Plant Ecology and Evolution 155 (1): 107–122, 2022
https://doi.org/10.5091/plecevo.84543

RESEARCH ARTICLE

Taxonomic and biogeographical analysis of diatom assemblages from historic bryophyte samples from Campbell Island (sub-Antarctic)

Charlotte Goeyers[1,2,*], Dale H. Vitt[3] & Bart Van de Vijver[1,2]

[1]Meise Botanic Garden, Research Department, Meise, Belgium
[2]University of Antwerp, Department of Biology, ECOSPHERE, Wilrijk, Belgium
[3]Southern Illinois University, School of Biological Sciences-Plant Biology, Carbondale, Illinois, United States of America
*Corresponding author: charlotte.goeyers@plantentuinmeise.be

Background and aims – The past two decades, the non-marine diatom flora in the sub-Aantarctic region has been intensively revised. Historic collections provide excellent tools for answering taxonomic, community-related, and biogeographical questions. This study analysed the moss-inhabiting diatom flora from sub-Antarctic Campbell Island in samples collected in 1969–1970 and retrieved from the British Antarctic Survey herbarium (Cambridge, UK). With this study we attempt to expand our, till now sparse, knowledge on the moss-inhabiting diatom flora in the southern Pacific Ocean.

Material and methods – In total, the diatom composition in 32 moss samples has been analysed using Light Microscopy (LM) and Scanning Electron Microscopy (SEM). A biogeographical analysis and community analysis of the Campbell Island diatom flora were conducted.

Key results – Analysis of the Campbell Island diatom flora revealed the presence of 141 taxa belonging to 45 genera. The species composition in the dominant genera *Planothidium*, *Humidophila*, and *Psammothidium*, the presence of *Epithemia*, *Rhopalodia*, *Cocconeis*, uncommon in the sub-Antarctic region, and many unidentified taxa point to the uniqueness of the Campbell Island diatom flora. The biogeographical analysis showed an overall low similarity with the other sub-Antarctic and the Maritime Antarctic islands. Four different diatom assemblages were distinguished following the community analysis. Moisture level and habitat type seem to be the main factors shaping the Campbell Island diatom assemblages.

Conclusion – The results of the Campbell Island diatom analysis highlight the importance of historic herbarium material. Since the examined flora is largely composed of unknown (presumably new) species, it is vital to analyse additional (historic) samples to complete the assessment of the moss diatom assemblages from Campbell Island.

Keywords – Antarctic realm; bryophytes; Campbell Island; diatoms; Maritime Antarctica; moss; new species; sub-Antarctica.

INTRODUCTION

Over the last two decades, there has been a growing interest in the taxonomy, ecology, and biogeography of the non-marine diatom assemblages in the Antarctic realm. This is not surprising, since diatoms are one of the most abundant and diverse algal groups in the Antarctic region (Jones 1996; Van de Vijver & Beyens 1999b; Verleyen et al. 2021). These extensive surveys and revisions greatly improved and increased our knowledge. The generally accepted view of diatoms being cosmopolitan had to be (partially) abandoned, and the non-marine Antarctic diatom flora proved to be highly unique (Vyverman et al. 2007; Verleyen et al. 2021), indicated by the presence of many endemic species (Van de Vijver et al. 2002a; Zidarova et al. 2016 and references therein). These studies also indicate that the non-marine Antarctic diatom flora shows a high degree of bioregionalism,

Plant Ecology and Evolution is published by Meise Botanic Garden and Royal Botanical Society of Belgium
ISSN: 2032-3913 (print) – 2032-3921 (online)

with large differences in species composition between the different parts of the Antarctic realm (sub-Antarctic Islands, Maritime Antarctic Region, Antarctic Continent) (Verleyen et al. 2021).

Since Polar ecosystems are expected to show large environmental shifts due to global change, these regions are important study areas to investigate long-term ecosystem changes (Pienitz et al. 2004). Although diatoms are excellent bio-indicators, their use depends on a thorough knowledge of their diversity and taxonomy. As historical force-fitting (Tyler 1996) and outdated taxonomy led to incorrect identifications in the past, a revision of the Antarctic diatom flora remains highly necessary. Despite the increased taxonomic effort, mainly concentrated on the islands in the southern Indian Ocean (Van de Vijver et al. 2002a) and the Maritime Antarctic Region (Zidarova et al. 2016), there are still considerable gaps in our knowledge on non-marine Antarctic diatoms. The islands in the southern Pacific Ocean, such as the Auckland Islands, Campbell Island, Macquarie Island, Antipodes Islands, Snares Islands, and Bounty Island, have received far less attention. Apart from the Australian Macquarie Island, the remote islands belonging to New Zealand are only very infrequently visited, resulting in a serious undersampling of the diatom flora.

The Macquarie Island diatom flora received most of the attention, with the oldest publication dating back to 1954 when Bunt recorded 64 terrestrial diatoms, most of which considered cosmopolitan or marine (Bunt 1954). Eighty-three diatom taxa were recorded by Evans (1970) in the lakes of Macquarie Island. In these first studies, pH and salinity input by sea spray were hypothesised to be the main factors shaping the diatom assemblages. McBride et al. (1999) used 131 non-marine diatom taxa to reconstruct the history of Macquarie's water bodies (McBride & Selkirk 1999; McBride et al. 1999). Ten years later, Saunders et al. (2009) recorded 208 benthic diatom species from 34 genera from 50 coastal and inland lakes, while McBride (2009) identified 102 species from 34 genera in 14 lakes and ponds. Campbell Island is even less studied. During a bryological visit in 1969–1970, one of the co-authors of the present paper (DV) visited the island and collected a large number of bryophyte samples in which 59 moss-inhabiting diatoms were observed (Vitt 1971; Hickman & Vitt 1974). The bryophyte samples were subsequently stored in the British Antarctic Survey Herbarium in Cambridge (UK). More than 40 years later, Saunders et al. (2015) assessed the aquatic diatom flora found in lakes and reported important differences with the nearby Macquarie Island diatom assemblages, despite a high floristic similarity between Campbell Island and the sub-Antarctic islands in the southern Indian Ocean (Van de Vijver et al. 2002a) and the diatom flora in the Tasmanian and New Zealand mountain lakes (Vyverman et al. 1995; Hodgson et al. 1997; Kilroy et al. 2007; John 2016a).

In 2019, the diatom flora in the historic moss samples collected in 1969–1970 was re-examined using a more fine-grained and updated taxonomy. This quickly led to the description of a handful of new species belonging to the genera *Psammothidium*, *Frankophila*, *Angusticopula*, *Ferocia*, and *Arcanodiscus* and a better taxonomic identity for several others (Van de Vijver 2019; Van de Vijver et al. 2019a, 2020a; Goeyers & Van de Vijver 2020a, 2020b).

The present study continues this reanalysis. In order to demonstrate the possible unique character of the diatom flora, its biogeographical links with the rest of sub-Antarctic region and nearby larger landmasses, 69 historic moss samples, retrieved during a visit to the British Antarctic Survey herbarium were analysed. The results will allow a better understanding of the biogeographical distribution and diversity of the sub-Antarctic diatom flora in the southern Pacific Ocean and highlight the importance of historic herbarium collections in answering taxonomic, community-related, and biogeographical questions.

MATERIAL AND METHODS

Study area and sampling

Campbell Island (52°33.7′S, 169°09′E) is a small island situated 700 km south of the New Zealand mainland (Clark & Dingwall 1985). The island is an eroded remnant of extensive Oligocene to Miocene basaltic volcanism (Quilty 2007) and is covered with large peat deposits, up to 10 m thick (Rainsley et al. 2019). A cloudy, moist, and cool climate prevails with minimal sunshine (Thorn 2008). The island has a total surface of 113 km^2 and reaches an elevation of 569 m. More details on the climate, geomorphology, and vegetation of the island can be found in Saunders et al. (2015).

