taxa, including planktonic ones). Tidal pools were the second most diverse habitat, with a total of 72 species present in the samples. Intertidal cobbles and artificial substrata were less diverse, with a total of 47 and 59 species, respectively. Rocks had the lowest diversity, with only 18 species found in the samples, however, only two

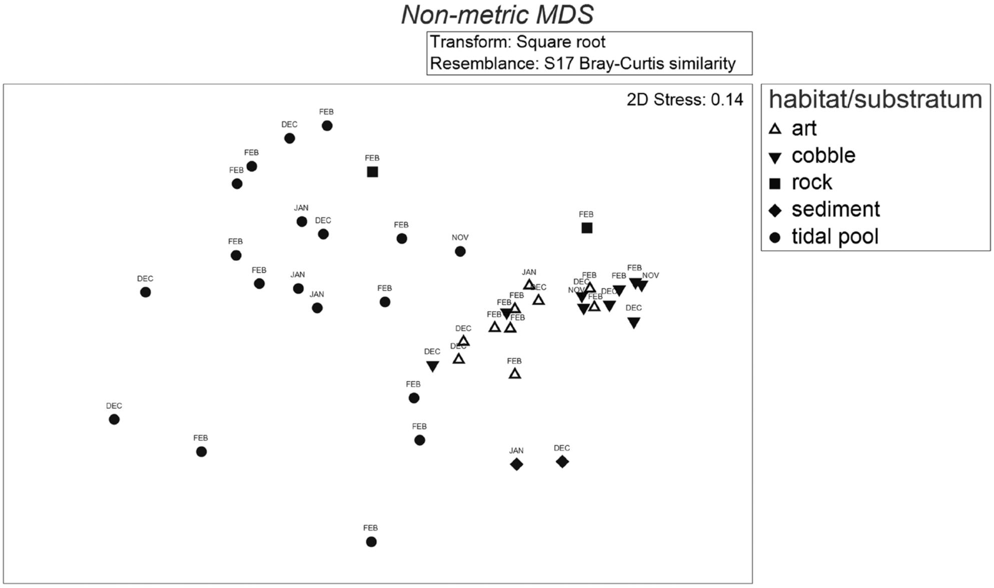

Figure 2 – nMDS graph based on the species abundances in samples. art = artificial substratum; letters indicate sampling month: NOV = November, DEC = December, JAN = January, FEB = February.

Table 2 – List of all taxa with their occurrences and abundances in the different sample groups. TP = tidal pool, CBL = cobbles, LR = large rock, BS = bottom sediments, ASB = artificial substrata; n = number of samples; x = species is recorded outside the counts; * indicates planktonic taxa.

Taxon	**TP (n = 19)**		**CBL (n = 9)**		**LR (n = 2)**		**BS (n = 2)**		**ASB (n = 10)**		**occurrence (total n of samples)**
	occurrence (n of samples)	**% abundance**	**occurrence (n of samples)**	**% abundance**	**occurrence (n of samples)**	**% abundance**	**occurrence (n of samples)**	**% abundance**	**occurrence (n of samples)**	**% abundance**	
Achnanthes bongrainii Perag.	9	0.5–3.4	9	0.5–45.0	1	x	2	0.25	7	0.25–0.75	28
Achnanthes brevipes C.Agardh s.l.	1	0.75									1
Achnanthes vicentii Manguin	2	0.5	6	0.5–0.75			2	0.25	4	0.25	14
Achnanthes sp.1	2	0.25	4	0.25–1.25			1	0.25	1	x	8
Achnanthes sp.2	1	0.25	5	0.25–0.75	1	47.25			3	0.5	10
Achnanthes sp.3	1	x									1
**Actinocyclus actinochilus* (Ehrenb.) Simonsen							1	0.25			1
Amphora cf. *biarcuata* Heiden							1	x			1
Amphora gourdonii Perag.	1	x					2	0.25–0.75			3
Amphora cf. *lunula* var. *parvula* Heiden							1	0.25			1
Amphora sp.1							1	x			1
Amphora sp.2			1	x			1	1.25	1	x	3
Amphora sp.3							1	x			1
Amphora sp.4							1	x	1	x	2
Amphora sp.5	7	0.5–17.5									7
Amphora sp.6	1	44.0									1
**Asteromphalus hookeri* Ehrenb.							1	0.25			1
Australoneis frenguelliae (Riaux-Gob. & J.M.Guerrero) J.M.Guerrero & Riaux-Gob.			2	x			2	0.25–0.5	1	x	5
Berkeleya cf. *rutilans* (Trentep. ex Roth) Grunow	3	0.5–62.0									3
Brandinia charcotii (Perag.) comb. nov.	15	0.4–18.5	6	0.75–9.25	1	34.0	2	0.25–0.5	6	0.25–11.75	30
**Chaetoceros* sp. fragments							1	x			1
Cocconeis antiqua Temp. & Brun	1	x	1	x			2	0.25			4
Cocconeis californica Grunow	1	0.25									1
Cocconeis californica var. *antarctica* Freng. & H.A.Orlando, nom. inval.	1	x							1	x	2

Table 2 (continued) – List of all taxa with their occurrences and abundances in the different sample groups. TP = tidal pool, CBL = cobbles, LR = large rock, BS = bottom sediments, ASB = artificial substrata; n = number of samples; x = species is recorded outside the counts; * indicates planktonic taxa.

	TP (n = 19)		**CBL (n = 9)**		**LR (n = 2)**		**BS (n = 2)**		**ASB (n = 10)**		
Taxon	**occurrence (n of samples)**	**% abundance**	**occurrence (n of samples)**	**% abundance**	**occurrence (n of samples)**	**% abundance**	**occurrence (n of samples)**	**% abundance**	**occurrence (n of samples)**	**% abundance**	**occurrence (total n of samples)**
Cocconeis californica var. *kerguelensis* Heiden	1	x	1	x			1	0.25	1	x	4
Cocconeis costata W.Greg. s.l.	6	0.25	4	0.25			2	1.0	3	x	15
Cocconeis dallmannii Al-Handal et al.	4	0.25	1	x			2	0.5–1.25	4	x	11
Cocconeis fasciolata (Ehrenb.) N.E.Br.	10	0.5	5	0.5	1	x	2	1.0–1.5	6	0.5	24
Cocconeis gausii Heiden							1	x	1	x	2
Cocconeis imperatrix A.W.F.Schmidt			4	x							4
Cocconeis melchioroides Al-Handal et al.	7	0.25	5	0.25			2	0.75–2.5	7	0.25	21
Cocconeis matsii (Al-Handal et al.) Riaux-Gob. et al.	1	x	1	0.25			2	1.25	3	x	7
Cocconeis pottercovei Al-Handal et al.	2	x					2	0.75	2	x	6
Cocconeis cf. *schmidtii* Heiden	1	x									1
Cocconeis sp.1	1	0.5					1	x			2
Cocconeis sp.2							1	x			1
Cocconeis sp.3									1	x	1
Cocconeis sp.4							1	x			1
Cocconeis sp.5			1	x							1
Cocconeis sp.6							1	x			1
Cocconeis sp.7							1	x			1
Cocconeis sp.8							1	0.25	1	x	2
**Corethron pennatum* (Grunow) Ostenf.							1	0.25			1
**Coscinodiscus asteromphalus* Ehrenb.							1	0.25			1
**Coscinodiscus subtilis* Ehrenb.							1	x			1
Craspedostauros laevissimus (W.West & G.S.West) K.Sabbe	11	0.25–32.75									11
Craspedostauros sp.	10	0.5–43.5									10
Diploneis sp.							1	x			1

Table 2 (continued) – List of all taxa with their occurrences and abundances in the different sample groups. TP = tidal pool, CBL = cobbles, LR = large rock, BS = bottom sediments, ASB = artificial substrata; n = number of samples; x = species is recorded outside the counts; * indicates planktonic taxa.

Taxon	TP (n = 19)		CBL (n = 9)		LR (n = 2)		BS (n = 2)		ASB (n = 10)		occurrence (total n of samples)
	occurrence (n of samples)	% abundance	occurrence (n of samples)	% abundance	occurrence (n of samples)	% abundance	occurrence (n of samples)	% abundance	occurrence (n of samples)	% abundance	
**Entomoneis* cf. *paludosa* (W.Sm.) Reimer							1	0.25			1
Fallacia marnieri (Manguin) Witkowski et al.			1	x			2	0.5–1.0	1	x	4
Fragilaria aff. *striatula* Lyngb.	14	0.5–92.0	3	0.25–8.5			1	0.75	7	0.25–6.5	25
Fragilaria islandica var. *adeliae* Manguin			1	x					1	x	2
Fragilaria sp.1									1	x	1
Fragilaria sp.2	3	0.25					2	0.5–1.5	2	x	7
**Fragilariopisis curta* (Van Heurck) Hust.	1	x					2	0.5–1.0	1	x	4
**Fragilariopsis* cf. *nana* (Steem.Niels.) Paasche							2	0.25–0.75	1	x	3
**Fragilariopsis kerguelensis* (O'Meara) Hust.							2	0.5			2
**Fragilariopsis rhombica* (O'Meara) Hust.							1	x			1
**Fragilariopsis separanda* Hust.	1	x					1	1.25			2
**Fragilariopsis* cf. *vanheurckii* (Perag.) Hust.							1	x			1
Gomphonemopsis ligowskii Al-Handal & E.W.Thomas	5	0.25–0.75	1	x			2	1.25–1.75	3	0.25–0.5	11
**Grammatophora* sp.	1	x					2	x			3
Gyrosigma cf. *fasciola* (Ehrenb.) J.W.Griff. & Henfr.							1	x			1
*cf. *Hemidiscus* sp.							2	1.5–3.75			2
Licmophora antarctica Perag.	8	0.25	2	x	1	x	2	0.25–0.75	6	0.25	19
Licmophora belgicae Perag.	1	0.25	2	0.5			1	0.25	4	0.25–3.25	8
Licmophora gracilis (Ehrenb.) Grunow	9	0.5	6	1.25	2	12.5	2	0.25–1.0	7	0.25–2.75	26
Licmophora luxuriosa Heiden									1	x	1
Luticola muticopsis Van Heurck	1	x									1
Melosira brandinii L.F.Fernandes & R.M.Souza-Mosimann	13	0.25–37.25			1	x			3	x	17
Melosira sp.1	12	0.25–28.5			1	0.25			2	x	15
Melosira sp.2									1	x	1

Table 2 (continued) – List of all taxa with their occurrences and abundances in the different sample groups. TP = tidal pool, CBL = cobbles, LR = large rock, BS = bottom sediments, ASB = artificial substrata; n = number of samples; x = species is recorded outside the counts; * indicates planktonic taxa.

Taxon	TP (n = 19)		CBL (n = 9)		LR (n = 2)		BS (n = 2)		ASB (n = 10)		occurrence (total n of samples)
	occurrence (n of samples)	% abundance	occurrence (n of samples)	% abundance	occurrence (n of samples)	% abundance	occurrence (n of samples)	% abundance	occurrence (n of samples)	% abundance	
**Minisdiscus* sp.			2	x			2	0.5–5.0	4	0.5	8
Navicula criophiliforma Witkowski et al.	7	0.75	2	x			1	x	4	x	14
Navicula directa (W.Sm.) Ralfs	8	0.25–1	2	x			2	0.25–1.25	4	x	16
Navicula cf. *hippodontaformis* Witkowski et al.	1	x					1	x			2
Navicula jejunoides Van Heurck							2	1.5	1	x	3
Navicula glaciei Van Heurck	19	0.5–29.3	9	0.25–27	2	0.5–8.25	2	6.75–8.0	10	1.0–50.0	42
Navicula aff. *perminuta* Grunow	19	0.25–51.0	9	62.5–100.0	2	6.25–51	2	36.25–45.25	10	17.5–98.25	42
Navicula sp.1			3	0.5			2	3.25–8.25	2	0.25–0.5	7
Navicula sp.2	14	0.75–80.5			1	12.5					15
Navicula sp.3	12	0.25–39.0									12
Navicula sp.4	1	0.5	4	0.5–0.75					6	0.125–0.5	11
Navicula sp.5	2	6.75–38.75									2
Navicula sp.6	1	x									1
Navicula sp.7			1	x			1	x			2
Navicula sp.8	2	0.25									2
Navicula sp.9							2	1.25			2
Navicula sp.10							1	0.5			1
Nitzschia homburgiensis Lange-Bert.	1	x					1	0.5			2
Nitzschia vandeputteana Hamsher et al.	4	0.25–4.5									4
Nitzschia cf. *chalonii* Van Heurck							1	0.25			1
Nitzschia sp.1	5	0.25	3	0.25–1.25			2	0.25	6	0.25	16
Nitzschia sp.2							1	x	1	x	2
Nitzschia sp.3	14	0.25–29.5	2	5.0			2	2.0	4	0.75–1.5	22
Nitzschia sp.4	9	0.25–1.0	3	x	1	0.75					13
Nitzschia sp.5	1	x					1	x			2
Nitzschia sp.6					1	0.75	1	0.25			2
Nitzschia sp.7							2	0.25–0.5			2
Nitzschia sp.8	1	33.5									1
Nitzschia sp.9									1	x	1

Table 2 (continued) – List of all taxa with their occurrences and abundances in the different sample groups. TP = tidal pool, CBL = cobbles, LR = large rock, BS = bottom sediments, ASB = artificial substrata; n = number of samples; x = species is recorded outside the counts; * indicates planktonic taxa.

	TP (n = 19)		**CBL (n = 9)**		**LR (n = 2)**		**BS (n = 2)**		**ASB (n = 10)**		
Taxon	**occurrence (n of samples)**	**% abundance**	**occurrence (n of samples)**	**% abundance**	**occurrence (n of samples)**	**% abundance**	**occurrence (n of samples)**	**% abundance**	**occurrence (n of samples)**	**% abundance**	**occurrence (total n of samples)**
Parlibellus rhombicus W.Greg. sensu Van Heurck (1909)	8	0.25–9.0			1	0.25					9
Parlibellus variabilis (Heiden) Simonsen							1	0.5			1
Petroneis aff. *plagiostoma* (Grunow) D.G.Mann	1	x	2	x			1	x	1	x	5
Petroneis sp.1 [cf. *Navicula cluthensis* var. *lanceolata* (Heiden) Simonsen]	2	x	1	x			2	0.25–0.5			5
Petroneis sp.2							1	0.25			1
Pinnularia parallelimarginata Simonsen							1	0.5–0.75			1
Pinnularia quadratarea (A.W.F.Schmidt) P.T.Cleve							2	1.0	1	x	3
Pinnularia sp.							1	x			1
Planothidium sp.1	4	0.25–6.4	2	0.25			2	0.25–0.75	2	x	10
Planothidium sp.2			1	x			1	x	2	0.25	4
Planothidium sp.3	3	0.25–0.5									3
Pleurosigma sp.			2	x			2	3.25–7.25			4
Pseudogomphonema kamtschaticum (Grunow) Medlin	10	0.25–1.75	9	0.25–4.0	2	0.25	2	3.75–4.25	10	0.25–28.5	33
Pteroncola carlinii Almandoz & Ferrario	10	0.5–2.25	3	0.5–1.0	2	0.75	2	1.25	2	x	19
cf. *Pteroncola* sp.							1	1.0	1	x	2
Rhoicosphenia michalii Ligowski	1	x							1	x	2
Synedropsis fragilis (Manguin) Hasle et al.			3	0.25–0.5			1	1.5	7	0.75–2.5	11
Synedropsis recta Hasle et al.	3	0.25–1.0	3	0.5			2	1.75–3.0	7	0.25–8.0	15
Synedropsis cf. *recta* Hasle et al.	5	0.25	6	1.0–2.75					6	0.25–8.0	17
Tabularia sp.	2	0.5–1.0			1	0.5					3
Tabulariopsis australis (Perag.) D.M.Williams	9	0.25–16.75	1	1.0	1	23.25			1	x	12

Table 2 (continued) – List of all taxa with their occurrences and abundances in the different sample groups. TP = tidal pool, CBL = cobbles, LR = large rock, BS = bottom sediments, ASB = artificial substrata; n = number of samples; x = species is recorded outside the counts; * indicates planktonic taxa.

	TP (n = 19)		**CBL (n = 9)**		**LR (n = 2)**		**BS (n = 2)**		**ASB (n = 10)**		
Taxon	**occurrence (n of samples)**	**% abundance**	**occurrence (n of samples)**	**% abundance**	**occurrence (n of samples)**	**% abundance**	**occurrence (n of samples)**	**% abundance**	**occurrence (n of samples)**	**% abundance**	**occurrence (total n of samples)**
Thalassionema gelida Perag.							2	0.75–2.5			2
**Thalassiosira gerloffii* P.Rivera							1	x			1
**Thalasiosira gracilis* (G.Karsten) Hust.							2	x			2
**Thalassiosira gracilis* var. *expecta* (VanLand.) G.A.Fryxell & Hasle							2	0.25			2
**Thalassiosira ritscheri* (Hust.) Hasle							1	x			1
Trachyneis cf. *aspera* (Ehrenb.) P.T.Cleve							2	x			2
Tripterion margaritae L.F.Fernandes & Sar	10	0.25–20									10
unidentified gomphoneid diatom	1	0.5	2	x			1	0.5	2	x	6
unidentified naviculoid diatom 1	2	x									2
unidentified naviculoid diatom 2	1	13.75	1	x							2
unidentified amphoroid diatom	2	x									2
number of taxa per sample in the group (min–max)	14–18		9–22		8–16		52–86		9–38		
total number of taxa in each group of samples	72		47		18		92		59		

Table 3 – Results of the PERMANOVA test. Resemblance: S17 Bray-Curtis similarity. Number of permutations: 9999. *Term has one or more empty cells.

	Main test					
	d.f.	**SS**	**MS**	**pseudo-F**	**p (perms)**	**unique perms**
habitat	4	26856	6713.9	3.9308	0.0001	9877
month	3	4482	1494	0.87472	0.6195	9914
habitat × month*	5	6697.1	1339.4	0.7842	0.8136	9891
Res	29	4953.2	1708			
Total	41	1.03E+0.5				

	Pair wise tests			
	t	**p (perm)**	**unique perms**	**den. d.f.**
artificial substrata & cobbles	1.7756	0.0508	9950	13
artificial substrata & rocks	1.4764	0.0881	9108	8
artificial substrata & tidal pools	2.7417	0.0001	9939	22
cobbles & rocks	1.3184	0.1411	9274	7
cobbles & tidal pools	2.4609	0.0001	9935	21
rock & sediments	no test d.f. = 0			
rocks & tidal pools	1.2523	0.1263	9934	16
sediments & artificial substrata	2.1199	0.0019	8579	7
sediments & cobbles	1.7128	0.134	9612	6
sediments & tidal pools	1.9794	0.0016	9937	15

	Average similarity between/within groups				
	artificial substrata	**cobbles**	**rock**	**sediments**	**tidal pools**
artificial substrata	59.625				
cobbles	54.618	62.149			
rock	34.817	34.22	14.704		
sediments	34.68	27.79	20.099	68.361	
tidal pools	24.409	18.232	24.261	16.762	32.881

samples were taken from the sides of large rocks, in only one sampling month and in a single season.

Results from nMDS

The nMDS (fig. 2) of all samples and with the relatively high 2D stress value of 0.14 visualized the samples based on their diatom abundance data. All samples from artificial substrata and cobbles were grouped together, whereas samples from tidal pools were scattered on the other side of the graph, with a few exceptions. The two bottom sediment samples were both nearer to the samples from cobbles and artificial substrata. The two samples from large rocks were very distantly placed on the graph, with one of the samples closer to those from tidal pools, and the second sample next to the samples from artificial substrata and cobbles. No separation between the samples from the different sampling months could be seen on the nMDS graph.

Two-way PERMANOVA analyses

The two-way PERMANOVA indicated that seasonality did not significantly influence the diatom communities, and that there was no significant interaction between the habitat/substratum type and sampling month ($p > 0.05$, table 3). In contrast, the habitat/substratum type had a significant effect (pseudo-F = 3.9308, $p < 0.01$, table 3). The pair wise test showed that significant differences exist between the communities in tidal pools and those on intertidal cobbles, artificial substrata, and sediments (all three pairs at $p < 0.01$, table 3). Sediments were also significantly different from artificial substrata ($p < 0.01$, table 3) in their communities. The similarity was highest between the communities on artificial substrata and intertidal cobbles (55%, table 3).

SIMPER analysis and taxa contributions

Navicula aff. *perminuta* was the most characteristic species for diatom communities on intertidal cobbles, contributing to almost 90% of the similarity between the samples (62% intra-group similarity, table 4). On artificial substrata, *N.* aff. *perminuta*, together with *N. glaciei* accounted for 81% of the similarity in this group of samples. The dissimilarity (45%) between cobbles and artificial substrata was related to the higher abundances of *N. glaciei* (with a contribution of 24%), as well as *Pseudogomphonema kamtschaticum* and fragilarioid diatoms on artificial substrata (table 5). The two bottom sediment samples, although taken in two different seasons, shared a number of species, which altogether

Table 4 – Results from SIMPER analysis of similarity of the communities inside each group of samples and their contributing species. Resemblance: S17 Bray-Curtis similarity. Cut off for low contributions: 90%. Species are ordered based on contribution.

		Artificial substrata			
		Average similarity = 59.63			
Species	**Av. abundance**	**Av. similarity**	**Sim/SD**	**Contribution %**	**Cum.%**
Navicula aff. *perminuta*	7.41	33.18	2.49	55.65	55.65
Navicula glaciei	4.63	15.10	1.49	25.33	80.99
Pseudogomphonema kamtschaticum	1.50	3.20	1.02	5.36	86.35
Fragilaria aff. *striatula*	0.97	1.89	0.77	3.17	89.52
Brandinia charcotii	0.88	1.17	0.47	1.96	91.48
		Cobbles			
		Average similarity = 62.15			
Species	**Av. abundance**	**Av. similarity**	**Sim/SD**	**Contribution %**	**Cum.%**
Navicula aff. *perminuta*	8.98	55.93	2.49	89.99	89.99
Pseudogomphonema kamtschaticum	0.73	2.11	0.79	3.39	93.38
		Tidal pools			
		Average similarity = 32.88			
Species	**Av. abundance**	**Av. similarity**	**Sim/SD**	**Contribution %**	**Cum.%**
Navicula glaciei	2.55	6.38	1.93	19.41	19.41
Navicula aff. *perminuta*	2.34	5.43	1.62	16.51	35.93
Navicula sp.2	2.84	5.13	0.85	15.59	51.52
Navicula sp.3	2.08	2.65	0.51	8.06	59.58
Melosira brandinii	1.75	1.91	0.46	5.82	65.39
Fragilaria aff. *striatula*	1.84	1.82	0.36	5.54	70.93
Melosira sp.1	1.38	1.72	0.54	5.23	76.16
Craspedostauros sp.	1.43	1.37	0.41	4.17	80.33
Tripterion margaritae	1.05	1.17	0.46	3.54	83.87
Craspedostauros laevissimus	1.01	1.10	0.52	3.36	87.23
Brandinia charcotii	0.92	1.10	0.61	3.34	90.57
		Sediments			
		Average similarity = 68.36			
Species	**Av. abundance**	**Av. similarity**	**Sim/SD**	**Contribution %**	**Cum.%**
Navicula aff. *perminuta*	6.37	11.46		16.77	16.77
Navicula glaciei	2.71	4.95		7.24	24.01
Pseudogomphonema kamtschaticum	2.00	3.69		5.39	29.40
Navicula sp.1	2.34	3.43		5.02	34.42
Pleurosigma sp.	2.25	3.43		5.02	39.44
Synedropsis recta	1.53	2.52		3.68	43.13
cf. *Hemidiscus* sp.	1.58	2.33		3.41	46.54
Cocconeis matsii	1.12	2.13		3.11	49.65
Gomphonemopsis ligowskii	1.22	2.13		3.11	52.77
Navicula sp.9	1.12	2.13		3.11	55.88
Cocconeis costata	1.00	1.90		2.79	58.66
Cocconeis fasciolata	1.11	1.90		2.79	61.45
Pinnularia quadratarea	1.00	1.90		2.79	64.24
Coconeis melchioroides	1.22	1.65		2.41	66.65
Cocconeis pottercovei	0.87	1.65		2.41	69.06
Thalassionema gelida	1.22	1.65		2.41	71.47
Cocconeis dallmannii	0.91	1.35		1.97	73.44
Fallacia marnieri	0.85	1.35		1.97	75.41
Fragilaria sp.2	0.97	1.35		1.97	77.38
Fragilariopisis curta	0.85	1.35		1.97	79.35
Minisdiscus sp.	1.47	1.35		1.97	81.32

Table 4 (continued) – Results from SIMPER analysis of similarity of the communities inside each group of samples and their contributing species. Resemblance: S17 Bray-Curtis similarity. Cut off for low contributions: 90%. Species are ordered based on contribution.

Sediments
Average similarity = 68.36

Species	Av. abundance	Av. similarity	Sim/SD	Contribution %	Cum.%
Pinnularia parallelimarginata	0.79	1.35		1.97	83.29
Achnanthes bongrainii	0.50	0.95		1.39	84.68
Amphora gourdonii	0.68	0.95		1.39	86.07
Brandinia charcotii	0.60	0.95		1.39	87.47
Australoneis frenguelliae	0.60	0.95		1.39	88.86
Fragilariopsis cf. *nana*	0.68	0.95		1.39	90.25

Large rocks
Average similarity = 14.70

Species	Av. abundance	Av. similarity	Sim/SD	Contribution %	Cum.%
Navicula aff. *perminuta*	4.82	11.46		77.95	77.95
Navicula glaciei	1.79	3.24		22.05	100.00

Table 5 – SIMPER pair wise comparisons of the sample groups and contributing species for the dissimilarity between the groups. ASB = artificial substrata, CBL = cobbles, BS = sediments, TP = tidal pools. Groups for which PERMANOVA indicated significant differences are highlighted. Resemblance: S17 Bray-Curtis similarity. Cut off for low contributions: 90%. Species are ordered based on contribution.

Artificial substrata & cobbles
Average dissimilarity = 45.38

Species	Av. abundance (ASB)	Av. abundance (CBL)	Av. dissimilarity	Sim/SD	Contribution %	Cum.%
Navicula glaciei	4.63	1.31	10.92	1.50	24.06	24.06
Navicula aff. *perminuta*	7.41	8.98	6.60	1.38	14.54	38.60
Pseudogomphonema kamtschaticum	1.50	0.73	3.38	1.08	7.45	46.05
Achnanthes bongrainii	0.44	1.10	3.06	0.73	6.74	52.79
Fragilaria aff. *striatula*	0.97	0.38	2.75	1.20	6.06	58.86
Brandinia charcotii	0.88	0.43	2.70	0.96	5.95	64.80
Synedropsis recta	0.81	0.08	2.08	0.87	4.58	69.38
Synedropsis cf. *recta*	0.52	0.30	1.75	0.83	3.85	73.24
Synedropsis fragilis	0.61	0.13	1.60	1.05	3.52	76.76
Licmophora gracilis	0.44	0.12	1.22	0.94	2.68	79.44
Nitzschia sp.3	0.21	0.25	1.04	0.56	2.29	81.73
Nitzschia sp.1	0.20	0.28	0.92	1.00	2.03	83.76
Navicula sp.1	0.12	0.24	0.78	0.83	1.72	85.48
Navicula sp.4	0.12	0.17	0.72	0.71	1.60	87.08
Licmophora belgicae	0.23	0.08	0.68	0.53	1.50	88.58
Achnanthes sp.1	0.00	0.24	0.64	0.60	1.42	90.00
Cocconeis melchioroides	0.20	0.06	0.62	0.82	1.37	91.36

Artificial substrata & sediments
Average dissimilarity = 65.32

Species	Av. abundance (ABS)	Av. abundance (BS)	Av. dissimilarity	Sim/SD	Contribution %	Cum.%
Navicula glaciei	4.63	2.71	3.60	1.5	5.52	5.52
Pleurosigma sp.	0.00	2.25	3.12	4.50	4.78	10.30
Navicula sp.1	0.12	2.34	3.07	3.60	4.71	15.00
Navicula aff. *perminuta*	7.41	6.37	2.49	1.23	3.82	18.82
cf. *Hemidiscus* sp.	0.00	1.58	2.19	4.25	3.35	22.17
Minisdiscus sp.	0.07	1.47	1.96	1.68	3.00	25.18
Pseudogomphonema kamtschaticum	1.50	2.00	1.74	1.41	2.67	27.85
Thalassionema gelida	0.00	1.22	1.69	3.31	2.59	30.44
Synedropsis recta	0.81	1.53	1.63	2.72	2.49	32.93

Table 5 (continued) – SIMPER pair wise comparisons of the sample groups and contributing species for the dissimilarity between the groups. ASB = artificial substrata, CBL = cobbles, BS = sediments, TP = tidal pools. Groups for which PERMANOVA indicated significant differences are highlighted. Resemblance: S17 Bray-Curtis similarity. Cut off for low contributions: 90%. Species are ordered based on contribution.

Artificial substrata & sediments
Average dissimilarity = 65.32

Species	**Av. abundance (ABS)**	**Av. abundance (BS)**	**Av. dissimilarity**	**Sim/SD**	**Contribution %**	**Cum.%**
Cocconeis matsii	0.00	1.12	1.55	14.17	2.37	35.31
Navicula sp.9	0.00	1.12	1.55	14.17	2.37	37.68
Gomphonemopsis ligowskii	0.12	1.22	1.54	3.57	2.36	40.04
Cocconeis melchioroides	0.02	1.22	1.42	2.30	2.17	42.21
Cocconeis costata	0.00	1.00	1.39	14.17	2.12	44.33
Pinnularia quadratarea	0.00	1.00	1.39	14.17	2.12	46.45
Fragilaria sp.2	0.00	0.97	1.34	3.60	2.05	48.50
Cocconeis fasciolata	0.17	1.11	1.32	3.00	2.01	50.52
Cocconeis dallmannii	0.00	0.91	1.26	4.25	1.93	52.45
Brandinia charcotii	0.88	0.60	1.21	1.37	1.86	54.31
Cocconeis pottercovei	0.00	0.87	1.20	14.17	1.84	56.15
Fragilariopisis curta	0.00	0.85	1.19	5.08	1.81	57.96
Fallacia marnieri	0.00	0.85	1.18	5.46	1.81	59.77
Fragilaria aff. *striatula*	0.97	0.43	1.16	1.24	1.78	61.56
Navicula directa	0.00	0.81	1.12	2.55	1.71	63.27
Pinnularia parallelimarginata	0.00	0.79	1.09	7.60	1.67	64.94
Nitzschia sp.3	0.21	0.71	0.98	1.03	1.49	66.43
Fragilariopsis cf. *nana*	0.00	0.68	0.95	3.44	1.45	67.89
Planothidium sp.1	0.00	0.68	0.95	3.44	1.45	69.34
Amphora gourdonii	0.00	0.68	0.95	3.60	1.45	70.79
Synedropsis fragilis	0.61	0.61	0.91	1.09	1.39	72.18
Navicula jejunoides	0.00	0.61	0.84	0.97	1.29	73.47
Australoneis frenguelliae	0.00	0.60	0.84	5.46	1.28	74.75
Nitzschia sp.7	0.00	0.60	0.84	5.46	1.28	76.03
Petroneis sp.1	0.00	0.60	0.84	5.46	1.28	77.31
Licmophora antarctica	0.10	0.68	0.81	2.09	1.24	78.55
Licmophora gracilis	0.44	0.75	0.79	1.55	1.21	79.76
Amphora sp.2	0.00	0.56	0.78	0.97	1.20	80.95
Fragilariopsis separanda	0.00	0.56	0.78	0.97	1.20	82.15
Pteroncola carlinii	0.00	0.56	0.77	0.97	1.18	83.33
cf. *Pteroncola* sp.	0.00	0.50	0.69	0.97	1.05	84.38
Synedropsis cf. *recta*	0.52	0.00	0.69	0.62	1.05	85.43
Achnanthes bongrainii	0.44	0.5	0.60	1.52	0.92	86.35
Licmophora belgicae	0.23	0.25	0.51	0.85	0.78	87.13
Navicula sp.10	0.00	0.35	0.49	0.97	0.76	87.89
Nitzschia homburgiensis	0.00	0.35	0.49	0.97	0.76	88.65
Parlibellus variabilis	0.00	0.35	0.49	0.97	0.76	89.40
unidentified gomphoneid diatom	0.00	0.35	0.49	0.97	0.76	90.16

Cobbles & sediments
Average dissimilarity = 72.21

Species	**Av. abundance (CBL)**	**Av. abundance (BS)**	**Av. dissimilarity**	**Sim/SD**	**Contribution %**	**Cum.%**
Navicula aff. *perminuta*	8.98	6.37	4.58	3.35	6.34	6.34
Pleurosigma sp.	0.00	2.25	3.31	4.50	4.58	10.92
Navicula glaciei	1.31	2.71	3.23	3.05	4.48	15.40
Navicula sp.1	0.24	2.34	3.09	3.17	4.28	19.68
cf. *Hemidiscus* sp.	0.00	1.58	2.32	4.27	3.21	22.89
Minisdiscus sp.	0.00	1.47	2.17	1.83	3.01	25.90

Table 5 (continued) – SIMPER pair wise comparisons of the sample groups and contributing species for the dissimilarity between the groups. ASB = artificial substrata, CBL = cobbles, BS = sediments, TP = tidal pools. Groups for which PERMANOVA indicated significant differences are highlighted. Resemblance: S17 Bray-Curtis similarity. Cut off for low contributions: 90%. Species are ordered based on contribution.