Approximately 1,100 specimens representing 123 taxa of mosses were collected as part of an expedition between December 1969 and January 1970 with the support of the National Science Foundation (USA) (Vitt 1974) (see fig. 1 for the sampling locations on Campbell Island). During a visit to the moss herbarium at the British Antarctic Survey collection (Cambridge, UK) in 2018, 69 of these historic bryophyte samples were selected based on the descriptions present on the labels, taking into account the availability of sufficient material for subsampling. Only samples showing an indication of moisture presence (e.g. waterfalls, seepage areas, streams) were chosen and included specimens collected from sea level to 550 m elevation and from all three of the physiographic zones present on the island (Vitt 1991). Specimen selection included material from habitats ranging from continuously wet (e.g. waterfalls) to those that are periodically dry (e.g. cliff faces). Although diatom presence was not analysed with SEM or light microscopy during the sampling campaign in 1969–1970, light microscope images of diatom occurrence as epiphytes on moss stems and leaves were shown by Hickman & Vitt (1974).

Sample treatment and diatom counting

Subsamples of the selected material were prepared for light microscopy (LM) following the method described in van der Werff (1955). Small parts of the subsamples were cleaned by adding 37% H_2O_2 and heating to 80°C for one hour. The reaction was completed with the addition of saturated $KMnO_4$. After digestion and centrifugation (3 times 10 minutes at 3700 g), the resulting cleaned material was diluted with distilled water to avoid excessive concentrations of diatom valves. Cleaned valves were mounted in Naphrax®. Samples and slides are stored in the BR collection (Meise, Belgium). Slides were analysed using an Olympus BX53 microscope, equipped with Differential Interference Contrast (Nomarski) and a UC30 camera connected to the Cell Sense Standard program. For each slide, 400 diatom valves were identified and enumerated on random transects at 1000× magnification.

For scanning electron microscopy, stubs were prepared by filtering drops of the oxidized suspension through 5 µm pore polycarbonate membrane filters (Whatman Cyclopore PC circles, 25 mm diameter). The filters were air-dried, and pieces were affixed to 12.7 mm aluminium specimen (Agar) stubs covered with double sided carbon stickers (Agar Carbon Tabs). The stubs were placed in a high-resolution fine sputter coater for FE-SEM (JFC-2300HR Coating Unit, JEOL) and coated with a layer of approximately 10 nm platinum (using Argon-gas under 0.05 mbar pressure). The SEM observations were performed using a JEOL JSM-7100FLV Field Emission SEM (at 1 kV and a working distance of 3.5–6.0 mm) and were used to help in the identification of taxa.

The identification of Antarctic and sub-Antarctic species was based on the following publications: Foged (1979); Lange-Bertalot & Moser (1994); Vyverman et al. (1995); Krammer (2000); Lange-Bertalot (2001); Van de Vijver et al. (2002b, 2004, 2011, 2013, 2014a, 2014b, 2016, 2017a, 2019b); Werum & Lange-Bertalot (2004); Flower (2005); Esposito et al. (2008); Sterken et al. (2015); John (2016a, 2016b); Zidarova et al. (2016); Van de Vijver (2019).

Figure 1 – Sampling locations on Campbell Island. The numbers are the numbers given to the moss samples that were collected during the 1969–1970 field campaign. Map created with Adobe PhotoShop.

Data analysis

The taxon richness per sample, the frequency classes of taxa occurrence, and the relative abundances of the taxa and genera in the Campbell Island samples were calculated in R v.1.4.1106 (R Development Core Team 2020). For a pairwise comparison of the Campbell Island diatom flora with similar assemblages in the sub-Antarctic Region (islands in the southern Indian and Atlantic Ocean) and the Maritime Antarctic Region (Livingston Island and James Ross Island), the community coefficient of Sørensen (1948) was used. This index has the following formula: 2c/(a+b+2c) where 'a' and 'b' are the numbers of species exclusively observed in each of the two sites and 'c' is the number of species shared by these sites. The comparison is based on the revised species lists of South Georgia (Van de Vijver & Beyens 1997b), Iles Kerguelen (Van de Vijver et al. 2001), Iles Crozet (Van de Vijver et al. 2002b), Heard Island (Van de Vijver et al. 2004), the Prince Edward Islands (Van de Vijver et al. 2008), and Livingston and James Ross Island (Kopalová et al. 2014).

To assess the biogeographical origin of the Campbell Island diatom flora, the geographic distribution of the observed taxa was determined based on literature. When the identity of a taxon could not be determined, this was shown using 'cf.' or 'spp.' and its distribution was listed as unknown (U). For Antarctic species (indicated as 'A'), the geographic distribution was further split in 'SA' when the species occurred only in the sub-Antarctic Region and 'SA/MA' when the taxon was present in both the sub-Antarctic and Maritime Antarctic Region. 'SH' indicates taxa that are present in the entire Southern Hemisphere and cosmopolitan taxa are indicated by 'C'.

To determine to which extent our sampling effort represented the total diatom flora of the island, the incidence-based species richness estimator (ICE; Chao et al. 2000) and the mean Chao2 richness estimator (Chao 1984) were calculated, both using the EstimateS program v.9.0 (Colwell 2013). The Shannon-Wiener diversity index (log10-based) and Hill's evenness index were used to assess the taxon diversity and were calculated using the statistical package MVSP v.3.2 (Multi-Variate Statistical Package, Kovach 1993).

Ordination was used to elucidate the principal patterns in the Campbell Island diatom flora. Square root transformed relative abundance data with downweighing of rare taxa were used in the ordinations. The statistical and numerical techniques used in this study are described in Jongman et al. (1995). Detrended correspondence analysis (DCA) was carried out to estimate gradient length. The results showed that one sample (CA-296) was entirely dominated by *Angusticopula cosmica* Goeyers & Van de Vijver and therefore turned out to be a clear outlier. This sample was removed from further statistical analysis. A DCA with the outlier omitted showed gradient lengths for the first four axes of 0.695, 0.470, 0.261, and 0.188, suggesting that methods based on unimodal models (DCA) would be appropriate for a subsequent ordination (ter Braak & Prentice 1988). All ordination analyses were performed using the CANOCO v.4.5 (ter Braak & Šmilauer 1998).

We related diatom occurrences and diversity to a number of environmental (A–E) and moss structural characteristics (F–K). Character states are marked by a number (1–8).

Environmental characteristics were categorised as follows with data taken from Dale Vitt's field notes:

(A) Elevation: elevation from which the moss samples were collected (1800 ft (550 m) maximum and to the nearest 50 ft (15 m));

(B) Moisture regime: Vitt (1979) argued that in Arctic and Antarctic environments, the water regime is the most important factor controlling the distribution of mosses. Here, we consider three hydrological regimes: (1) wet = habitats with continuous water availability wherein moss plants rarely experience drought, (2) mesic = shaded forest floor habitats and those where moss plants may experience periodic drought for short periods of time, or (3) periodically dry = habitats that are hydrologically variable with periodic pronounced drought. Moss plants are physiologically drought tolerant in these habitats (Vitt et al. 2014);

(C) Salinity: (1) near ocean = moss samples collected at zero elevation along the coastline were considered to be affected by salt spray, (2) away from ocean = samples collected inland with freshwater inputs only;

(D) Habitat: (1) waterfalls including surrounding spray zones, (2) forests, scrub, and tussock-grassland, (3) open tundra, (4) disturbed areas, (5) cliff faces and boulders, (6) streams and stream banks;

(E) Substrate: moss populations occurring on (1) soil (including peat), (2) rocks (cliff sides and boulders), (3) scrub (mostly *Dracophyllum*) trunks and branches, or (4) humus.

Next, moss structural characteristics were considered that contribute to moss canopy complexity (or lack thereof) or provide microhabitats for diatoms on stems and leaves, and considered to potentially exsert influence on diatom occurrences (data taken from Sainsbury 1955, with attributes defined by Malcolm & Malcolm 2006):

(F) Branching: (1) moss plants with no or a few sympodial branches, generally growing erect, (2) plants with occasional lateral branches (either sympodial or monopodial), or (3) plants with numerous branches (pleurocarpous);

(G) Growth form: (1) cushion, (2) mat, (3) frond, (4) clump, (5) tuft, (6) turf, (7) gregarious, or (8) weft;

(H) Leaf cell ornamentation: (1) smooth, or (2) papillose/mamillose;

(I) Plant size: (1) tiny = leaves < 1 mm long on very slender stems, (2) small = leaves 1–2 mm long, (3) medium = leaves 2–3 mm long, or (4) large = robust plants with leaves > 3 mm long;

(J) Stem ornamentation: (1) smooth or with a few rhizoids, (2) tomentose (with matted rhizoids), or (3) with abundant paraphyllia;

(K) Leaf cell shape: (1) rounded to isodiametric, (2) oblong to rectangular, or (3) linear.