Cobbles & sediments

Average dissimilarity = 72.21

Species	**Av. abundance (CBL)**	**Av. abundance (BS)**	**Av. dissimilarity**	**Sim/SD**	**Contribution %**	**Cum.%**
Synedropsis recta	0.08	1.53	2.14	4.33	2.96	28.86
Pseudogomphonema kamtschaticum	0.73	2.00	1.89	1.92	2.61	31.47
Thalassionema gelida	0.00	1.22	1.80	3.32	2.49	33.96
Gomphonemopsis ligowskii	0.00	1.22	1.79	9.66	2.48	36.44
Cocconeis melchioroides	0.06	1.22	1.71	2.92	2.37	38.81
Navicula sp.9	0.00	1.12	1.64	14.76	2.28	41.09
Achnanthes bongrainii	1.10	0.50	1.57	0.67	2.18	43.27
Cocconeis matsii	0.06	1.12	1.56	6.16	2.16	45.43
Cocconeis fasciolata	0.08	1.11	1.52	3.91	2.10	47.53
Pinnularia quadratarea	0.00	1.00	1.47	14.76	2.04	49.57
Fragilaria sp.2	0.00	0.97	1.42	3.61	1.96	51.53
Cocconeis costata	0.06	1.00	1.39	5.52	1.92	53.45
Cocconeis dallmannii	0.00	0.91	1.34	4.27	1.86	55.31
Fragilariopisis curta	0.00	0.85	1.26	5.09	1.74	57.05
Fallacia marnieri	0.00	0.85	1.25	5.49	1.74	58.79
Cocconeis pottercovei	0.06	0.87	1.19	4.80	1.65	60.43
Navicula directa	0.00	0.81	1.19	2.55	1.64	62.08
Pinnularia parallelimarginata	0.00	0.79	1.16	7.65	1.60	63.68
Nitzschia sp.3	0.25	0.71	1.16	1.03	1.60	65.28
Brandinia charcotii	0.43	0.60	1.09	1.43	1.51	66.80
Licmophora gracilis	0.12	0.75	1.05	2.36	1.46	68.25
Fragilariopsis cf. *nana*	0.00	0.68	1.01	3.43	1.39	69.65
Amphora gourdonii	0.00	0.68	1.00	3.61	1.39	71.04
Licmophora antarctica	0.00	0.68	1.00	3.61	1.39	72.43
Planothidium sp.1	0.06	0.68	0.92	2.46	1.28	73.70
Fragilaria aff. *striatula*	0.38	0.43	0.92	0.91	1.28	74.98
Synedropsis fragilis	0.13	0.61	0.91	1.07	1.26	76.23
Navicula jejunoides	0.00	0.61	0.89	0.97	1.24	77.47
Australoneis frenguelliae	0.00	0.60	0.89	5.49	1.23	78.70
Nitzschia sp.7	0.00	0.60	0.89	5.49	1.23	79.93
Petroneis sp.1	0.00	0.60	0.89	5.49	1.23	81.16
Amphora sp.2	0.00	0.56	0.83	0.97	1.15	82.30
Fragilariopsis separanda	0.00	0.56	0.83	0.97	1.15	83.45
Pteroncola carlinii	0.19	0.56	0.82	1.06	1.13	84.58
cf. *Pteroncola* sp.	0.00	0.50	0.73	0.97	1.01	85.59
Nitzschia sp.1	0.28	0.50	0.65	2.52	0.91	86.50
Navicula sp.10	0.00	0.35	0.52	0.97	0.73	87.22
Nitzschia homburgiensis	0.00	0.35	0.52	0.97	0.73	87.95
Parlibellus variabilis	0.00	0.35	0.52	0.97	0.73	88.68
unidentified gomphoneid diatom	0.00	0.35	0.52	0.97	0.73	89.40
Fragilariopsis kerguelensis	0.00	0.35	0.52	0.97	0.71	90.12

Sediments & tidal pools

Average dissimilarity = 83.24

Species	**Av. abundance (BS)**	**Av. abundance (TDP)**	**Av. dissimilarity**	**Sim/SD**	**Contribution %**	**Cum.%**
Navicula aff. *perminuta*	6.37	2.34	5.24	2.62	6.30	6.30
Navicula sp.2	0.00	2.84	3.59	1.09	4.31	10.61
Navicula sp.1	2.34	0.00	2.97	4.28	3.57	14.18

Table 5 (continued) – SIMPER pair wise comparisons of the sample groups and contributing species for the dissimilarity between the groups. ASB = artificial substrata, CBL = cobbles, BS = sediments, TP = tidal pools. Groups for which PERMANOVA indicated significant differences are highlighted. Resemblance: S17 Bray-Curtis similarity. Cut off for low contributions: 90%. Species are ordered based on contribution.

Sediments & tidal pools **Average dissimilarity = 83.24**						
Species	**Av. abundance (BS)**	**Av. abundance (TDP)**	**Av. dissimilarity**	**Sim/SD**	**Contribution %**	**Cum.%**
Pleurosigma sp.	2.25	0.00	2.86	4.63	3.44	17.62
Navicula sp.3	0.00	2.08	2.57	0.87	3.09	20.71
Fragilaria aff. *striatula*	0.43	1.84	2.42	0.63	2.91	23.62
Pseudogomphonema kamtschaticum	2.00	0.17	2.33	4.71	2.80	26.42
Melosira brandinii	0.00	1.75	2.16	0.78	2.60	29.02
cf. *Hemidiscus* sp.	1.58	0.00	2.01	4.34	2.41	31.44
Minisdiscus sp.	1.47	0.00	1.88	1.87	2.26	33.70
Synedropsis recta	1.53	0.12	1.80	3.89	2.16	35.85
Craspedostauros sp.	0.00	1.43	1.79	0.66	2.15	38.01
Melosira sp.1	0.00	1.38	1.72	0.84	2.06	40.07
Navicula glaciei	2.71	2.55	1.69	1.89	2.02	42.10
Thalassionema gelida	1.22	0.00	1.55	3.37	1.87	43.96
Cocconeis melchioroides	1.22	0.03	1.52	3.18	1.82	45.79
Cocconeis matsii	1.12	0.00	1.42	16.38	1.71	47.50
Navicula sp.9	1.12	0.00	1.42	16.38	1.71	49.21
Cocconeis fasciolata	1.11	0.04	1.36	5.45	1.64	50.84
Nitzschia sp.3	0.71	0.96	1.34	0.92	1.61	52.46
Gomphonemopsis ligowskii	1.22	0.18	1.32	3.08	1.59	54.04
Tripterion margaritae	0.00	1.05	1.31	0.78	1.57	55.61
Craspedostauros laevissimus	0.00	1.01	1.28	0.68	1.53	57.15
Pinnularia quadratarea	1.00	0.00	1.27	16.38	1.53	58.68
Cocconeis costata	1.00	0.08	1.16	5.34	1.40	60.07
Fragilaria sp.2	0.97	0.05	1.16	3.02	1.39	61.47
Cocconeis dallmannii	0.91	0.03	1.13	3.71	1.35	62.82
Cocconeis pottercovei	0.87	0.00	1.10	16.38	1.32	64.14
Fragilariopisis curta	0.85	0.00	1.09	5.24	1.31	65.45
Fallacia marnieri	0.85	0.00	1.09	5.61	1.30	66.75
Brandinia charcotii	0.60	0.92	1.03	1.01	1.24	68.00
Pinnularia parallelimarginata	0.79	0.00	1.00	8.00	1.20	69.20
Navicula directa	0.81	0.11	0.92	2.06	1.11	70.31
Planothidium sp.1	0.68	0.3	0.90	2.22	1.08	71.39
Fragilariopsis cf. *nana*	0.68	0.00	0.87	3.51	1.05	72.43
Amphora gourdonii	0.68	0.00	0.87	3.67	1.04	73.47
Licmophora antarctica	0.68	0.03	0.83	3.02	1.00	74.48
Tabulariopsis australis	0.00	0.69	0.83	0.58	1.00	75.47
Berkeleya cf. *rutilans*	0.00	0.64	0.82	0.34	0.98	76.46
Licmophora gracilis	0.75	0.14	0.80	1.81	0.96	77.41
Synedropsis fragilis	0.61	0.00	0.78	0.98	0.94	78.36
Navicula jejunoides	0.61	0.00	0.77	0.98	0.93	79.29
Australoneis frenguelliae	0.60	0.00	0.77	5.61	0.92	80.21
Nitzschia sp.7	0.60	0.00	0.77	5.61	0.92	81.13
Petroneis sp.1	0.60	0.00	0.77	5.61	0.92	82.05
Pteroncola carlinii	0.56	0.25	0.73	1.10	0.88	82.93
Amphora sp.2	0.56	0.00	0.72	0.98	0.86	83.79
Fragilariopsis separanda	0.56	0.00	0.72	0.98	0.86	84.65
cf. *Pteroncola* sp.	0.50	0.00	0.63	0.98	0.76	85.41
Achnanthes bongrainii	0.50	0.23	0.61	1.73	0.73	86.14
Navicula sp.5	0.00	0.46	0.60	0.31	0.72	86.86

Table 5 (continued) – SIMPER pair wise comparisons of the sample groups and contributing species for the dissimilarity between the groups. ASB = artificial substrata, CBL = cobbles, BS = sediments, TP = tidal pools. Groups for which PERMANOVA indicated significant differences are highlighted. Resemblance: S17 Bray-Curtis similarity. Cut off for low contributions: 90%. Species are ordered based on contribution.

Sediments & tidal pools
Average dissimilarity = 83.24

Species	Av.abundance (BS)	Av.abundance (TDP)	Av.dissimilarity	Sim/SD	Contribution %	Cum.%
Nitzschia sp.1	0.50	0.08	0.53	2.26	0.64	87.50
Amphora sp.5	0.00	0.44	0.52	0.46	0.63	88.13
Navicula sp.10	0.35	0.00	0.45	0.98	0.54	88.67
Nitzschia homburgiensis	0.35	0.00	0.45	0.98	0.54	89.22
Parlibellus variabilis	0.35	0.00	0.45	0.98	0.54	89.76
unidentified gomphoneid diatom	0.35	0.04	0.45	0.98	0.54	90.31

Artificial substrata & tidal pools
Average dissimilarity = 75.59

Species	Av. abundance (ABS)	Av. abundance (TDP)	Av. dissimilarity	Sim/SD	Contribution %	Cum.%
Navicula aff. *perminuta*	7.41	2.34	11.76	1.84	15.56	15.56
Navicula glaciei	4.63	2.55	6.49	1.46	8.58	24.14
Navicula sp.2	0.00	2.84	6.20	1.05	8.21	32.35
Fragilaria aff. *striatula*	0.97	1.84	4.68	0.69	6.19	38.54
Navicula sp.3	0.00	2.08	4.38	0.86	5.80	44.34
Melosira brandinii	0.00	1.75	3.67	0.78	4.86	49.20
Craspedostauros sp.	0.00	1.43	3.08	0.67	4.08	53.27
Pseudogomphonema kamtschaticum	1.50	0.17	2.96	1.07	3.91	57.18
Melosira sp.1	0.00	1.38	2.93	0.83	3.88	61.06
Brandinia charcotii	0.88	0.92	2.44	1.09	3.22	64.29
Tripterion margaritae	0.00	1.05	2.23	0.78	2.95	67.24
Craspedostauros laevissimus	0.00	1.01	2.21	0.67	2.92	70.16
Nitzschia sp.3	0.21	0.96	2.13	0.73	2.81	72.98
Synedropsis recta	0.81	0.12	1.63	0.89	2.16	75.13
Berkeleya cf. *rutilans*	0.00	0.64	1.43	0.34	1.90	77.03
Tabulariopsis australis	0.00	0.69	1.38	0.58	1.83	78.86
Synedropsis fragilis	0.61	0.00	1.23	0.95	1.63	80.49
Achnanthes bongrainii	0.44	0.23	1.11	0.91	1.46	81.95
Synedropsis cf. *recta*	0.52	0.03	1.07	0.67	1.42	83.37
Navicula sp.5	0.00	0.46	1.06	0.31	1.40	84.77
Licmophora gracilis	0.44	0.14	0.90	0.95	1.19	85.96
Amphora sp.5	0.00	0.44	0.87	0.47	1.15	87.10
Amphora sp.6	0.00	0.35	0.76	0.23	1.01	88.11
Nitzschia sp.8	0.00	0.30	0.66	0.23	0.87	88.98

Cobbles & tidal pools
Average dissimilarity = 81.77

Species	Av. abundance (CBL)	Av. abundance (TDP)	Av. dissimilarity	Sim/SD	Contribution %	Cum.%
Navicula aff. *perminuta*	8.98	2.34	16.66	2.43	20.37	20.37
Navicula sp.2	0.00	2.84	6.82	1.04	8.34	28.71
Navicula glaciei	1.31	2.55	5.22	1.44	6.39	35.10
Fragilaria aff. *striatula*	0.38	1.84	5.07	0.61	6.19	41.29
Navicula sp.3	0.00	2.08	4.80	0.86	5.87	47.16
Melosira brandinii	0.00	1.75	4.02	0.78	4.92	52.08
Craspedostauros sp.	0.00	1.43	3.38	0.67	4.14	56.22
Melosira sp.1	0.00	1.38	3.21	0.83	3.93	60.15
Nitzschia sp.3	0.25	0.96	2.49	0.76	3.04	63.19
Achnanthes bongrainii	1.10	0.23	2.47	0.63	3.02	66.21

Table 5 (continued) – SIMPER pair wise comparisons of the sample groups and contributing species for the dissimilarity between the groups. ASB = artificial substrata, CBL = cobbles, BS = sediments, TP = tidal pools. Groups for which PERMANOVA indicated significant differences are highlighted. Resemblance: S17 Bray-Curtis similarity. Cut off for low contributions: 90%. Species are ordered based on contribution.

	Cobbles & tidal pools Average dissimilarity = 81.77					
Species	**Av. abundance (CBL)**	**Av. abundance (TDP)**	**Av. dissimilarity**	**Sim/SD**	**Contribution %**	**Cum.%**
Tripterion margaritae	0.00	1.05	2.45	0.78	2.99	69.20
Craspedostauros laevissimus	0.00	1.01	2.43	0.67	2.97	72.17
Brandinia charcotii	0.43	0.92	2.37	0.93	2.89	75.06
Pseudogomphonema kamtschaticum	0.73	0.17	1.68	1.15	2.06	77.12
Tabulariopsis australis	0.11	0.69	1.59	0.62	1.95	79.07
Berkeleya cf. *rutilans*	0.00	0.64	1.58	0.34	1.93	81.00
Navicula sp.5	0.00	0.46	1.17	0.30	1.43	82.42
Amphora sp.5	0.00	0.44	0.94	0.47	1.15	83.58
Amphora sp.6	0.00	0.35	0.83	0.23	1.02	84.60
Pteroncola carlinii	0.19	0.25	0.83	0.77	1.02	85.62
Planothidium sp.1	0.06	0.30	0.73	0.54	0.89	86.51
Nitzschia sp.8	0.00	0.30	0.73	0.23	0.89	87.39
Synedropsis cf. *recta*	0.30	0.03	0.72	0.54	0.88	88.28
Nitzschia sp.1	0.28	0.08	0.67	0.79	0.82	89.09
Achnanthes sp.1	0.24	0.03	0.57	0.64	0.69	89.79
Navicula sp.1	0.24	0.00	0.56	0.70	0.68	90.47

contributed almost 74% for the high similarity between them (68%, table 4). These samples included almost all of the planktonic species found in the study, but also the highest number of *Cocconeis* taxa, various *Amphora* sensu lato and *Navicula* species (e.g. *N. directa*, *N. jejunoides*, and several unidentified *Navicula* species), *Petroneis* and *Nitzschia* taxa (tables 2 & 5). In addition, *Parlibellus variabilis*, *Pinnularia quadratarea*, *Thalassionema gelida*, and *Trachyneis* cf. *aspera*, were only found in the bottom sediment samples, while *Pleurosigma* sp. reached up to 7.5% of the counted valves from sediments (tables 2 & 5). All these species with their occurrences and abundances differentiated the bottom sediment samples from all other groups (tidal pools, artificial substrata, and cobbles), contributing between 30 and 35% of the dissimilarity in the pair wise tests (table 5). The contribution of the planktonic taxa to the dissimilarity between the sediment samples and other groups was smaller, ranging from 8% to 11%. In tidal pools, the dominant taxa and species abundances varied between the pools (table 2), resulting in a lower similarity within this sample group (33%, table 4). The largest proportion of the similarity (54%, table 4) within tidal pools communities was related to the presence and higher abundances of *Navicula* sp.2 and *Navicula* sp.3, fragilariod and centric diatoms (i.e. *Melosira brandinii*), *Craspedostauros* spp., and *Tripterion margaritae* (table 4). With the addition of *Berkeleya* cf. *rutilans*, these taxa were completely absent on intertidal cobbles. Other species, such as *Fragilaria* aff. *striatula*, *Navicula glaciei*, and *Tabulariopsis australis* had higher abundances in tidal pools, compared to cobbles, whereas *Pseudogomphonema kamtschaticum* and *Achnanthes bongrainii* were more numerous on cobbles than in the tidal pools. All these species together were responsible for more than 60% of the high dissimilarity between the communities on cobbles and tidal pools (82%, table 5). The lower abundances of *Navicula* aff. *perminuta* in tidal pools alone contributed 20% of the dissimilarity between the groups (table 5). Similarly, the high average dissimilarity between communities on artificial substrata and in tidal pools (76%, table 5) was again due to the absence on the artificial substrata of the typical species for the tidal pools, including *Tabulariopsis australis*. The higher average abundances of *Navicula* aff. *perminuta* and *N. glaciei* on artificial substrata added another 27% to the dissimilarity between the communities in these two groups (table 5). Finally, the two samples taken from the walls of large coastal rocks differed a lot, and the small percentage of similarity between them (15%, table 4) was mostly due to the presence of *Navicula* aff. *perminuta* and *N. glaciei* in small numbers in the samples (tables 2 & 4). These samples, only two and heterogenic with regard to their communities, were excluded from further comparisons.

Environmental parameters

Of the measured environmental parameters, salinity was markedly different between the two sampling seasons, as well as between the tidal pools and coastal localities (table 1). In November–December 2018 salinity of the sea water near the coast varied between 29.5 and 33.9 PSU, whereas in January–February 2020 it dropped to between 12 and 21.3 PSU (table 1). The highest variability in salinity was evident in tidal pools, with the lowest values recorded for sample LT10 (6.5 PSU) in 2020 and the highest for sample S3 (34.4 PSU) in 2018 (table 1). The water temperature in the tidal pools also varied, from 2.8°C (sample LT6) to 18.8°C (sample LT10) (table 1). Secchi depth was only measured for Johnsons Dock and Mongolian (Reserve) Port, and it was always lower inside the glacier-influenced Johnsons Dock (0.5–1.4 m), whereas in Mongolian (Reserve) Port, it was always above 2 m (table 1).

DISCUSSION

Habitat/substratum type and the distribution of benthic diatoms

There are many factors that influence the distribution and abundances of surface-associated diatoms in marine realm, including, but not limited to the substratum type, its chemistry, and even the microstructure of its surface, depth position, and orientation of the substrata, light conditions, wave action, and the effects of currents (Desrosiers et al. 2014 and references therein). Moreover, in the Antarctic coastal waters, benthic communities are subjected to changes in salinity due to glacier and snow meltwater inflow during the summer months (e.g. Brandini & Rebello 1994; Rakusa-Suszczewski 1995), often combined with the mechanical stress of waves forces and frequent ice-scouring (Barnes & Conlan 2007). Compared to the other sampled habitats and substrata, the communities on intertidal cobbles had a low diversity and were entirely dominated by only one small naviculoid diatom, *Navicula* aff. *perminuta*, sometimes reaching even up to 100% of the counted valves in a sample (table 2). Small naviculoid diatoms, such as *N.* aff. *perminuta*, have fast reproduction cycles and are able to rapidly (re-) colonize denuded habitats (Morin et al. 2008); they are highly resistant to mechanical stresses (Majewska et al. 2016 and references therein) and therefore typical for environments with recurrent unfavourable conditions (Hudon & Bourget 1983; Tuji 2000). The intertidal cobbles are unstable substrata, positioned directly under the scouring of ice pieces and wave forces and this could explain the clear dominance of small motile diatoms, such as *N.* aff. *perminuta*. One hypothesis for the observed similarity in the communities on artificial substrata with those on intertidal cobles could be the short period of exposure of the artificial substrata, as prevalence of small naviculoid taxa is also typical for the early stages of colonization (Hudon & Bourget 1983). Few studies in Antarctica have included artificial substrata and so far, only one study addressed the colonization rate of benthic diatoms in Antarctica (Zidarova et al. 2020). Results between the studies that included artificial substrata in Antarctica are difficult to compare due to the different nature of the substrata used in the studies and the different environmental conditions for the substrata (Desrosiers et al. 2014). For instance, on the ceramic tiles exposed for more than 100 days in the intertidal zone in Potter Cove, Al-Handal & Wulff (2008a, site PU) recorded 47 taxa, but mostly *Cocconeis* spp. dominated the diatom communities; *Navicula* cf. *perminuta* was frequent and *Pseudogomphonema kamtschaticum* was not observed on their ceramic tiles. Daglio et al. (2018) found 21 diatom taxa on ceramic tiles after 25 days of colonization, but in a controlled, artificial environment. For comparison, the total number of species on the artificial substrata from only two locations at South Bay was more than twice higher than the number of species observed by Daglio et al. (2018) for about the same period of their substrata exposure. For a much shorter period of exposure, compared to that used by Al-Handal & Wulff (2008a, site PU), the number of species at South Bay was again higher, with a quarter (59 vs 47 for PU). Further, Zidarova et al. (2020) in their colonization experiment with plexiglass tiles submerged at a depth of 1 m into the water column, found that the dominant diatom species in the communities on tiles were established after the first days of substrata exposure and did not change during the entire experimental period and at both sites (38 and 45 days of substrata exposure); the initially higher species richness, diversity and evenness were gradually decreasing, reaching levels similar to that of the natural epilithon in the region after 22–25 days of substrata exposure; and an equilibrium in the number of valves on the substrata was achieved after day 25, at least inside Johnsons Dock. In our opinion, the similarity in the communities on cobbles and on artificial substrata seems to reflect the disturbance by waves and ice-scouring on the substrata, due to their position at small depths (up to 6.5 m) but not underdevelopment of the communities due to short exposure time. At such small depths in Antarctica (up to 6.5 m for the experiment), the effects of waves and ice over the benthos are still very pronounced (Barnes & Conlan 2007).

Tidal pools are common habitats for the Antarctic shores (Rakusa-Suszczewski 1995). In these habitats, located in the intertidal zone and fed twice daily by water with the tides (Vidal et al. 2011), diatoms are subjected to a number of different stress factors, such as frequent fluctuations in water level, water temperature, and salinity. For King George Island, Rakusa-Suszczewski (1993) reported that in tidal pools salinity may vary from only a few to more than 40 PSU, while the water temperature can reach over 12°C. These observations generally conform to ours from Livingston Island. In addition to the unstable salinity and temperature conditions, benthic algae can also be exposed to high irradiances during low tide (Zacher et al. 2007). Many of the species, which were present in higher numbers in the communities of tidal pools, are known to form mucilage tubes or stalked colonies. The cells of *Melosira brandinii*, typically present in tidal pools, are joined together by mucilage stalks (Fernandes & de Souza-Mosimann 2001). Another characteristic species for the tidal pools, *Tripterion margaritae*, forms branched mucilage colonies (Fernandes & Sar 2009). *Parlibellus* and *Berkeleya*, the latter reaching up to 62% of the counted valves in some of the tidal pools (table 2), as well as other naviculoid diatom taxa (broad sense), live in large mucilage tubes (e.g. Lobban 1985; Houpt 1994). Experimentally, it has been shown that the extracellular polymeric substances produced by diatoms can protect the cells from fluctuations in salinity (Steele et al. 2014), or from both temperature and salinity stresses (Aslam et al. 2012). The tube formation provides the cells with protection against desiccation (Majewska et al. 2016 and references therein), also present in the dynamic environment of the shallow tidal pools in Antarctica. Earlier, Klöser (1998) found abundantly *Parlibellus* and *Melosira* species in tidal pools, and suggested that other diatom species were unable to cope with such variable conditions, i.e. temperatures and salinity changes, in these habitats. On the other hand, the mucilage forming species belonging to the high guild profile as defined by Passy (2007), are also vulnerable to mechanical/physical disturbances. Tidal pools are much less exposed to mechanical stresses (compared to the intertidal cobbles) and provide a shelter for the species from severe wave and ice-scouring effects. Finally, as suggested by Klöser (1998), the substratum properties seem to contribute to diatom abundances and distributions as well, as long as species living on the rock surfaces of the tidal pools may not be able to survive on more unstable substrata, such as mud and small sand grains (Passy 2007). The typical taxa for tidal pools were absent on sediments. As for the sediments, notably two taxa, *Trachyneis* cf. *aspera* and *Pleurosigma* sp., were recorded in the two bottom sediment samples from higher depths inside the glacier-influenced Johnsons Dock. *Trachyneis aspera* is usually reported from Antarctic sediments (Klöser 1998; Al-Handal & Wulff 2008a), as living in very low light conditions at depths below 20 m (summarized data by Gómez et al. 2009). The second taxon, *Pleurosigma* sp. (fig. 10D, table 2), is most likely the same diatom that was found to dominate some of the microphytobenthic communities at depths of 20–30 m inside the glacier-influenced Marian Cove on King George Island (Ha et al. 2019). Although data in the Antarctic literature for these two species are scarce, we did not observe them on the hard artificial substrata, placed at the same location even at depths of 6.5 m, suggesting that these two species could be typical for the deep-water sedimentary assemblages.

When studying the habitat distributions of benthic diatoms from Potter Cove, Klöser (1998) concluded that the Antarctic marine benthic diatoms do not show the typical distribution associated with a particular substratum type, such as epiphyton, epipelon, and epipsammon, but their distribution across the different habitats is related to the habitat properties and the levels of stress factors. Indeed, the most common taxa found on hard substrata have also been recorded living epiphytically or epizoically. These include *Navicula* aff. *perminuta*, *Navicula glaciei*, and *Pesudogomphonema kamtschaticum* (e.g. Majewska et al. 2013, 2015). But for many other taxa that were resposible for the dissimilarities in the communities from habitat/substratum type of South Bay, records and data in the literature are scarce. In our opinion, and based on our findings from South Bay, diatom species distributions specifically on hard substrata in the Antarctic coastal waters are related mostly to the disturbing factors that shape the habitat and the ability of the species to resist their combined effect. Moreover, seasonality that may have a significant effect on shallow water epiphytic communities in Antarctica (Majewska et al. 2016), had no strong effect on diatom species distribution and abundances on the studied hard substrata, neither significant dissimilarities were found between the two sediment samples in the study, taken from the same locality but in different months during two consecutive seasons. The question how climate change may influence the epilithic marine diatoms in Antarctica is open, as changes in the levels of disturbance of any of the stress factors shaping their habitat could provoke changes in communities.

Notes on some rarely reported Antarctic species and taxa with complex taxonomic history

Achnanthes bongrainii (Perag.) A.Mann (fig. 3)

Achnanthes antarctica Perag. (Peragallo 1921: 13, Pl. I, figures 25–26), **syn. nov.**

Achnanthepyla bongrainii var. *parallela* Perag. (Peragallo 1921: 50, Pl. II, figure 1), **syn. nov.**

Achnanthes brevipes var. *intermedia* f. *gaussii* Heiden (Heiden & Kolbe 1928: 579; Simonsen 1992: 30, Pl. 30, figures 1–5), **syn. nov.**

Achnanthes charcotii Perag. (Peragallo 1921: 13, Pl. I, figures 10–11), **syn. nov.**

Nitzschia granulata var. *gelida* Perag. (Peragallo 1921: 64, Pl. III, figure 22), **syn. nov.**

Taxonomic history and remarks – Described as *Achnanthepyla bongrainii* Perag. by Peragallo (1921), the species was transferred to the genus *Achnanthes* by Mann (1937). The original description of Peragallo's taxon discusses a large-celled species, with a valve length ranging from 60 to 100 µm and a valve width of 12 µm. Another taxon, *Achnanthepyla bongrainii* var. *parallela* Perag., found as part of the population of *A. bongrainii* ("avec le type à l'île Petermann", Peragallo 1921: 50; see also fig. 3A here), was separated from the nominate variety based on its parallel valve margins. In 1921, Peragallo also described two other *Achnanthes* species, which are morphologically similar to *A. bongrainii*: *A. charcotii* Perag., having a smaller valve length and a slightly smaller valve width (length 35 µm × width 11 µm) and 7 striae in 10 µm, and *A. antarctica* Perag., which dimensions and stria density (length 45–65 µm, width 8–10 µm, 6–6.5 striae in 10 µm, Peragallo 1921: 13) are intermediate between those of *A. charcotii* and *A. bongrainii*, although its width is slightly smaller. All the three taxa, described by Peragallo, have similar valve outline with more or less elliptic valves with parallel to convex margins; they also have similar striae arrangement on both the raphe and rapheless valves, with weakly radiate striae in the valve middle, becoming more radiate toward the apices; the central area on the raphe valve, as well as the narrow sternum on the rapheless valve, located along the axial axis of the valve are other overlapping features between the three taxa (fig. 3A). All the three species were described from mosses, but Peragallo (1921) defined *A. bongrainii* and *A. charcotii* as "obviously marine", while he also reported the third taxon, *A. antarctica*, as present in marine samples as well. There is no doubt that these three taxa are marine, and so far, none of them has been recorded during the extensive recent surveys on the non-marine diatom flora of Maritime Antarctica (Zidarova et al. 2016). In our opinion, all the three, *A. antarctica*, *A. charcotii*, and *A. bongrainii*, including its variety *parallela*, are conspecific, and should be regarded as one taxon, *A. bongrainii* (see fig. 3A), due to the following reasons: valves from the populations, identified as *A. bongrainii* from Potter Cove, King George Island (Al-Handal & Wulff 2008a) had a length between 44 and 84 µm and a width of 9.2–11 µm, with 6–7 striae in 10 µm, which range corresponds to the dimensions and stria density ranges of (at least) both the original *A. charcotii* and *A. antarctica*.