A Chi-square goodness of fit analysis was used to compare all environmental and structural characteristics as nominal values (calculated in R). With the exception of elevation, all environmental and structural characteristics were assessed, comparing expected and observed distributions for Diatom Assemblages 1–3 (with diatoms) with Diatom Assemblage 4 (with few or no diatoms) and for both Diatom Assemblages 1 and 2 to those in the combined Diatom Assemblages 1–3 (Diatom Assemblage 3 had too few samples to compare).

RESULTS

Species composition and diversity

Of the 69 historic moss samples from Campbell Island, only 32 contained sufficient diatoms and were included in the multivariate analyses. The remaining 37 samples contained (almost) no diatoms and were removed from the multivariate analysis. These removed samples will later be grouped as a fourth group to allow further discussion of the entire sample set. In total, 141 diatom taxa (including species, subspecies, varieties, and forms) belonging to 45 genera were observed. The taxon richness per sample (fig. 2) varied from 3 to 37 taxa, with most samples containing between 11 and 15 taxa. Many taxa were restricted to a limited number of samples (fig. 3). More than 50% of all taxa occurred in less than 5% of the samples. Very few taxa (2%) occurred in 50% or more of the samples.

Humidophila R.L.Lowe et al. (present in 75% of the samples), *Pinnularia* Ehrenb. (72%), *Psammothidium* Bukht. & Round (69%), *Angusticopula* Houk, Klee & H.Tanaka (59%), *Planothidium* Round & Bukht. (59%), *Diatomella* Grev. (50%), and *Frustulia* Rabenh. (41%) were the most frequently observed genera. The most taxon-rich genera include *Pinnularia* (17 taxa), *Psammothidium* (10 taxa), and *Humidophila* (9 taxa). In terms of relative abundance, *Planothidium* (19% of all counted valves), *Humidophila* (15%), *Psammothidium* (13%), *Pinnularia* (6%), *Angusticopula* (5%), *Ferocia* Van de Vijver & Houk (5%), and *Eunotia* Ehrenb. (4%) were the most important genera (table 1). Together, these seven genera represented 67% of all counted valves, with the remaining 38 genera accounting for 61% of all observed taxa. Some of the genera, such as *Planothidium* or *Angusticopula,* were very abundant in the total valve count, but were represented by only a very small number of taxa (3% and 2% of the total number of taxa, respectively).

The most common taxa include *Planothidium renei* (Lange-Bert. & Rol.Schmidt) Van de Vijver (15% of the total counted valves), *Humidophila costei* (Le Cohu & Van de Vijver) R.L.Lowe et al. (5%), *Ferocia houkiana* Goeyers & Van de Vijver (5%), *Psammontidium* cf. *confusiforme* Van de Vijver & Beyens (4%), *Cocconeis placentula* s.l. Ehrenb. (4%), *Diatomella balfouriana* Grev. (4%), and *Psammothidium* cf. *confusum* (Manguin) Van de Vijver (3%). *Planothidium renei* represented more than 15% of all counted valves and was also observed in 50% of the samples. Similarly, *Diatomella balfouriana* was present in 50% of the samples, but represented only 4% of all counted valves. None of the taxa occurred in all analysed samples. Together, the seven most abundant taxa accounted for 39% of all counted diatom valves (see fig. 4 for an overview of the 26 most abundant taxa). On the other end of the abundance range, 45 taxa (almost one third of all observed taxa) together accounted for only 1% of all counted diatom valves. Seventeen percent of the taxa are locally rare and were only observed once or twice. A high number of taxa (50 taxa or 36% of total) could only be identified to genus level, two additional taxa (1.4%) could not be identified to genus level and 24 taxa (17%) were identified to species level but with a high degree of uncertainty, even after comparison with the currently available literature and detailed analysis using scanning electron microscopy. The majority of these taxa can most likely be considered as new to science.

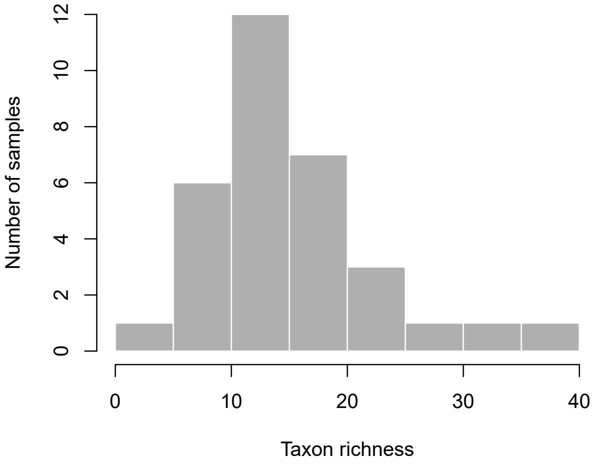

Figure 2 – Distribution of the moss samples based on their diatom taxon richness, expressed as the number of taxa (e.g. 20 indicates number of taxa between 16 and 20).

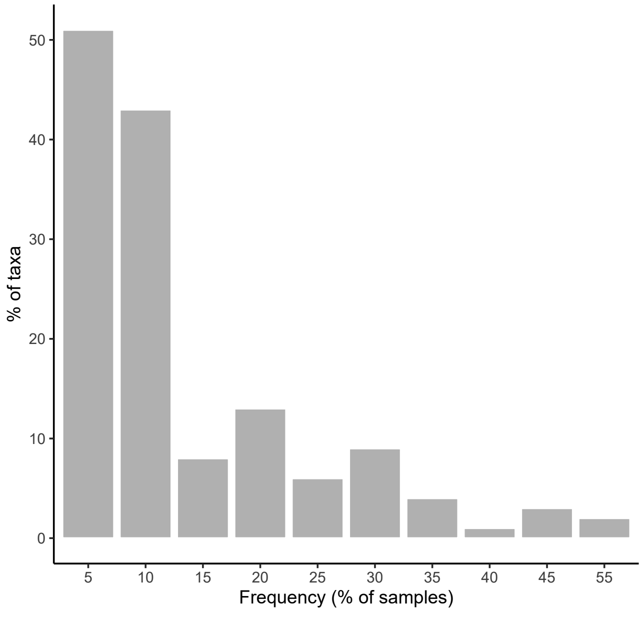

Figure 3 – Frequency classes of diatom taxa occurrence in the moss samples (e.g. 10 indicates 6–10% of all samples).

Table 1 – Summary of the genera and their relative abundance (%) in the 32 Campbell Island samples. Relative abundance refers to the percentage of valves counted for that genus relative to the total valve count.

Genera Campbell Island	Relative abundance (%)
Planothidium Round & Bukht.	19.2
Humidophila (Lange-Bert. & Werum) R.L.Lowe et al.	15.2
Psammothidium Bukht. & Round	13.0
Pinnularia Ehrenb.	5.5
Angusticopula Houk et al.	5.3
Ferocia Van de Vijver & Houk	4.5
Eunotia Ehrenb.	4.3
Cocconeis Ehrenb.	3.7
Diatomella Grev.	3.5
Fragilaria Lyngb.	2.7
Other	23.2

Biogeographical analysis

When comparing the species accumulation curve of Campbell Island to those of previously investigated Antarctic localities, it is clear that the moss-inhabiting diatom flora on the island is different (fig. 5). While the species accumulation curves of the other localities reach a plateau, indicating that these datasets represent most of their (theoretical) total diatom flora, the Campbell Island curve does not reach a plateau yet, indicating that a considerable number of additional samples will be needed to obtain a representative dataset. Using species richness estimators, it is possible to evaluate how well the sampling effort reflects the true diatom richness. The expected total number of taxa in all samples is 188 (Chao2), suggesting that our counting (i.e. 141) scored only 75% of the (theoretical) total number of taxa (contrary to the other localities: 84–99%).