The depicted valves of *A. bongrainii* in Daglio et al. (2018, figure 3a) had a length of 53 µm, a width of 10–10.2 µm, and 6–7 striae in 10 µm on both valves (measured by us), fitting entirely into the dimensions and stria density, reported in Al-Handal & Wulff (2008a). Measurements of the valves (n = 37) identified as *A. bongrainii* from various populations at South Bay, Livingston Island (fig. 3B–M), including the samples used in the study of Zidarova et al. (2020), gave a valve length of 16–50 µm, a width of 6–9.6 µm, and 6–7 striae in 10 µm on both the raphe and rapheless valves, all again overlapping with both *A. antarctica* and *A. charcotii*. The latter (*A. charcotii*), given the single dimensions and stria density reported in Peragallo (1921), is apparently described based on a single valve. In regard to the original description of *A. bongrainii* and his higher valve length, we did not observe valves reaching 100 µm in length, neither Al-Handal & Wulff (2008a) reported such long valves, and therefore these long valves seem a rarity, or at the end of the

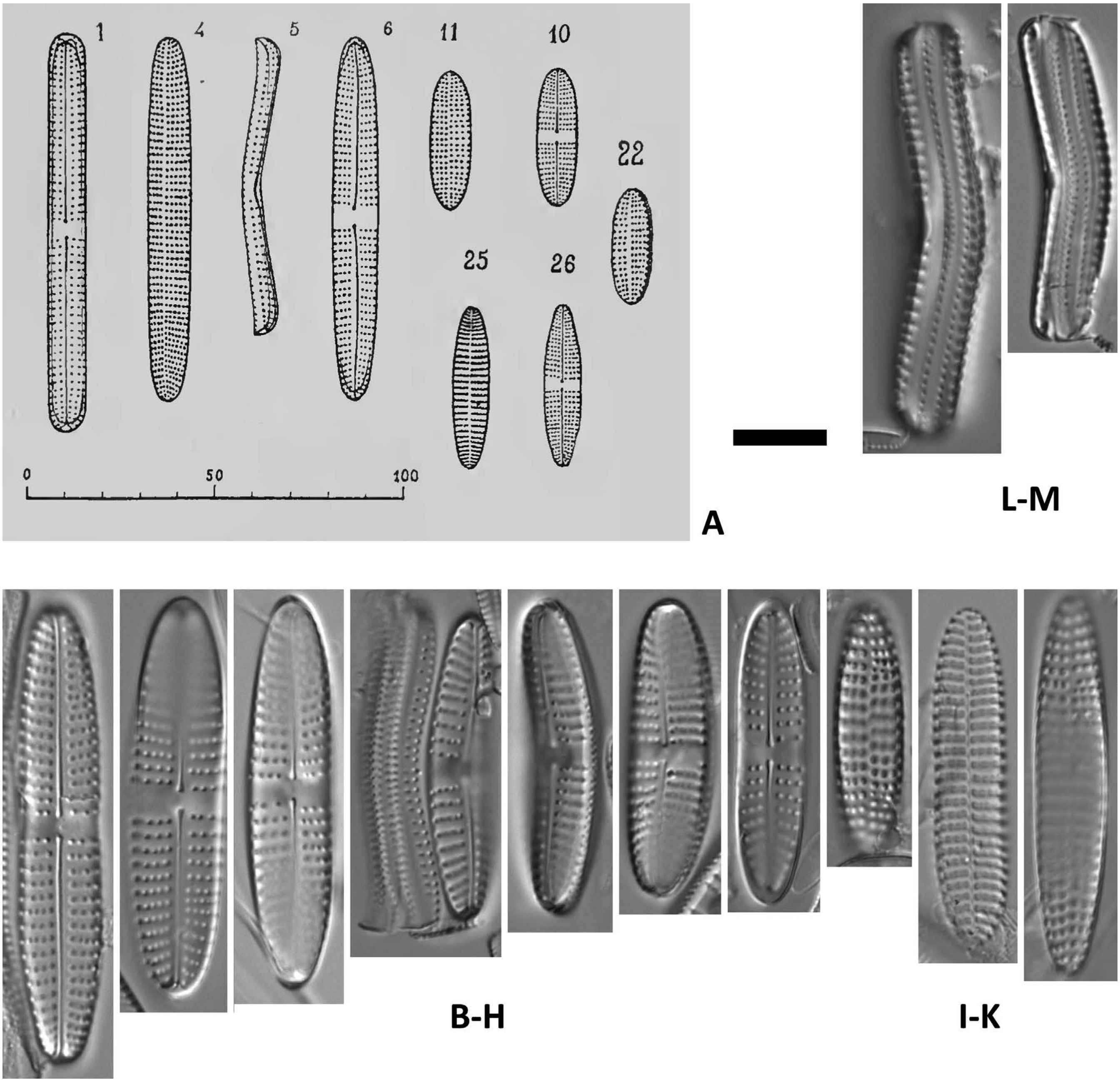

Figure 3 – *Achnanthes bongrainii*. **A**. Reproductions of the original drawings of *A. bongrainii*, its variety *parallela*, *A. antarctica*, *A. charcotii*, and *Nitzschia granulata* var. *gelida*: 1, *A. bongrainii* var. *parallela* (Peragallo 1921: Pl. II, figure 1); 4–6, *A. bongrainii* (Peragallo 1921: Pl. I, figures 4–6); 10–11, *A. charcotii* (Peragallo 1921: Pl. I, figures 10–11); 22, *Nitzschia granulata* var. *gelida* (Peragallo 1921: Pl. III, figure 22), 25–26, *A. antarctica* (Peragallo 1921: Pl. I, figures 25–26). **B**–**H**. Raphe valves of *A. bongrainii* from several populations from South Bay, Livingston Island. **I**–**K**. Rapheless valves of *A. bongrainii* from South Bay, Livingston Island. **L**–**M**. Girdle views of valves from South Bay, Livingston Island. Scale bars: A = 100 µm (original scale bar in Peragallo 1921); B–M = 10 µm.

range for the species. The other features, such as the striae arrangement of both raphe and rapheless valves of the three Peragallo's species, their central areas, the narrow sternum and its position along the axis of the rapheless valve, clearly overlap with the populations from South Bay (see fig. 3A for comparisons). Finally, Peragallo (1921) also described another taxon, named *Nitzschia granulata* var. *gelida* Perag. The depicted valve in Peragallo (1921, Pl. III, figure 22), having narrow hyaline area along the axis of the valve, with its dimensions (length of 25–35 µm, width 10 µm, with "6 points carénaux et lignes de granules en 10 µ", Peragallo 1921: 64) seems to be described due to the observations of only rapheless valves of actually *A. charcotii* (fig. 3A). We believe this variety should also be included into the synonymy of *A. bongrainii* (see also fig. 3A).

Furthermore, Heiden in Heiden & Kolbe (1928) described *A. brevipes* var. *intermedia* f. *gaussii* Heiden. Simonsen (1992), analyzing Heiden's original material, concluded that this taxon should be placed within *A. parvula* Kütz., but did not consider *A. bongrainii* when making this suggestion. There is no doubt that the valves of the Heiden's taxon, shown in Simonsen (1992: Pl. 30, figures 1–5), belong to *A. bongrainii* as well. Moreover, populations worldwide identified as *A. brevipes* C.Agardh, *A. brevipes* var. *intermedia* (Kütz.) Cleve, or as *A. parvula*, all have a different valve outline with usually more or less constricted valves in the middle with cuneate apices, as well as a different valve structure, with a narrow, more eccentrically (i.e. laterally) placed sternum on the rapheless valve, in contrast to *A. bongrainii* (fig. 3), a higher number of striae in 10 µm (above 7) and generally a narrower central area on the raphe valve (i.e. Witkowski et al. 2000; Toyoda & Williams 2004; Toyoda et al. 2005), compared to *A. bongrainii*.

In short, at least till SEM observations of various populations of *A. bongrainii* in Antarctica are available, we propose the following taxa to be considered and included into the synonymy of *Achnanthes bongrainii*: *Achnanthes antarctica*, *Achnanthepyla bongrainii* var. *parallela*, *Achnanthes brevipes* var. *intermedia* f. *gaussii*, *Achnanthes charcotii*, and *Nitzschia granulata* var. *gelida*.

Two other *Achnanthes* species, whose raphe valves show some morphological similarity to *A. bongrainii* were found in this study: *Achnanthes* sp.1 (having also similarity to *A. groenlandica* (Cleve) Grunow) and *Achnanthes* sp.2. These taxa need further investigation and evaluation, since the striation of their rapheless valves differs from that of *A. bongrainii* (fig. 4L–M, 4O, 4N). The first taxon has coarse areolae and an irregular striation of the rapheless valves (e.g. fig. 4L), while the second possesses one, quite enlarged areola on the rapheless valve (fig. 4O).

Ecology and distribution – *A. bongrainii* has been certainly reported several times from Antarctica under the name of *A. brevipes* and varieties (i.e. Roberts & McMinn 1999: Pl. 1, figures 3–4, as *A. brevipes* C.Agardh; Cremer et al. 2003: figures 8–10, as *A. brevipes* var. *intermedia*; Bae et al. 2021: supplementary information, figure S4c–f and figure S6c–d). It has been found mostly in the epilithon (Frenguelli & Orlando 1958; Al-Handal & Wulff 2008a; Daglio et al. 2018), and based on the existing literature records it is a quite widespread species in both Maritime Antarctica and the shores of the Antarctic Continent (e.g. Peragallo 1921; Frenguelli & Orlando 1958; Roberts & McMinn 1999). At South Bay, it was regularly observed on the artificial substrata and in tidal pools, with a maximum abundance on cobbles (table 2).

Achnanthes vicentii Manguin (fig. 4D–G)

Taxonomic remarks – Manguin (1957) described two *Achnanthes* species from Adélie Land (East Antarctica): *A. vicentii* Manguin and *A. sapini-jaloustrei* Manguin. The two species have identical valve outline, similar striation, and overlapping dimensions, and the main difference is in the raphe and rapheless valves, with the features of the raphe valve of the first matching the features of the rapheless valve of the second (Manguin 1957, see figures 25 & 26). Whether these two taxa are indeed different or it was a mistake in Manguin's observations at that time (and they are conspecific), could only be clarified with analyses of the original material. Unlike *A. vicentii*, often reported from different locations in Antarctica (e.g. Al-Handal & Wulff 2008a; Majewska & De Stefano 2015; Majewska et al. 2015), we could not find any records of *A. sapini-jaloustrei*. As for *A. vicentii*, it definitely does not belong to the genus *Achnanthes* s.s. (Toyoda et al. 2005), but most likely to *Planothidium* Round & Bukht., as the observations on a single rapheless valve in SEM from our populations suggest (fig. 4G). Al-Handal & Wulff (2008a) reported the same taxon from King George Island as *Planothidium vicentii*, an invalid name since the transfer was never validly published.

Ecology and distribution – *Achnanthes vicentii* was found in small numbers (< 1% of the counts) in almost all types of samples: artificial substrata, cobbles in the intertidal zone, tidal pools, and on bottom sediments (table 2). It seems to be present in larger numbers as an epiphyte or as an epibiont on sessile fauna (Majewska et al. 2013). It is a widespread species in entire Antarctica, from the South Shetland Islands to the Ross Sea (Majewska et al. 2013) and Adélie Land (Manguin 1957).

Australoneis frenguelliae **(**Riaux-Gob. & J.M.Guerrero) J.M.Guerrero & Riaux-Gob. (fig. 4A–C)

Taxonomic history – The species was originally discovered by Frenguelli & Orlando (1958) and named *Cocconeis orbicularis* Freng. & H.A.Orlando. The description was invalid due to the lack of a Latin diagnosis (Riaux-Gobin et al. 2019). Riaux-Gobin et al. (2019) proposed its inclusion within the genus *Campyloneis*, as *C. frenguelliae* Riaux-Gob. & J.M.Guerrero, based on the reticulate internal structure of the raphe valve with transapical pillars, and the presence of areolae arranged in rectangular sectors on the sternum valve, all clearly visible in LM. Another invalidly described taxon by Frenguelli & Orlando (1958), *Cocconeis reticulata* var. *deceptionensis* Freng. & H.A.Orlando, was considered a heterotypic synonym of *Cocconeis orbicularis* (Riaux-Gobin et al. 2019). SEM analyses of *Cocconeis orbicularis* from Potter Cove, King George Island, showed that *Campyloneis frenguelliae* possesses a combination of unique features, including the hollow structure of the raphe valve valvocopula, presence of marginal multiple pores at the end of each sternum valve stria and differentiation of two areolation patterns on the raphe valve, and it was transferred to a new genus, *Australoneis* (Guerrero et al. 2021).

Ecology and distribution – The ecology of *A. frenguelliae* is not well known, but it was originally found as an epiphyte on turf (Riaux-Gobin et al. 2019). In our samples, it was quite rarely observed, usually outside of the counts (table 2), and it was mostly recorded in the two samples, taken from the bottom sediments of Johnsons Dock at larger depths (> 20 m). A few valves were also present on artificial substrata and occasionally on cobbles in the intertidal zone (table 2); apparently the studied habitats and/or types of substrata were not typical for this species. Its currently known distribution includes the Maritime Antarctic (South Shetland Islands and South Orkney Islands) and south up to Melchior Archipelago (Riaux-Gobin et al. 2019), and the South Pacific Ocean (Chile) (Guerrero et al. 2021)

Brandinia charcotii (Perag.) Zidarova & P.Ivanov, **comb. nov.** (fig. 5)

Basionym – *Fragilaria charcotii* Perag., Diatomées d'eau douce et diatomées d'eau salée. In: Deuxième Expédition Antactique Française (1908–1910) commandée par le Dr. Jean Charcot: 68, Pl. III, figure 5. 1921. (Peragallo 1921: 68).

Brandinia mosimanniae L.F.Fernandes & Procopiak (Fernandes et al. 2007: 47, figures 1–6, 11–28).

Taxonomic history and remarks – The genus *Brandinia* L.F.Fernandes was separated from morphologically similar genera, such as *Fragilaria* Lyngb., *Ulnaria* (Kütz.) Compère, *Fossula* Hasle et al., and *Synedropsis* Hasle et al., in having

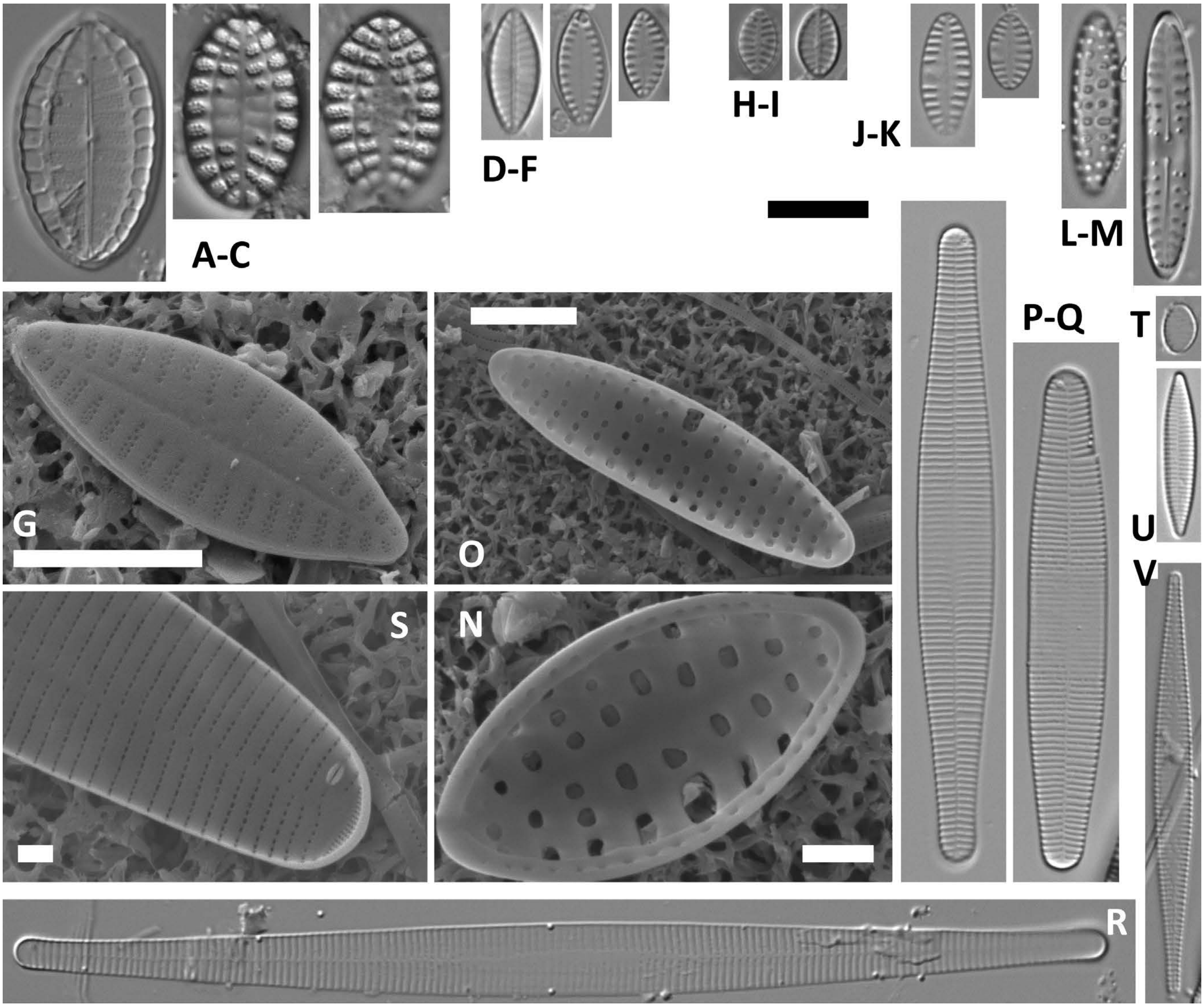

Figure 4 – **A**–**C**. *Australoneis frenguelliae*. **D**–**F**. *Achnanthes vicentii*. **G**. *Achnanthes vicentii*, SEM of a rapheless valve. **H**–**I**. *Planothidium* sp.1. **J**–**K**. *Planothidium* sp.2. **L**–**M**. *Achnanthes* sp.2. **N**. *Achnanthes* sp.2, SEM of an entire valve internally. **O**. *Achnanthes* sp.1, SEM of an entire valve internally. **P**–**R**. *Fragilaria* aff. *striatula*. **S**. *Fragilaria* aff. *striatula*, SEM of the apex internally with the rimoportula. **T**. *Fragilaria* sp.2. **U**. *Fragilaria* sp.1. **V**. *Fragilaria islandica* var. *adeliae*. Scale bars: A–F, H–M, P–R, T–V = 10 µm; G, O = 5 µm; N = 1 µm; S = 2 µm.

a combination of open girdle bands, two rimoportulae (one at each valve apex), and an ocellulimbus (Fernandes et al. 2007). The type species, *Brandinia mosimanniae* L.F.Fernandes & Procopiak, was found in the epilithon of Martel Bay, King George Island, and Elephant Island, Antarctica, and is still the only known species in the genus.

Based on the original description of *Brandinia mosimanniae* in Fernandes et al. (2007), it is a species having linear valves with "curved" or parallel margins, rounded to subcapitate apices, a narrow sternum with "opposing" striae; the central area is more or less rectangular, "masking or partially excluding the areolae". Valve dimensions and stria density of the species are quite variable: valve length 27–125.5 µm, width 7.5–10.8 µm, and 12–20 uniseriate striae in 10 µm. The valves possess two rimoportulae, one at each apex, visible in LM. The valves found at South Bay (fig. 5B–I) fit the description of the valves of the original *Brandinia mosimanniae*: valves (n = 25) are linear to linear-elliptic, with parallel to weakly convex margins in the middle, rostrate or subcapitate apices, and having a narrow sternum with "opposing striae" (Fernandes et al. 2007), a large more or less rectangular central area with faint striae, and one rimoportula at each apex; valve dimensions and stria density fit the range, given for the original *Brandinia mosimanniae*: a valve length of 42.5–77.2 µm, width of 7.0–8.7 µm, and 14–17 striae in 10 µm (see above).

When describing *Brandinia mosimanniae*, Fernandes et al. (2007) compared their new taxon with only *Fragilaria striatula* Lyngb. as the most similar species. However, in 1921 Peragallo described another *Fragilaria* species, named *F. charcotii* Perag. from Iles Argentines. The original description of this species is given on page 68 in his work: "Valve longuement elliptique, à extrémités rostrées, capitées, pseudo-raphé invisible. Stries transversales faibles, non

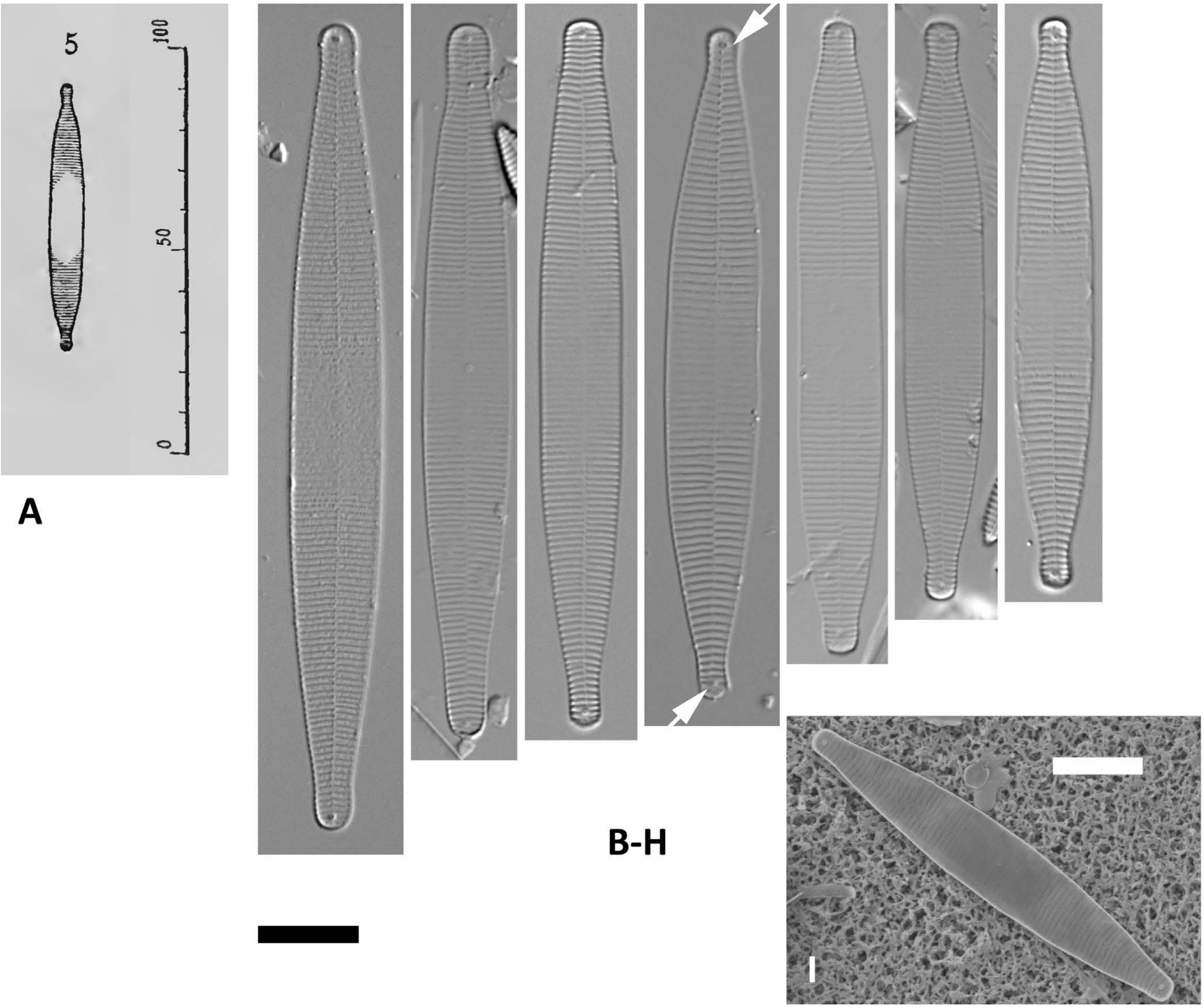

Figure 5 – *Brandinia charcotii*. **A**. Reproduction of the original drawing of *Fragilaria charcotii* in Peragallo (1921: Pl. III, figure 5). **B**–**H**. LM view of several valves of *Brandinia charcotii* (= *Brandinia mosimanniae*) from South Bay, Livingston Island. Arrows indicate the typical for *Brandinia* rimoportulae at the valve apices. **I**. SEM view of an entire valve internally with the rimoportulae at the apices. Scale bars: A = 100 µm (original scale bar in Peragallo 1921); B–I = 10 µm.

visiblement granulées, laissant au centre de la valve un area elliptique touchant les bords et dont la longueur est d'environ un tiers de celle de la valve. Longueur 60–65 µ; largeur 8 µ; 14 à 15 stries en 10 µ". Peragallo (1921) provided a drawing of this species as well, which is reproduced here on fig. 5A. The presented valve is linear elliptic, with subcapitate apices, as in *Brandinia mosimanniae* (see above), with dimensions and stria density exactly into the range of both our populations of *Brandinia mosimanniae* and its type (i.e. length 60–65 µm, width 8 µm, 14–15 striae in 10 µm, see above for the type and our populations). *Fragilaria charcotii* also has the same striation pattern as in the valves from the South Shetland Islands, although Peragallo was unable to see the "masking striae" in the central area and to recognize the rimoportulae at that time (fig. 5 for comparisons). No SEM studies are available for *F. charcotii* (and Peragallo's material seems to be lost, Bart Van de Vijver, pers. comm.), but based on the comparisons of the original Peragallo's drawing and description of the species, with the populations identified as *Brandinia mosimanniae* from South Bay and the original description of the latter (Fernandes et al. 2007: figures 1–6, 11–13, see above), there is no doubt that these two species are conspecific. In this sense, the name *Brandinia mosimanniae* is a later heterotypic synonym of *Fragilaria charcotii*. The latter name would have priority over the name *Brandinia mosimanniae*, but the affiliation to the genus *Fragilaria* is apparently incorrect. Therefore, we propose a new combination for this taxon: *Brandinia charcotii* (Perag.) Zidarova & P.Ivanov.

Ecology and distribution – *Brandinia charcotii* was often found in the samples, including on the artificial substrata during the initial stages of colonization (Zidarova et al. 2020), but it was most abundant on the sides of large coastal rocks and on the sides and bottom of tidal pools (table 2). Apart from observations in the epilithon (Fernandes et al. 2007), the species is also present in the Antarctic marine epiphyton, although in small numbers (< 1.6% of the counted valves; Majewska et al. 2013, 2015, 2016). It has an apparently wide distribution on the Antarctic marine coasts, from the South Shetland Islands (Fernandes et al. 2007; Majewska et al. 2015; Zidarova et al. 2020) to the islands around the Antarctic Peninsula (Peragallo 1921) and further south to the Ross Sea (Majewska et al. 2013, 2016). In Adélie Land, Frenguelli & Orlando (1958) and Frenguelli (1960) erroneously identified and reported *Brandinia charcotii* as *Fragilaria bongrainii* Perag. and "*F. bongrainii* var. *planctonica* Heiden & Kolbe" (Frenguelli & Orlando 1958: Pl. IV, figures 17–20), the latter being actually an errounesly reported *Fragilaria planctonica* Heiden (see under *Fragilaria* aff. *striatula* below).

Fragilaria* aff. *striatula Lyngb. (fig. 4P–S)

(*Grammonema* aff. *striatula* (Lyngb.) C.Agardh)

Taxonomic remarks – The Antarctic populations of this species are reported in the Antarctic literature with several different names, reflecting the histories of its numerous discoveries. The most commonly used name is perhaps *Synedra kerguelensis* Heiden (e.g. *Synedra* cf. *kerguelensis* in Zidarova et al. 2020), although it is a later heterotypic synonym of *Fragilaria bongrainii*. When studying the types of Heiden in Heiden & Kolbe (1928), Simonsen (1992) noted the presence of a single rimoportula at one of the valve apices in both *S. kerguelensis* and another taxon, *Fragilaria planctonica*, as well as the overlapping number of striae in 10 µm between the two (originally given as 15–18 in 10 µm in *F. planctonica* and 12–18 µm in *S. kerguelensis*). Therefore, Simonsen (1992) concluded that *S. kerguelensis* and *F. planctonica* are conspecific, proposing the inclusion of several other taxa within *F. planctonica* as well: the Antarctic *F. bongrainii*, *F. californica* var. *antarctica* Perag., *S. kerguelensis* var. *antarctica* Freng. & H.A.Orlando, *F. bongrainii* var. *planctonica* (Heiden) Freng. & H.A.Orlando, and *S. camtschatica* var. *antarctica* sensu Krebs (non sensu Manguin 1960), an opinion that seems correct. However, Simonsen (1992) observed a much larger range in the stria density in *S. kerguelensis* and *F. planctonica*, reporting up to 27 striae in 10 µm for the valves from Heiden's populations. This range, to some extent, overlapped with the range reported for another morphologically similar *Fragilaria* species, *F. striatula*. Based on the stria density and the overall morphological similarity between the Antarctic populations in the Heiden's material and *F. striatula*, the latter examined by Hasle & Syversten (1981) and having 17–28 striae in 10 µm, Simonsen (1992) concluded that *F. planctonica* and related Antarctic taxa should in fact be all included within *F. striatula*. Later, Cremer et al. (2003) also suggested that *F. striatula* and *S. kerguelensis* (a later synonym of *F. planctonica*) might be conspecific. However, Simonsen (1992) noted that the valves having a coarser striation, i.e. a smaller number of striae in 10 µm, also have more the outline of Heiden's *F. planctonica* with slightly capitates apices, whereas the finely striated valves had more linear valve outline, as in *S. kerguelensis*. At South Bay, both slender valves with a coarser striation and slightly capitates apices, similar to Heiden's *F. planctonica* were observed, as well as linear valves with more bluntly rounded apices, more as in *F. striatula* and Heiden's *S. kerguelensis* (figs 4P–S). So far, we have not found valves with more than 17–18 striae, and our populations better fit the original Antarctic populations, named *F. bongrainii* or *S. kerguelensis*. More studies are needed in order to clarify whether all Antarctic populations indeed belong to *F. striatula*.

Ecology and distribution – *Fragilaria* aff. *striatula* is a widespread benthic species all over the Antarctic marine coasts, found in almost all studies from the region and reported either as *Fragilaria striatula* or *Synedra kerguelensis*. It is known to form spring blooms on stones and rocks (Klöser 1998; Bae et al. 2021), but is also related to the sea ice and possibly an indicator for cooler waters (Cremer et al. 2003). At South Bay, *Fragilaria* aff. s*triatula* was present on almost all substrata, but it was most abundant in tidal pools (table 2).

Parlibellus variabilis (Heiden) Simonsen (fig. 9S–T)

Taxonomic history – The species was described by Heiden in Heiden & Kolbe (1928) as *Libellus variabilis* Heiden. Cox (1988) doubted its placement in *Parlibellus* E.J.Cox, but suggested that it could belong to *Scoliotropis* Cleve instead. Simonsen (1992), analyzing Heiden's material, disagreed with this opinion, because the species does not show the typical valve symmetry of *Scoliotropis*, but possesses numerous copulae with double rows of areolae typical for *Parlibellus*, although the areola arrangement as in *Parlibellus* could not be observed. The few valves found at South Bay fit the description in Simonsen (1992).

Ecology and distribution – At South Bay, the species was extremely rare, found on the bottom sediments in Johnsons Dock (table 2). We were unable to find other records of this taxon, except from its type locality.

Pinnularia parallelimarginata Simonsen (fig. 10H–I)

Taxonomic history and remarks – This is another enigmatic species, also described by Heiden in Heiden & Kolbe (1928), as *P. parallela* Heiden. A new specific epithet was later given by Simonsen (1992) because the epithet *parallela* was already taken. As noted by Simonsen (1992), with its fine striation and somewhat dorsiventral, i.e. apically asymmetrical valves and eccentrically placed raphe, it belongs neither to *Pinnularia*, nor to *Caloneis*. No SEM observations for this taxon are available at present, and its accurate generic affiliation remains unclear.

Ecology and distribution – *Pinnularia parallelimarginata* was extremely rare in our samples, with only a few valves found on bottom sediments in Johnsons Dock (table 2). The literature search yielded no other records, except from the original locality, Kerguelen Archipelago, Southern Indian Ocean. Its finding in the Southern Atlantic Ocean suggests it has a wider geographic distribution range.