The similarity analysis (table 2) showed that the Campbell Island diatom flora has a very low similarity with the other sub-Antarctic and Maritime Antarctic localities. The lowest similarities were found between Campbell Island and Maritime Antarctica (13%) and Campbell Island and Iles Kerguelen (13%), whereas the highest similarity was observed between Campbell Island and the sub-Antarctic Iles Crozet archipelago (36%). The islands of the southern Indian Ocean (Iles Crozet, the Prince Edward Islands, Iles Kerguelen, and Heard Island) showed very high intra-similarities, with the highest similarity observed between Iles Kerguelen and Heard Island (86%). South Georgia, located in the southern Atlantic Ocean, had a very low similarity with Campbell Island (19%), although it also shares a low number of taxa with the islands of the southern Indian Ocean islands (49–52%).

Supplementary file 1 provides an alphabetical list of all observed taxa together with their biogeographical distribution. Forty taxa (28.4% of all taxa observed in this study) had a Southern Hemisphere distribution (comprising SH, A, SA, and SA/MA). Of these, 23 taxa or 16.3% were restricted to the Antarctic region (comprising A, SA, and SA/MA), with one taxon or 0.7% limited to the whole Antarctic region (indicated by A). Seventeen taxa or 12% were confined to only the sub-Antarctic region (indicated by SA) and 5 taxa or 3.5% found in both the sub-Antarctic and Maritime Antarctic region (indicated by SA/MA). Twenty-three taxa or more than 16% had a cosmopolitan distribution, such as *Platessa oblongella* (Østrup) C.E.Wetzel et al., *Psammothidium abundans* (Manguin) Bukht. & Round, and *Humidophila biceps* (Grunow) Furey et al. Seventy-eight taxa or 55.3% have an unknown distribution.

Table 2 – Results of the similarity analysis based on the Sørensen community index. Numbers are in %. CI = Campbell Island, MA = Maritime Antarctic, KE = Iles Kerguelen, CR = Iles Crozet, HE = Heard Island, PE = Prince Edward Islands, SG = South Georgia.

	CI	MA	KE	CR	HE	PE	SG
CI		13.4	13.3	36.0	32.7	32.3	18.6
MA			16.3	17.3	14.3	13.8	16.0
KE				81.3	86.3	80.7	50.8
CR					76.0	71.4	48.8
HE						79.5	52.1
PE							48.7

Community analysis

The DCA ordination analysis (fig. 6) divided the Campbell Island moss samples into three Diatom Assemblages (DA). Although not being part of the community analysis, a fourth 'leftover' assemblage (DA4) should be considered containing all samples with no or very few (= less than 20 observed valves after analysing an entire slide) diatoms. The first two DCA axes ($\lambda_1 = 0.695$, $\lambda_2 = 0.470$) explained 16.3% of the variation in the diatom composition with an additional 6.3% explained on the next two axes. The distinction between the three assemblages containing sufficient diatoms is clearly reflected in the species composition of each assemblage. Table 3 provides an overview of the dominant taxa for each of these assemblages.

The first assemblage (13 samples in total) is located on the lower left of the DCA diagram. Most of the moss samples were collected in wet habitats (77%) away from the ocean (61.5%). Waterfalls including spray zones (46%) were the dominant habitat. The substrate of the samples was mostly rock (69%). Moss host species were not or sparsely branched (54%), growing predominantly in mats (46%). Leaf cell ornamentation was mostly papillose/mamillose (62%), and moss host species were mostly of medium (85%) size with a stem ornamentation containing paraphyllia (46%). Leaf cell shape was mostly oblong or rectangular (69%). Indicator genera include *Planothidium* (42% of total counted valves in this group), *Psammothidium* (13%), and *Cocconeis* Ehrenb. (8%), with *Planothidium renei* (34%) as dominating taxon and *Cocconeis placentula* s.l. (8%), *Psammothidium* cf. *confusum* (7%), *Fragilaria* sp.A (6%), and *Rossithidium* sp.1 (6%) as sub-dominant taxa.

The second assemblage (14 samples in total) is located in the middle of the DCA diagram. Most samples were

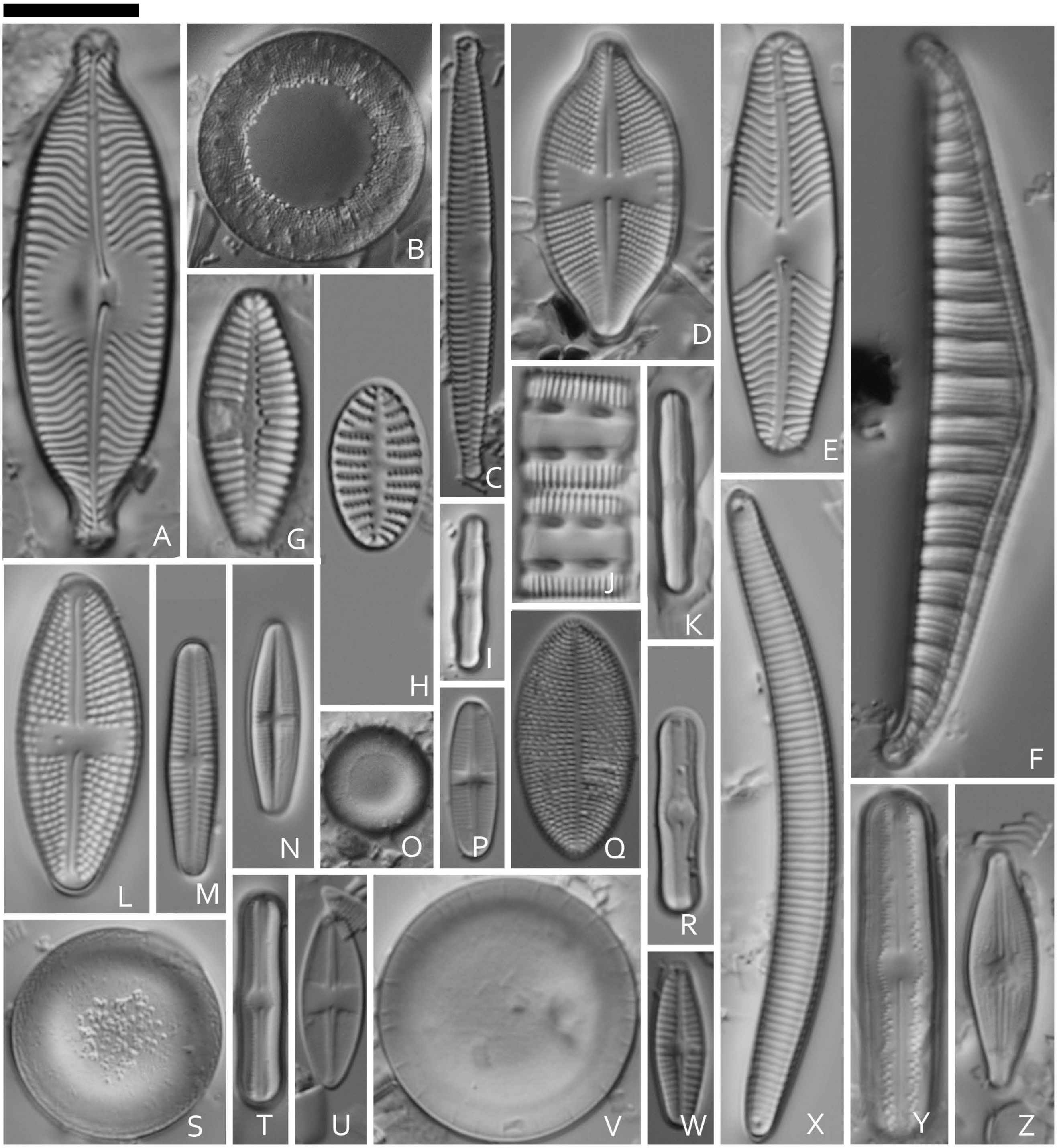

Figure 4 – The 26 most abundant diatom taxa (based on valve counts). **A**. *Pinnunavis genustriata*. **B**. *Angusticopula cosmica*. **C**. *Fragilaria* sp.A. **D**. *Psammothidium mannensianum*. **E**. *Pinnularia austroshetlandica*. **F**. *Rhopalodia* cf. *rupestris*. **G**. *Planothidium subantarcticum*. **H**. *Platessa oblongella*. **I**. *Humidophila nienta*. **J**. *Diatomella balfouriana*. **K**. *Humidophila* sp.B. **L**. *Luticola crozetensis*. **M**. *Rossithidium* sp.1. **N**. *Psammothidium* cf. *confusum*. **O**. *Arcanodiscus desmetianus*. **P**. *Psammothidium* cf. *confusiforme*. **Q**. *Cocconeis placentula* s.l. **R**. *Humidophila* sp.6. **S**. *Ferocia houkiana*. **T**. *Humidophila costei*. **U**. *Psammothidium* cf. *incognitum*. **V**. *Angusticopula chilensis*. **W**. *Planothidium renei*. **X**. *Eunotia* sp.1. **Y**. *Humidophila arcuata*. **Z**. *Nupela* sp.1. Scale bar = 10 µm.