Tabulariopsis australis (Perag.) D.M.Williams (fig. 6B–E)

Taxonomic history – This species was discovered in Antarctica by Peragallo (1921) and described as *Ceratoneis australis* Perag. based on the features of its central area and

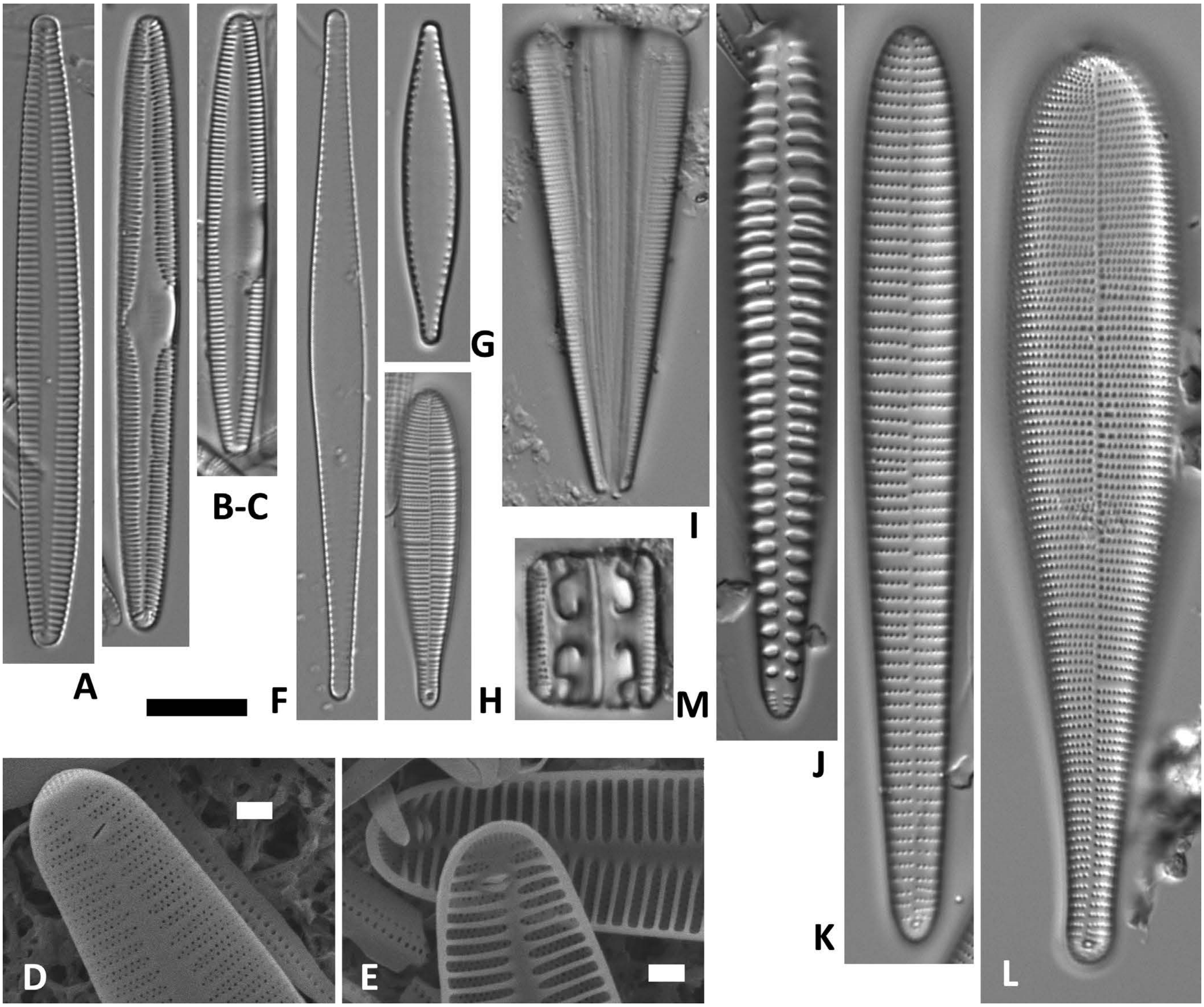

Figure 6 – **A**. *Tabularia* sp. **B**–**C**. *Tabulariopsis australis*. **D**. *Tabulariopsis australis*, SEM, valve apex with the external opening of the rimoportula. **E**. *Tabulariopsis australis*, SEM, valve apices internally with rimoportula. **F**. *Synedropsis fragilis*. **G**. *Synedropsis recta*. **H**. *Licmophora gracilis*. **I**. *Licmophora gracilis*, girdle view in LM. **J**. *Licmophora luxuriosa*. **K**. *Licmophora antarctica*. **L**. *Licmophora belgicae*. **M**. *Grammatophora* sp. (girdle view). Scale bars = A–C, F–M =10 µm; D–E = 2 µm.

striation in LM. Following the examination of materials from Heard Island, containing the same taxon, and based on the combination of biseriate striae, the shape and size of the ocellulimbus, and the unilateral central area, it was placed in a new genus, *Tabulariopsis*, by D.M.Williams in 1988. The Peragallo's variety *gracilis* was also included within the synonymy of the species.

Ecology and distribution – Due to possible misidentification with either *Fragilaria* or *Tabularia* species, the ecology of *T. australis* is not well known. Williams (1988) suggested that the species is an epiphyte but we have found it abundantly in tidal pools (table 2), often together with diatoms forming mucilage colonies, i.e. *Melosira* spp., *Parlibellus rhombicus*, and *Tripterion margaritae*. It is possible that it lives attached on their mucilage as well, as observed for other fragilarioid diatoms (Houpt 1994). Although not often reported, *T. australis* seems to have a wide distribution range in the Southern Ocean, from the Southern Indian Ocean (Heard Island) to the Maritime Antarctic Region (Klöser 1998; Fernandes et al. 2014b; Bae et al. 2021) and the Antarctic Peninsula area (Peragallo 1921).

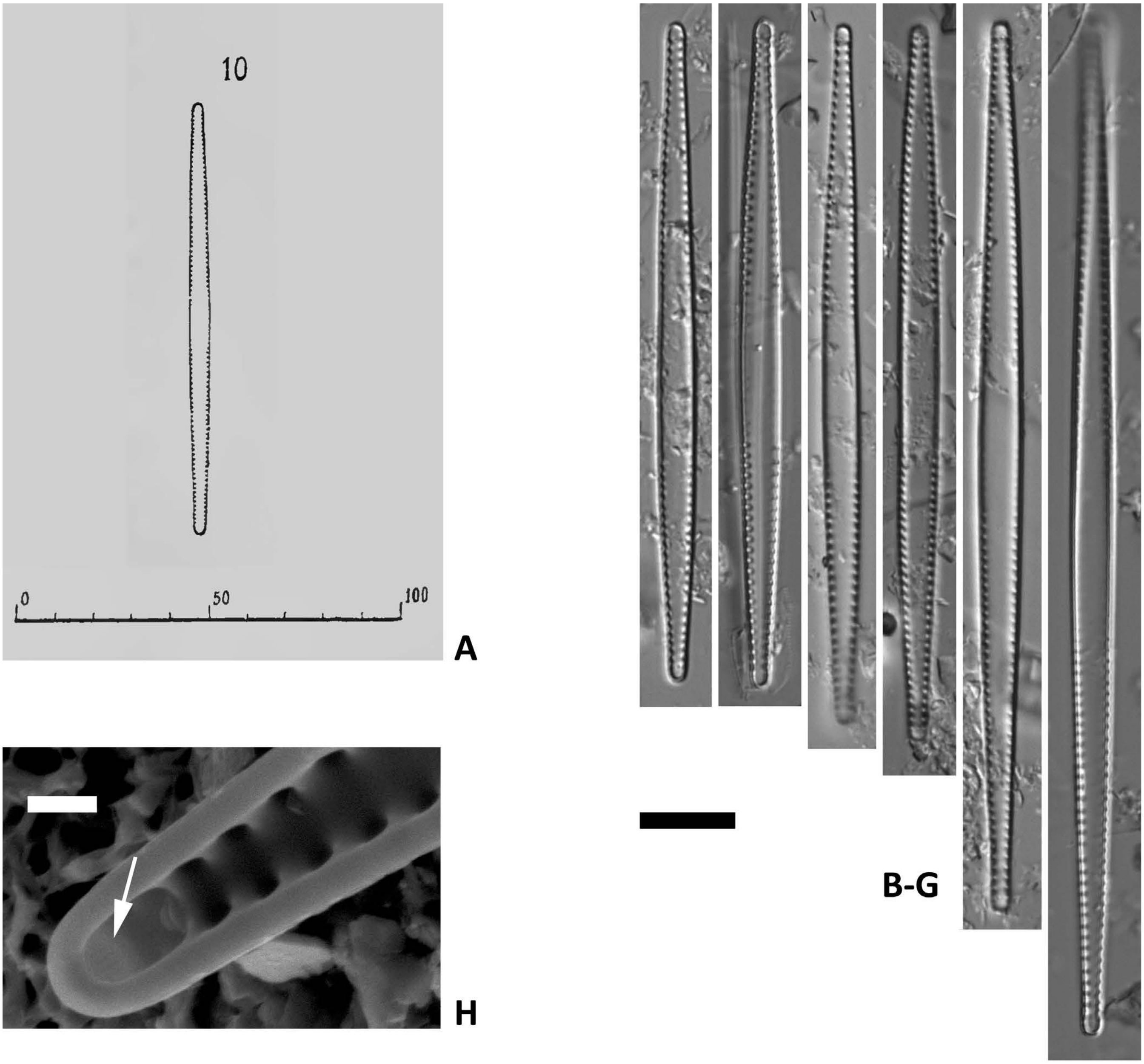

Figure 7 – *Thalassionema gelida*. **A**. Reproduction of the original drawing of *Thalassionema gelida* in Peragallo (1921: Pl. III). **B**–**G**. LM view of several valves from South Bay, Livingston Island. **H**. SEM view of a valve apex internally of a valve from the South Bay population, with the rimoportula clearly visible. Arrow points to the faintly visible, but clearly present ocellulimbus. Scale bars: A = 100 µm (original scale bar in Peragallo 1921); B–G = 10 µm; H = 1 µm.

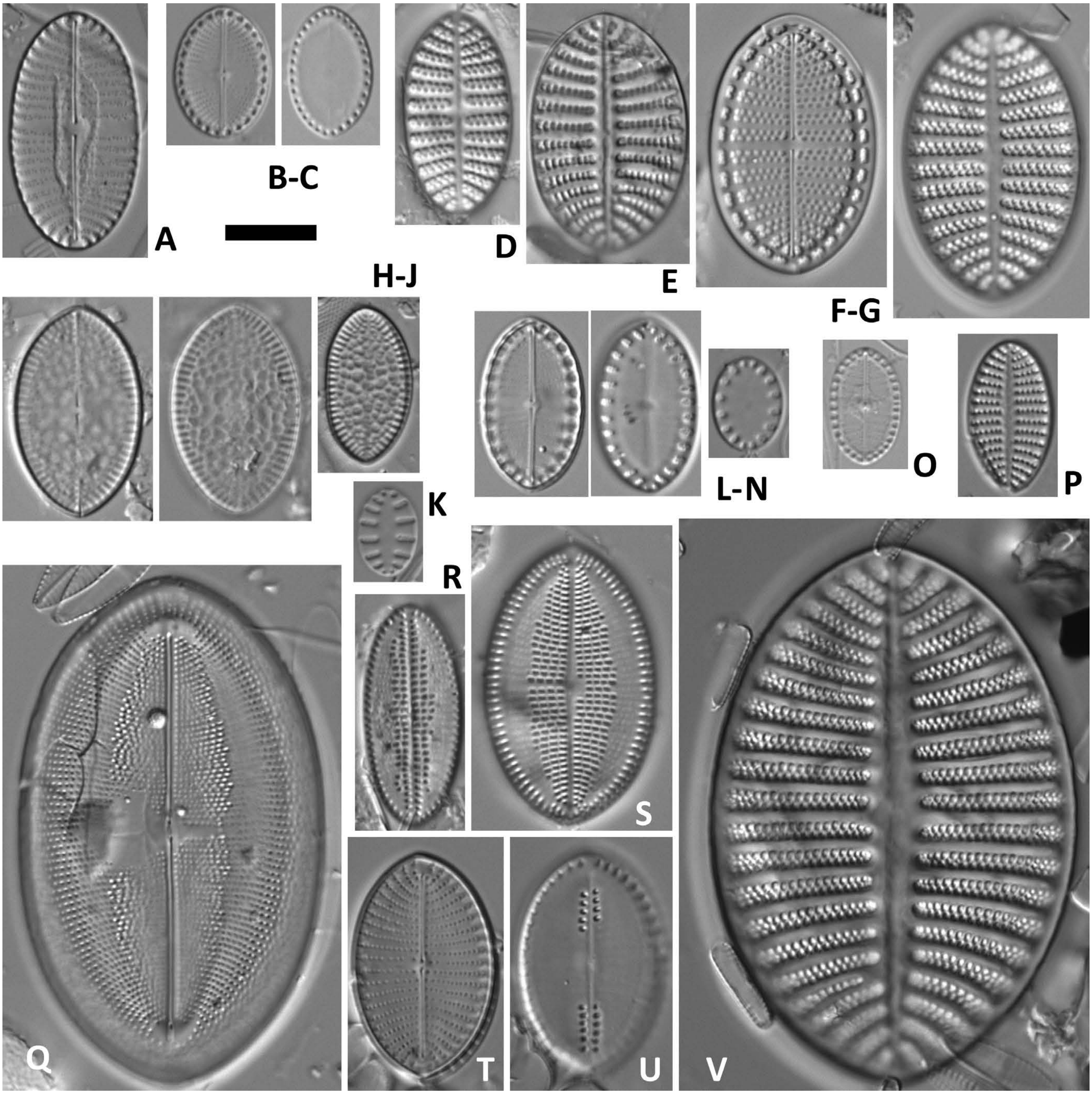

Figure 8 – **A**. *Cocconeis* sp.3. **B**–**C**. *Cocconeis dallmannii*. **D**. *Cocconeis costata*. **E**. *Cocconeis* sp.6. **F**–**G**. *Cocconeis fasciolata*. **H**–**J**. *Cocconeis* sp.1. **K**. *Cocconeis matsii*. **L**–**N**. *Cocconeis melchioroides*. **O**. *Cocconeis pottercovei*. **P**. *Cocconeis gausii*. **Q**. *Cocconeis antiqua*. **R**. *Cocconeis californica* var. *kerguelensis*. **S**. *Cocconeis californica*. **T**–**U**. *Cocconeis californica* var. *antarctica*. **V**. *Cocconeis imperatrix*. Scale bar = 10 µm.

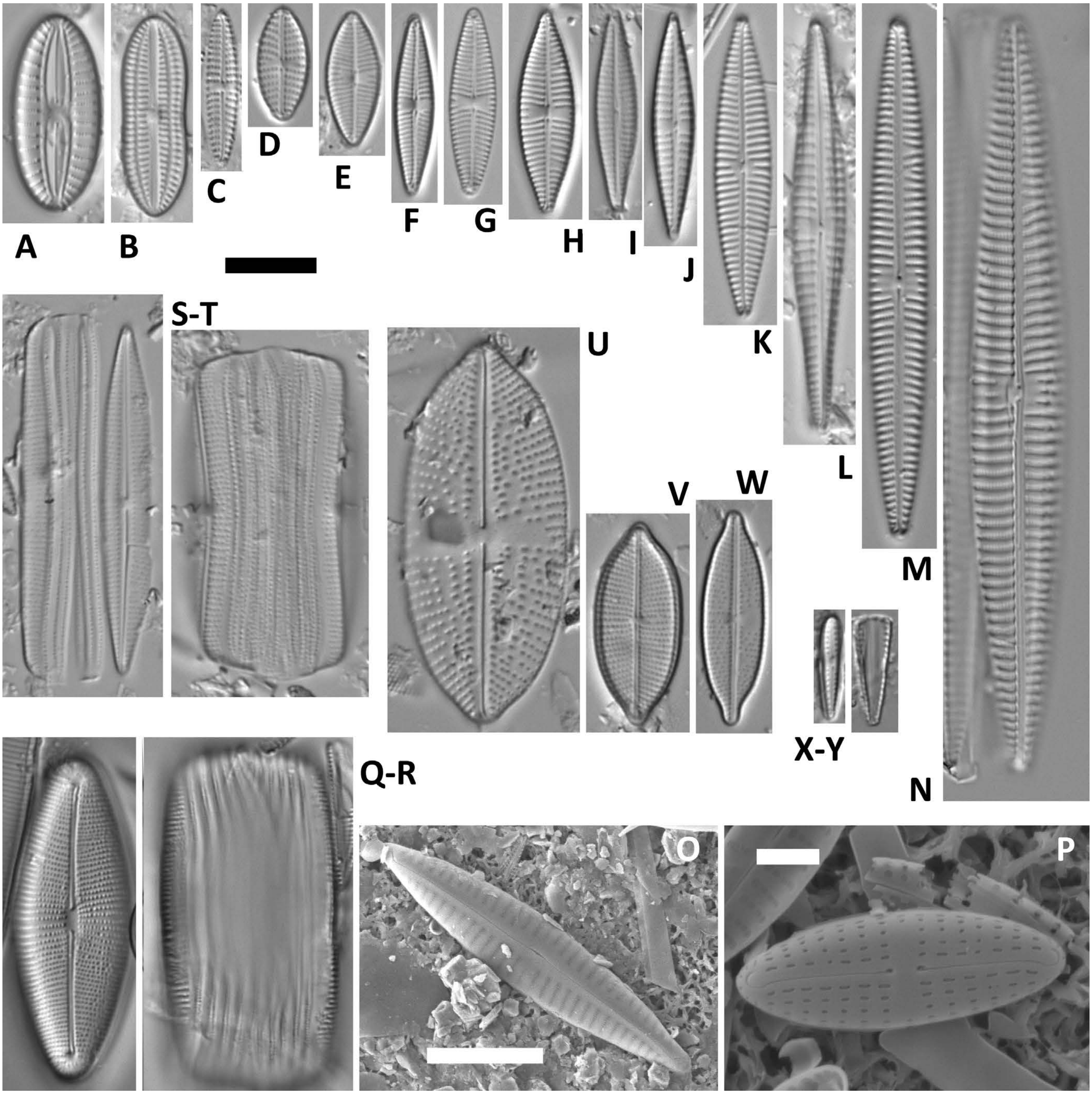

Figure 9 – **A**. *Fallacia marnieri*. **B**. *Diploneis* sp. (*D. sejunta* var. *constricta* sensu Cremer et al. 2003). **C**. *Navicula* aff. *perminuta*. **D**. *Navicula* sp.4. **E**. *Navicula* sp.5. **F**. *Navicula* sp.2. **G**. *Navicula* sp.3. **H**. *Navicula glaciei*. **I**. *Navicula* sp.7. **J**. *Navicula* sp.1. **K**. *Navicula criophiliforma*. **L**. *Navicula* cf. *hippodontaformis*. **M**. *Navicula jejunoides*. **N**. *Navicula directa*. **O**. *Navicula* cf. *hippodontaformis* (SEM, entire valve externally). **P**. *Navicula* aff. *perminuta* (SEM, entire valve, externally). **Q**–**R**. *Parlibellus rhombicus* sensu Van Heurck (1909), valve view and girdle view with the typically numerous copulae. **S**–**T**. *Parlibellus variabilis*, valve view and girdle view with numerous copulae. **U**. *Petroneis* sp.1 (cf. *Navicula cluthensis* var. *lanceolata*). **V**. *Petroneis* aff. *plagiostoma*. **W**. *Petroneis* sp.2. **X**–**Y**. *Gomphonemopsis ligowskii*. Scale bars: all LM (A–N, Q–R) and O = 10 µm; P = 2 µm.