Table 3 – Summary of the most abundant taxa in the three diatom assemblages, according to the cluster analysis. Symbols indicate the mean overall abundance of the taxa in each group. Legend: ■ = > 10%, □ = 5–10%, ○ = 2–5%, ● = < 2%.

Taxon	Code	DA1	DA2	DA3
Planothidium renei	PLANRENE	■	●	●
Cocconeis placentula s.l.	COCCPLAC	□	●	●
Psammothidium cf. *confusum*	PSAMCONF	□	●	●
Fragilaria spA-CA	FRAGSPCA	□	●	●
Rossithidium sp1-CA	ROSSSPC1	□	●	●
Humidophila costei	HUMICOST	●	■	●
Humidophila sp6-CA	HUMISPC6	●	□	●
Diatomella balfouriana	DIATBALF	●	□	●
Humidophila arcuata	HUMIARCU	●	□	●
Psammothidium mannensianum	PSAMMANN	●	○	●
Ferocia houkiana	FEROHOUK	●	●	■
Pinnularia austroshetlandica	PINNAUST	●	●	■
Eunotia sp1-CA	EUNOSPC1	●	○	■
Humidophila spB-CA	HUMISPCB	●	●	■
Pinnunavis genustriata	PINVGENU	●	●	□

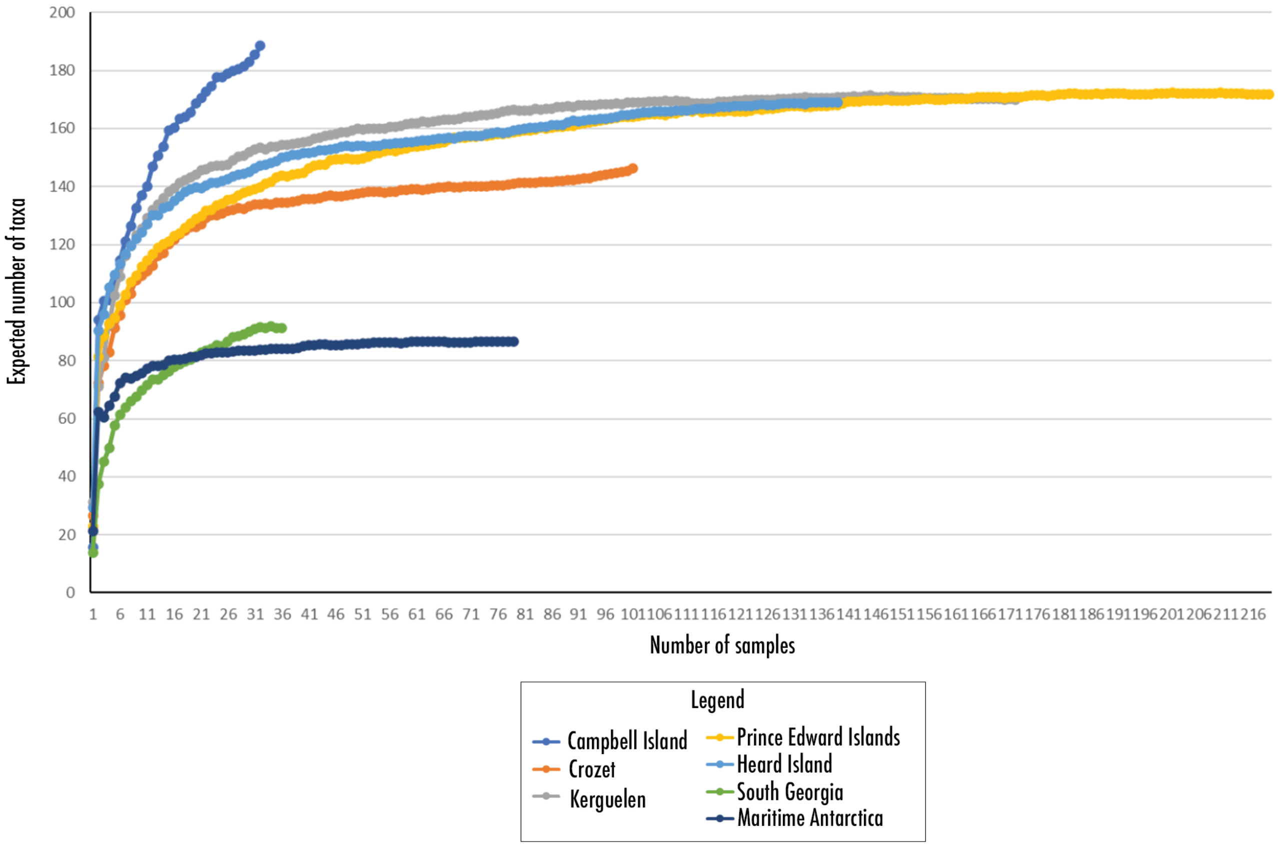

Figure 5 – Species accumulation curve of Campbell Island compared to those of other previously investigated Antarctic localities.

collected in periodically dry (54%) habitats, away from the ocean (87%). The dominant habitat types were cliff faces and boulders (73%). Substrate was mostly rock (73%). Moss host species were not or sparsely branched (40%) or had many branches (40%) and grew in mats (27%) or fronds (27%). Leaf cell ornamentation was mostly smooth (60%), and moss hosts species were mostly of small size (47%) with a stem ornamentation that was smooth or contained few rhizoids (87%). Leaf cell shape was mostly oblong or rectangular (40%). The second assemblage is dominated by the genera *Humidophila* (32%), *Psammothidium* (18%), *Diatomella* (8%), and *Eunotia* (5%) and shows a high species abundance of *Humidophila costei* (12%), *Humidophila* sp.6 (9%), *Diatomella balfouriana* (8%), *Humidophila arcuata* (6%), and *Psammothidium mannensianum* (4%).

The third assemblage (four samples in total) is located on the right side of the diagram. Samples were mainly collected in wet habitats (50%) near (50%) or away from (50%) the ocean. Habitats varied from waterfalls (25%) and disturbed areas (25%) to cliffs (25%) and streams (25%). Substrate was mostly rock (75%). Moss host species were not or sparsely branched (50%) or had occasional lateral branches (50%) and growth form was mostly in turfs (50%). Leaf cell ornamentation was smooth (75%) and plant size was small (50%) to medium (50%). Stem ornamentation was always smooth or with few rhizoids (100%) and leaf cell shape was rounded (50%). Indicator genera are *Ferocia* (33%), *Pinnularia* (29.6%), *Eunotia* (13%), and *Humidophila* (13%). *Ferocia houkiana* (33%) proved to be the dominant taxon. *Pinnularia austroshetlandica* (G.W.F.Carlson) A.Cleve (14%), *Eunotia* sp.1 (13%), *Humidophila* sp.B (11%), and *Pinnunavis genustriata* (Hustedt) Lange-Bert. & Krammer (6%) were sub-dominant.

The fourth assemblage containing 37 samples in total was formed by all samples that contained little or no diatoms. Samples in this assemblage were collected in periodically dry habitats (60%) away from the ocean (92%) in forests, scrubs, or tussock-grasslands (32%). Substrate was mostly soil

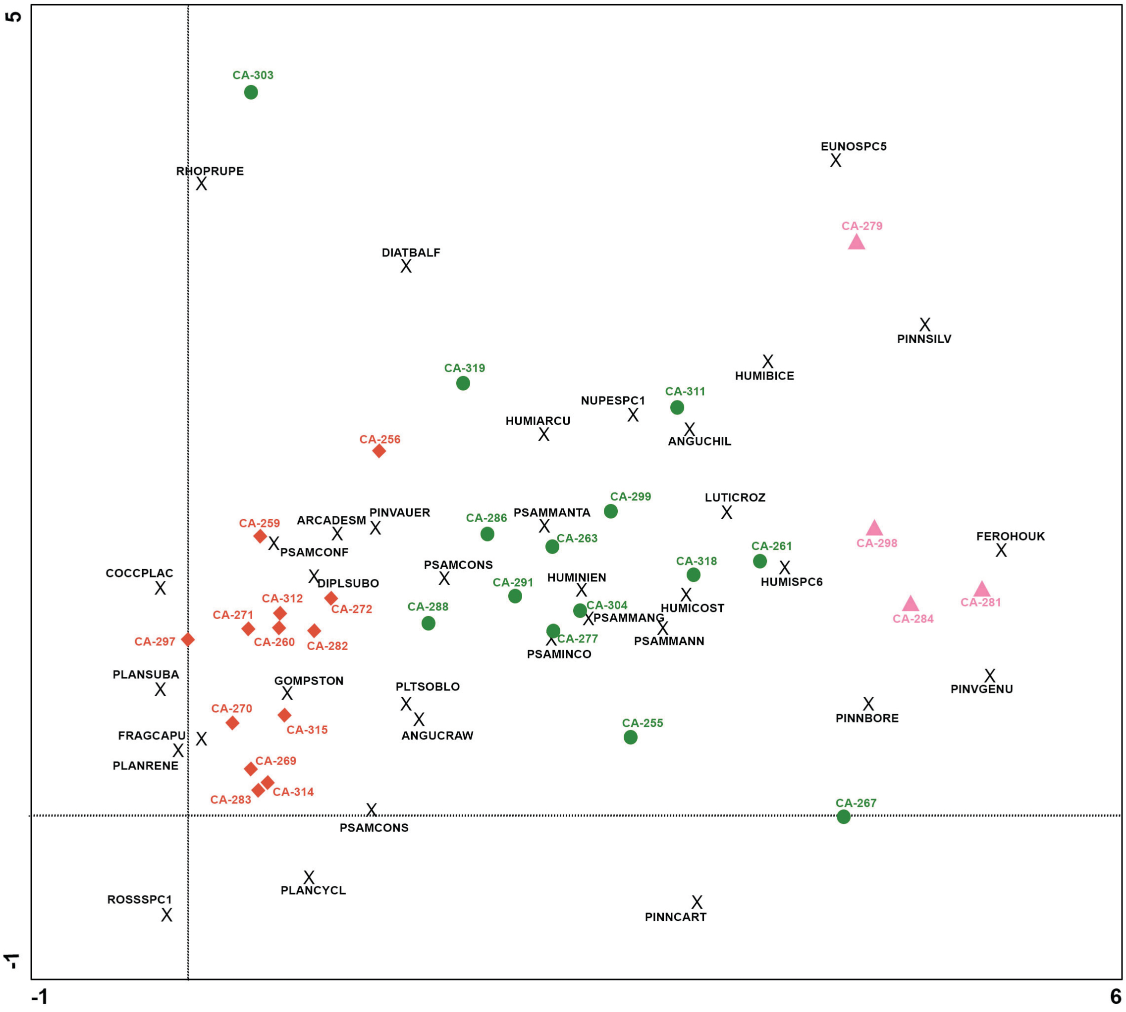

Figure 6 – DCA analysis showing the Campbell Island samples plotted on the first two axes. The outlier CA-296 was removed. Separation of the groups was based on the cluster analysis, performed with MVSP: DA1 = red diamonds, DA2 = green circles, DA3 = pink triangles. Black crosses indicate taxa that determine the position of the samples in the DCA diagram. Full names of these taxa can be found in supplementary file 1.

(35%) or rock (35%). Moss host species were not or sparsely branched (51%) and grew mostly in mats (35%). Leaf cell ornamentation was smooth (89%) and moss hosts were of medium size (46%). Stem ornamentation was smooth or with few rhizoids (76%) and leaf cell shape was linear (54%).

For the Chi-square goodness of fit analysis (see supplementary file 2), the first three assemblages (DA1–3) were compared to DA4, which contained little or no diatoms. Both environmental characteristics (moisture regime, salinity, habitat, and substrate) and moss structural characteristics (branching, growth form, leaf cell ornamentation, plant size, stem ornamentation, and leaf cell shape) were compared. The analyses revealed that nine out of the ten characteristics were significantly different. Only branching had a similar distribution for DA1–3 and DA4.

Secondly, it was examined if both DA1 and DA2 had observed distributions that differed from those expected from all groups that possessed diatoms (DA1–3). In this case, DA1 had significantly different distributions from those in the overall diatom assemblages in nine of the ten characteristics. Only substrate showed no significant difference. Major differences were moisture regime (77% of the samples in DA1 were from wet habitats vs 53% of the samples in DA1–3), habitat (in DA1, 46% of the samples were collected in waterfalls, 23% from cliffs, and 23% from streams vs 31%, 47%, and 13% in DA1–3). Among the moss structural characteristics, sparsely branched (54%), medium-sized plants (85%) in mats (46%) with papillose leaf cell ornamentation (62%) and ornamented stems (69%) of DA1 contrasted sharply to the overall dataset (DA1–3) wherein moss structural characteristics were mostly sparsely branched (66%), medium-sized plants (53%) in mats (34%) with papillose leaf cell ornamentation (47%) and ornamented stems (38%).

When DA2 was compared to DA1–3, seven of the ten characteristics had different distributions, and one additional characteristic (substrate, $p = 0.042$) had a marginally significant distribution. Major differences were that 54% of the samples in DA2 were from periodically dry habitats vs only 8% from DA1 and 31% in D1–3. Seventy-three percent of the samples were collected from cliffs and 20% from waterfalls vs 23% and 46% in DA1, and 47% and 31% in DA1–3. Among moss structural characteristics with strong differences, growth form had a high abundance of fronds (27%) and mats (27%), vs 0% and 46% in DA1, and 13% and 34% in DA1–3. Leaf cell ornamentation was smooth (60%) in DA2 vs 38% in DA1 and 53% in DA1–3. Moss plant size was small (47%) compared to 8% in DA1 and 31% in DA1–3.

DISCUSSION

Species diversity and biogeography

Of the 69 historic samples, 37 did not contain sufficient diatom valves. Most of these empty samples were prepared from mosses that were collected in relatively dry, terrestrial environments. As the moisture content of the mosses plays a fundamental role in shaping diatom assemblages (Van de Vijver & Beyens 1997a, 1999b; Van de Vijver et al. 2004, 2008; Kopalová et al. 2014) and desiccation is poorly tolerated by diatoms (Souffreau et al. 2010), dry areas may contain only a few or even no diatom valves. Only a handful of species, such as *Pinnularia borealis* Ehrenb., can survive in dry habitats (Van de Vijver & Beyens 1997a).

Only 32 samples were analysed in the present study, a number that is rather low compared to other sub-Antarctic localities, except when comparing with South Georgia. To illustrate, the number of samples from the Prince Edward Islands is almost seven times higher (219 samples). A similar observation can be made for the other southern Indian Ocean islands. One of the reasons for this undersampling is that sampling campaigns on the southern Indian Ocean islands were entirely designed for diatom analysis, whereas on Campbell Island, the initial rationale for the expedition was a bryophyte-based study. On the other islands, less focus was put on collecting different moss taxa, meaning that more typical diatom habitats were sampled. Unfortunately, sampling campaigns on the southern Pacific Ocean islands are not easy to organise and bound to a lot of logistic constraints, regulations, and permit restrictions, making new expeditions solely focused on diatom sampling unlikely in the near future. A second explanation for this low number is the way the samples were selected prior to this study. The Campbell Island moss collection initially contained more than 1,100 specimens, all collected during the 1969–1970 field campaign. Only a fraction ended up in the British Antarctic Survey moss herbarium (< 200 according to the BAS specimen catalogue) and out of these samples, 69 were selected, merely based on the description on the labels or on the availability of sufficient moss material for subsampling. Preference was given to samples showing an indication of the presence of moisture (such as neighbouring waterfalls). A more thorough sampling of this historic moss collection will most likely yield more interesting samples for further diatom analysis.