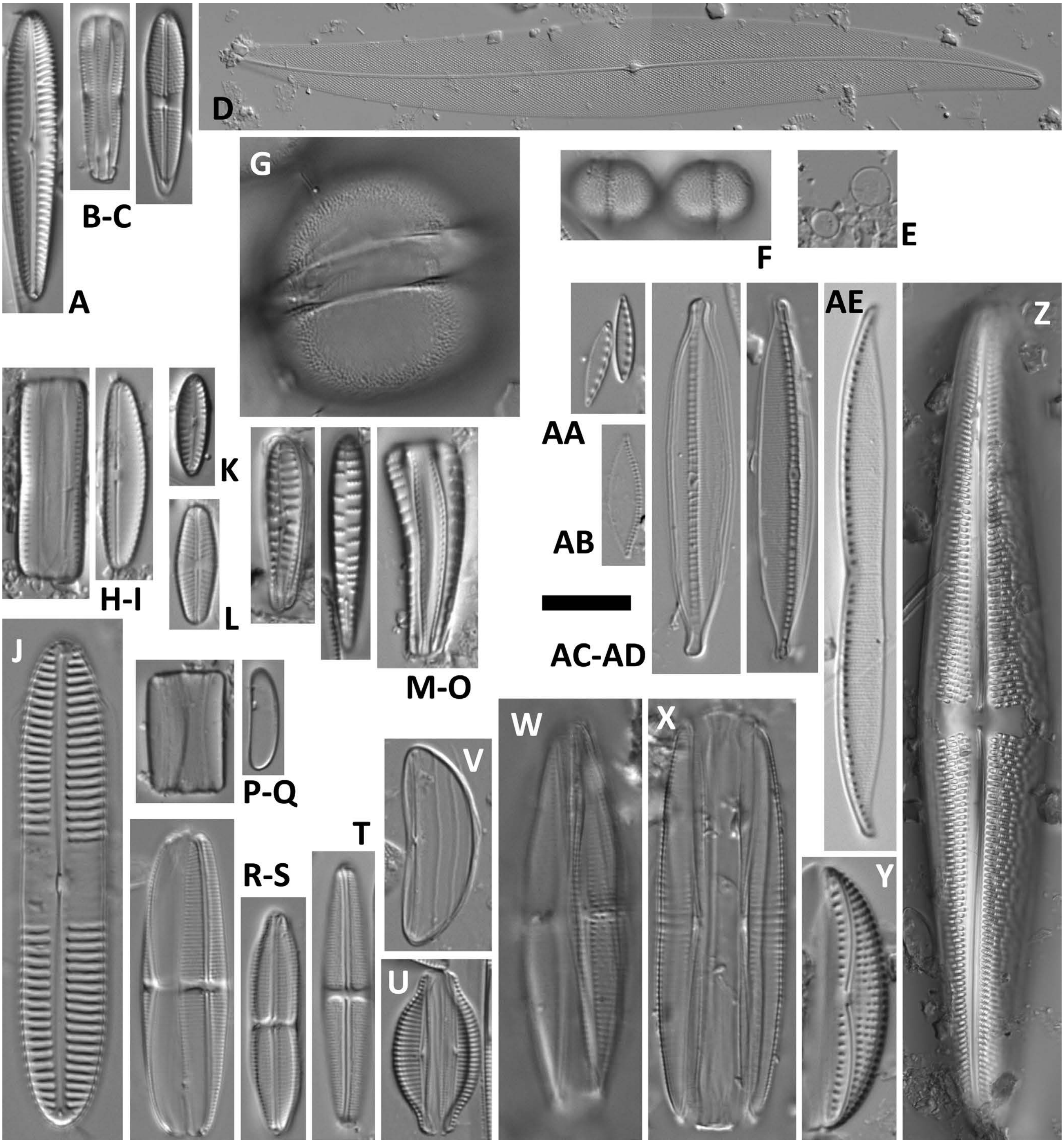

Figure 10 – **A**. *Pseudogomphonema kamtschaticum*. **B**–**C**. *Tripterion margaritae*. **D**. *Pleurosigma* sp. **E**. *Minidiscus* sp. **F**. *Melosira* sp. **G**. *Melosira brandinii*. **H**–**I**. *Pinnularia parallelimarginata*, girdle view and valve view. **J**. *Pinnularia quadratarea*. **K**. Unidentified gomphoneid diatom. **L**. Unidentified naviculoid diatom 2. **M**–**O**. *Rhoicosphenia michalii*. **P**–**Q**. *Pteroncola carlinii*. **R**–**S**. *Craspedostauros* sp. **T**. *Craspedostauros laevissimus*. **U**. *Amphora* (sensu lato) sp.5. **V**. Unidentified amphoroid diatom. **W**. *Amphora lunula* var. *parvula*. **X**. *Amphora* cf. *biarcuata*. **Y**. *Amphora gourdonii*. **Z**. *Trachyneis* cf. *aspera*. **AA**. *Nitzschia* sp.7. **AB**. *Nitzschia* sp.3. **AC**–**AD**. *Nitzschia* sp.4. **AE**. *Nitzschia* sp.1. Scale bar: A–C, E–Y, AA–AE = 10 µm; D, Z = 20 µm.

Thalassionema gelida Perag. (fig. 7)

Synedra camtschaticum var. *antarctica* Manguin (1960: 300, Pl. 13, figures 139–140), **syn. nov.**

Taxonomic history – Mann (1937) transferred this species to *Synedra*, stating that (at that time) "there is no reason for considering this species other than a normal *Synedra*". Since the time of Mann (1937), there have been many uncertainties around the genus *Synedra* and many genera, especially the marine ones, were separated from the genus (Williams & Round 1986; Williams 2011). Considering the marine origin of the species and the needle-shaped valves with short marginal striae, i.e. marginal areolae in LM (Hallegraeff 1986), the original affiliation to the genus *Thalassionema*, as given by Peragallo (1921), seemed more appropriate. However, we were able to observe in SEM one valve end of this species internally, and it certainly possesses a large, well-developed rimoportula on the valve face close to the apex, but also an ocellulimbus (fig. 7H), suggesting an affiliation to other araphid needle-shaped genera, such as *Catacombas* D.M.Williams & Round (Williams & Round 1986). Further, Manguin (1960) described *Synedra camtschaticum* (*camtschatica*) var. *antarctica* Manguin from Adélie Land (non *S. camtschatica* var. *antarctica* sensu Krebs). Manguin's variety on his drawing (Manguin 1960: Pl. 13, figures 139–140) is quite similar to Peragallo's *Thalassionema gelida*. Peragallo's original taxon has a length of 100–120 µm and 8 striae in 10 µm. Peragallo (1921) did not provide any information for the valve width, but our measurements of the valve he depicted (Peragallo 1921, Pl. 3, figure 10) showed a length of 110 µm, a width of ca 5 µm, and 8–9 striae in 10 µm. Manguin's *S. camtschaticum* var. *antarctica* shows similar dimensions (valve length of 122 µm, width of 4.5–5 µm in the valve middle and 3.5 µm towards the apices, Manguin 1960: 300), but Manguin (1960) reported a higher stria density, 13 in 10 µm. The valves (n = 6) of *Thalassionema gelida* from South Bay had a length of 69 to 106 µm, width of 3.5 to 4.5 µm, while the stria density was variable and intermediate between the reported for Peragallo's and Manguin's species, 9–11 striae in 10 µm (fig. 7B–G). Taking into account the observations from South Bay and the original descriptions and drawings of the two taxa, *T. gelida* and *S. camtschaticum* var. *antarctica*, they seem conspecific, with the former name having priority. Therefore, we propose the inclusion of *Synedra camtschaticum* var. *antarctica* into the synonymy of *Thalassionema gelida*.

When describing *Catacombas*, Williams & Round (1986) transferred *Synedra camtschatica* Grunow and several of its varieties into the genus *Catacombas*, as *C. camtschatica* (Grunow) D.M.Williams & Round. They did not include the var. *antarctica* in the synonymy. Nevertheless, the valves of the Antarctic populations are smaller than those of *C. camtschatica*, which are both longer (above 120 µm) and broader (above 7 µm) according to Williams & Round (1986), and we propose to keep them as a separate entity, at present as *Thalassionema gelida*, till more observations in SEM are done and its generic affiliation to *Catacombas* is confirmed.

Ecology and distribution – Species of the genus *Thalassionema* are actually planktonic and are often found in the Antarctic (paleo)sediments (Tanimura et al. 2007). At present we do not know whether *T. gelida* is planktonic. It was only present in small numbers in the bottom sediment samples, taken inside Johnsons Dock (table 2). Since its discovery in 1921, it has rarely been reported in Antarctic studies. Peragallo (1921) found it on the coasts in the Antarctic Peninsula area (Iles Argentines, Ile Booth-Wandel, Ile Petermann), while north of the Peninsula, it is present in the near shore of the South Shetland Islands (King George Island, Fernandes et al. 2014b, and Livingston Island, this study). Southernmost, it was reported from Adélie Land by Frenguelli in Frenguelli & Orlando (1958). There are several records of a species, reported as *Catacombas camtschatica* (e.g. Klöser 1998 and references therein) from Antarctic sediments, and it is possible that these records actually represent *T. gelida*.

Tripterion margaritae (Freng. & H.A.Orlando) L.F.Fernandes & Sar (fig. 10B–C)

Taxonomic history – *Tripterion margaritae* is another species of Frenguelli & Orlando (1958, as *Gomphonema margaritae* Freng. & H.A.Orlando), validated by Fernandes & Sar (2009) with its transfer to the genus *Tripterion* R.W.Holmes et al.

Ecology and distribution – Frenguelli & Orlando (1958) described the species from a sample taken with a plankton net at Bahia Esperanza, but they reported it as frequent on coastal rock surfaces on islands of Melchior Archipelago. It was later also found living on rocks (Fernandes & Sar 2009). In our samples it was exclusively present on the bottom or sides of the tidal pools, sometimes reaching 20% of the counted valves, and completely absent so far from the other studied habitats (table 2). Based on the few existing historical records, and apart of the South Shetland Islands, the species is also present in the epilithon of the South Orkney Islands, and south to Melchior Archipelago (Frenguelli & Orlando 1958).

Diatom diversity and problems related to Antarctic marine benthic diatom species identification

Despite the use of a large number of taxonomic publications, we were unable to identify a large number of taxa up to species level, while several others could only be provisionally identified. Although some of these taxa include monoraphid species, such as *Cocconeis* spp., for which the observation of a single valve in samples is not sufficient for their correct identification (Romero 2011), while other, often rare, species need further SEM analysis (i.e. some *Amphora*, *Navicula*, and *Nitzschia* species), the number of unidentified or uncertainly identified taxa remains high. The taxonomy of benthic marine diatom species in Antarctica is highly confused. During our literature survey for species identification, it quickly became clear that some of the taxa, in the past described from the Antarctic realm, have been re-described several times by different authors or even by the same author, as is the case for several species in the genus *Cocconeis* and related genera (e.g. Romero 2011; Riaux-Gobin et al. 2019), and subsequently reported in the literature with different names. Another problem, already noted by Al-Handal & Wulff (2008a) and Majewska et al. (2013), is the often sparse information provided in the original descriptions and illustrations of the taxa in the early Antarctic literature. These descriptions were, of course, solely based on LM observations due to the limited technical capabilities a hundred years ago. For a large number of small-celled or finely striated species, the observed and reported morphological details a hundred years ago are at present often insufficient for the clear separation of species. Therefore, a lot of uncertainty currently exists in species identities even for the most widespread Antarctic marine benthic taxa. A good example is *Navicula* aff. *perminuta*, reported in almost every study of the Antarctic marine benthic diatom flora. Apart from being a dominant species in the Antarctic epilithon, it has also been reported in high numbers living epizoically and epiphytically (Majewska et al. 2013; Bae et al. 2021). Despite the numerous reports, its exact identity is still unknown, as most probably it includes several taxa, or represents other species but not the original *Navicula perminuta* Grunow, as discussed by Al-Handal & Wulff (2008a) and Majewska et al. (2013). The species has also been reported as being highly morphologically variable (Al-Handal & Wulff 2008a; Majewska et al. 2013). It is not unlikely that in some studies other small-celled *Navicula* taxa have been included within *Navicula* aff. *perminuta*. Several small *Navicula* species were detected in this study, which, if present in small numbers, might have been included within the variability of *Navicula* aff. *perminuta* in other studies (e.g. fig. 9F, J). Finally, and strikingly, in our attempt to study a small number of samples with DNA metabarcoding, another enigmatic taxon, *Navicula vara* Hust. was identified with a high similarity with the reference sequence (over 99%) and a significant sequence number in addition to *N. perminuta* (Nina Dzhembekova, unpubl. res.). Further research on the small *Navicula* taxa, which are common for Antarctica, is definitely necessary to reveal their identities and real diversity.

The overall number of species recorded at South Bay is higher than the number reported from sediments, ceramic tiles, and rocks by Al-Handal & Wulff (2008a), who in a larger set of samples in near shore waters of Potter Cove, King George Island, only found 84 taxa (or 35% less compared to this study). Similarly, Bae et al. (2021) reported again a lower diatom diversity (92 species, or 30% less) from sediments, rocks, cobbles, macroalgae, and shells of limpets from Marion Cove of the same island. However, in both studies, tidal pools, hosting a diverse and specific diatom flora, were not surveyed. The number of recorded species from South Bay is comparable to the recent estimates from the stony littoral of King George Island (108 species, Ligowski 2002) and for the Antarctic epiphyton (109 species, Majewska et al. 2016), and proves the presence of a highly diverse (but still unknown) marine benthic diatom flora in the region.

CONCLUSION

Marine benthic diatom species show distinct distributions in the Antarctic coastal waters and habitats, but current knowledge of the species' identities is quite incomplete. Further research, including a thorough analysis of both the historical Antarctic literature and where possible the original materials of the early described Antarctic taxa is necessary in order to discover their identities, to be able to separate the so far unrecognized possibly new taxa, to solve the nomenclature problems, and to better understand the ecology and distribution of the diatom species from the Antarctic marine benthos.

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