A high number of taxa could only be identified to genus level or to species level but with a high degree of uncertainty. Two taxa could not be identified to genus level and might belong to marine taxa, for which the taxonomic knowledge in this region is rather limited due to a lack of sufficient in-depth studies. This lack of species-level identifications is not uncommon in recent Antarctic diatom studies, especially when a more critical, fine-grained taxonomy is applied. To illustrate, in the study of the Prince Edward Islands diatom flora (Van de Vijver et al. 2008), 26 taxa (12% of total) could only be identified to genus level, with some of them described as new (Van de Vijver & Gremmen 2006). Over the past 20 years, the non-marine diatoms of the southern Indian Ocean islands have been revised, resulting in the description of a large number of new taxa (e.g. Van de Vijver et al. 2002a, 2017a, 2017b; Romero & Van de Vijver 2011; Van de Vijver & Le Cohu 2017). In the past, most of these taxa were commonly force-fitted into European or North American names due to the lack of appropriate taxonomic literature (Tyler 1996). A similar effort was recently made for some islands in the Maritime Antarctic region (Zidarova et al. 2016), but the islands in the southern Pacific Ocean have only rarely been the subject of thorough and critical taxonomic revisions. The recent description of new taxa and the revision of several others (Goeyers & Van de Vijver 2020a, 2020b; Van de Vijver et al. 2019a, 2020a) clearly demonstrate the need for a better analysis of the diatom flora on the southern Pacific Ocean Islands. Taxonomic efforts will have to be increased to reach the same level of taxonomic accuracy as on the Indian Ocean islands. This problem is, however, not unique for the sub-Antarctic region, and was recently also detected in the Northern Hemisphere, where force-fitting and a too broad interpretation of species descriptions led to identifications errors (Van de Vijver et al. 2020b). These past taxonomic uncertainties make comparisons between recently acquired data and historical records not straightforward. Based solely on the analysis of 32 samples, it is clear that the Campbell Island moss diatom flora is highly diverse. Hickman & Vitt (1974), the only historic record on Campbell Island diatoms, reported 59 epiphytic diatom taxa in only five moss samples. Unfortunately, a comparison of their species list that was illustrated by a handful of line drawings and a few LM pictures with our new results is, given our improved taxonomic knowledge, not feasible. Most of the reported names in Hickman & Vitt (1974) were never reported again in the Antarctic realm (Kellogg & Kellogg 2001) and are most likely the result of force-fitting. The only taxon that was observed with certainty in both studies is *Diatomella balfouriana*, illustrated in Hickman & Vitt (1974: figures 8–10). For all other taxa, comparisons were not possible.

The similarity analysis showed that the islands in the southern Indian Ocean share many taxa among them, which may point to the presence of a specific moss diatom flora. The highest number of taxa was found on Iles Kerguelen (165 taxa in 174 samples) and the Prince Edward Islands (162 taxa in 219 samples). These higher numbers were reached not only due to a much higher number of investigated samples, but also because those surveys sampled a broader range of habitats. Aquatic mosses were not included in the Campbell Island dataset but represented a considerable fraction of the other sub-Antarctic sample sets and proved to contain a lot of diatoms (Van de Vijver et al. 2004, 2008).

The similarity of the southern Indian Ocean diatom flora with the flora from Campbell Island is rather low, although the southern Indian Ocean diatom flora was analysed following the same taxonomic concepts, using the most up-to-date literature. The similarity is limited to species that are generally accepted to be cosmopolitan (e.g. *Navicula gregaria* Donkin) or widespread in the entire sub-Antarctic region (e.g. several *Psammothidium* taxa). Only on South Georgia, the number was much lower (76 taxa in 36 samples), but this is clearly an effect of underreporting due to a lack of taxonomic consistency rather than a reflection of the real diversity. Moreover, the South Georgian diatom flora also seems to be qualitatively different from the other localities. The South Georgia study was performed in 1997, well before an elaborate taxonomic revision took place. Therefore, this low similarity may not reflect the actual similarity. A preliminary revision of the South Georgian moss diatom flora, revealed the presence of a more diverse flora on the island, but composed of different taxa than observed on Campbell Island (Bart Van de Vijver unpubl. res.).

The species richness on the sub-Antarctic islands is in clear contrast with the lower richness observed in more southernly-situated locations, such as Maritime Antarctica (Kopalová et al. 2014), or the Antarctic continent (Sabbe et al. 2003; Gibson et al. 2006; Bishop et al. 2020). The difference between the Maritime and sub-Antarctic region is also reflected in the rather low similarity value, which can be explained by the large differences in climate and geology, both having a severe impact on the different diatom microhabitats (Kopalová et al. 2014; Zidarova et al. 2016). The observed trend of decreasing species richness, moving southwards, has been attributed to the harshness of the environment, geographic isolations, and factors related to latitude, e.g. period of ice cover and light intensity (Jones 1996; Sabbe et al. 2003).

The diatom flora on Campbell Island is unique in many aspects. Several typically epiphytic genera (Lange-Bertalot et al. 2017), such as *Epithemia*, *Rhopalodia*, and *Cocconeis*, are almost entirely absent on the other sub-Antarctic islands, but are present in often large populations on Campbell Island. Several genera, such as *Frustulia*, *Sellaphora*, *Psammothidium*, and some centric genera, also seem to be more species-rich on Campbell Island. The fact that most of these taxa could not be identified using the currently available literature can point to a possible higher level of speciation on the island, although it is unclear why and when this speciation might have taken place. Molecular phylogenetic analysis may be helpful in solving this question, but for this, new sampling will be necessary.

This uniqueness can be explained in various ways. Campbell Island is a small, oceanic island and therefore all botanical organisms that are present there today had to reach the island via passive dispersion. Once arrived, primitive organisms such as microscopic algae could spread and undergo speciation. Campbell Island is situated in the circum-Antarctic current and diatoms can easily disperse from the southern Indian Ocean islands. The fact that several of the at present unidentified taxa show some resemblance to their Indian Ocean relatives may be an indication of ongoing speciation. Several taxa such as *Psammothidium mannensianum*, of which *P. manguinii* is the Indian Ocean relative, are very similar to Indian Ocean island species, except for being triple in size (Van de Vijver 2019). An additional argument for the possible dispersion of aerophilic diatoms to Campbell Island may be found in a relatively high number of taxa that are shared with southern South America (Patagonia, Tierra del Fuego). The tip of South America is also situated in this circumpolar current and winds blow from South America, via the southern Atlantic and Indian Ocean to the Pacific Ocean. Taxa such as *Nupela chilensis*, *Adlafia tenuis*, and *Planothidium aueri* have been described in the past from South America and were found during the analysis of the Campbell Island flora (Lange-Bertalot 1996; Van de Vijver et al. 2019a). Campbell Island is also located close to New Zealand and Tasmania, but unfortunately, the diatom flora of these larger landmasses is barely known. Published literature (Foged 1979; John 2016a) is far from complete and filled with taxonomic inconsistencies. Nevertheless, several taxa from the genera *Stauroneis* and *Actinella* were found to be present on Tasmania as well, e.g. *Stauroneis kriegeri* R.M.Patrick and *Actinella parva* Vanhoutte & Sabbe. A better knowledge of the diatom flora of these nearby larger landmasses will most likely lead to a higher similarity with the diatom flora on Campbell Island. In the future, it will also be interesting to sample and study the diatom floras on Macquarie, Auckland, Bounty, and Antipodes Island (all located close to Campbell Island in the southern Pacific Ocean) and compare them with both Campbell Island and the other sub-Antarctic locations. This might lead to the delineation of a similar typical diatom flora in the southern Pacific Ocean and hence confirm the biogeographical zonation of the southern zone.

Campbell Island diatom assemblages

The samples that were used in this study were collected during a campaign that was organised for the sampling of mosses, liverworts, and lichens. Detailed ecological information necessary for a thorough diatom analysis was not available and measurements that could be explanatory for the separation of the diatom assemblages, such as temperature, pH, salinity, nutrients, water level fluctuation, etc. are lacking. Nevertheless, three assemblages plus one leftover assemblage could be distinguished. This study hypothesises that moisture regime and habitat play a pivotal role in the delineation of the groups.

Samples from Diatom Assemblage 1 (the 'wet' group) were collected in wet habitats on rock, mostly nearby waterfalls. It showed the highest mean taxon richness and the highest number of taxa observed in one sample. *Planothidium* and *Psammothidium* are the dominant genera. Both show an often-restricted biogeographical distribution in the (Sub) antarctic region (Van de Vijver et al. 2002b; Zidarova et al. 2016; Van de Vijver 2019). *Psammothidium* is often found in epilithic environments, which can be confirmed by their abundance in this group. *Psammothidium* cf. *confusum*, a dominant taxon in this assemblage, was found on wet cliffs, rocks in waterfalls, and submerged edges nearby waterfalls. It belongs to the *P. confusum*-group, a complex of species that is typically found in moss vegetations (Van de Vijver & Beyens 1997b, 1999a). *Planothidium renei*, another diatom with a restricted sub-Antarctic distribution, was the dominant taxon. *Cocconeis placentula* s.l. was regularly present in DA1 as well. It is one of the most common taxa found in freshwater bodies and its distribution seems cosmopolitan (Jahn et al. 2009), considering *C. placentula* was first described 170 years ago by Ehrenberg from freshwater localities in Berlin. It was found in three samples from DA2 but never in DA3. Furthermore, unidentified representatives of *Fragilaria* and *Rossithidium* have been observed in DA1 as well. The taxonomic status of the genus *Fragilaria* is problematic, which can blur ecological distinctions between species. Since *Fragilaria* sp.A had the highest abundance in DA1 and was only found in one sample of DA2 (and never in DA3), this study tentatively concludes that *Fragilaria* sp.A has a preference for moist and epilithic environments, e.g. rocks and wet cliffs in and next to waterfalls. Within the sub-Antarctic region, the genus *Fragilaria* typically dominates diatom assemblages in running water bodies such as rivers, waterfalls, and brooks (Van de Vijver & Beyens 1999b; Van de Vijver et al. 2008). The taxonomic status of the genus *Rossithidium* is also not resolved, e.g. the validity of the separation of *Rossithidium* and *Achnanthidium* has been challenged (Kingston 2003; Kulikovskiy et al. 2016; Jüttner et al. 2019). However, since *Rossithidium* sp.1 has only been found in this first assemblage, it is possible that this taxon prefers this moist epilithic environments.

The second Diatom Assemblage (the 'rocky' group) was mainly collected in periodically dry and rocky habitats on cliff faces and boulders on high elevation. This assemblage showed the highest mean diversity and mean evenness and is dominated by the genera *Humidophila*, *Psammothidium*, *Diatomella*, and *Eunotia.* A high abundance of *Humidophila costei*, *Humidophila* sp.6, and *Humidophila arcuata* was found, with *H. costei* being the most dominant. Only *H. costei* was found in other assemblages, however, only scarcely. Most taxa of the genus *Humidophila* are often found in moist, humid, and aerophilous habitats (Lowe et al. 2014), which can be confirmed by the findings in this study. Similar results were found on other sub-Antarctic islands. On the Prince Edward Islands, *Humidophila* taxa (previously identified as *Diadesmis*) dominated fellfield diatom flora (Van de Vijver et al. 2008). On Amsterdam Island, shaded areas had high abundances of several *Humidophila* taxa (although not the same taxa as on Campbell Island were found) (Chattová et al. 2021). *Diatomella* had only one representative taxon, *Diatomella balfouriana*. This diatom genus has a typical biogeographical distribution in polar and mountainous regions, while *D. balfouriana* is its most reported and widespread taxon (Van de Vijver et al. 2012). Although *D. balfouriana* was very dominant in DA2, it was frequently observed in DA1 as well but never in DA3. This can be explained by the often dry and saline areas in which samples from DA3 were collected. *Psammothidium mannensianum* was also abundant in DA2 and the previous observation that *P. mannensianum* often co-occurs with *P. manguinii* (Van de Vijver 2019) can be confirmed here. *Psammothidium mannensianum* was never found in the other assemblages, although *P. manguinii* was observed in one sample from DA1. Species of the *P. manguinii* complex are often found in dry, terrestrial areas (Van de Vijver 2019). On Ile de la Possession, the main island of the Iles Crozet, *P. manguinii* is mainly observed in bare soils in caves and on fellfields (Van de Vijver et al. 2002b).

The third Diatom Assemblage was composed of moss samples collected in wet habitats near or away from the ocean in terrestrial habitats such as waterfalls, disturbed areas, cliffs, and nearby streams. The lowest mean taxon richness and mean diversity were recorded in this group, which can be explained by the moisture-dependence of diatoms. The genera *Ferocia*, *Pinnularia*, *Eunotia*, and *Humidophila* showed the highest abundance in this assemblage, with *Ferocia houkiana* being the dominant taxon. *Ferocia houkiana* was present in all three assemblages, although it was only counted twice with two valves in DA1. In DA2, *F. houkiana* was observed in samples that were collected in crevices, while in DA3, it was most abundant in samples collected on rocks and recesses. This could suggest a tolerance for drier environments. *Pinnularia austroshetlandica* is very dominant in DA3 as well, although it was only found in one sample that was collected on rocks above the ocean. This suggests that *P. austroshetlandica* is a salt-tolerant taxon, because assemblages living on rocks nearby and above oceans are often influenced by salty sea- spray. *Pinnunavis genustriata*, another sub-dominant taxon in DA3, was found in this sample as well and thus seems to co-occur with *P. austroshetlandica*. *Pinnunavis genustriata* was also observed in the other assemblages, in samples that were collected on cliff ledges and rocks beneath overhangs. This again could suggest the influence of sea-spray in shaping the community. Furthermore, two unknown members of *Eunotia* and *Humidophila* (*Eunotia* sp.1, *Humidophila* sp.B) were observed. *Eunotia* sp.1 was present in all groups, while *Humidophila* sp.B was only observed in DA2 and DA3, in samples collected on rock ledges, cliff ledges, and a recess close to a waterfall. It can be argued that this unknown *Humidophila* is tolerant for drier environments or environments with shifting moisture levels. Members of the *Eunotia* genus are often confined to epiphytic habitats on a wide range of bryophytes and show a range of tolerances to nutrient concentrations (Pinseel et al. 2016). This was reflected in the unknown *Eunotia* sp.1, which was present in various samples collected in wet cliffs next to waterfalls, boggy soils in streams, dark wet recesses, rocks, rock ledges, and cliff ledges.

Finally, the fourth 'leftover' assemblage contained 37 samples in total and was formed by all samples that did not fit in the other assemblages and contained little or no diatoms. These samples were collected mostly in periodically dry habitats such as forests, scrubs and tussock-grasslands on mostly rock or soil substrate. The absence of moisture is the defining characteristic of the samples belonging to this assemblage.

Unlike vascular plants, bryophytes, especially mosses, are physiologically drought tolerant. This physiological ability provides a high level of desiccation tolerance, and is coupled to morphological traits that enable mosses to inhabit a wide range of moisture conditions. Complex canopies and pleurocarpous growth forms are associated with forest floor habitats, ectohydric water conduction (with stem outgrowths) occurs predominantly in mosses occurring emergent from permanent water supplies (wetlands springs and seepages), and enhanced leaf cell protuberances (papillae) occur in mosses in periodically dry habitats (Vitt et al. 2014). Many of these morphological adaptations occur predominantly in different phylogenetic lineages (Vitt 1991). The ability provided by these morphological traits to prolong water availability in moss populations also provides potentially suitable habitats for diatoms.

The Chi-square goodness of fit analysis showed that diatom diversity, diatom occurrence, and moss structural characteristics are closely related to environmental characteristics. The assemblages containing diatoms differed significantly for almost all characteristics of the leftover assemblage. Significant differences were also observed when comparing both the first and second assemblage with the combined three assemblages. DA1 showed significant differences on nine out of ten characteristics, while DA2 showed significant differences on seven out of ten characteristics. The two first diatom assemblages that ordinate separately are associated with different moisture regimes and habitats, and moss hosts with many different structural characteristics. Moss structural characteristics clearly separate out along both moisture and habitat gradients and form a complex set of characteristics that are associated with different diatom assemblages. We suggest that moisture regimes (wet or periodically dry) and habitat (waterfalls or cliffs) are among the most critical factors that control diatom assemblage distributions. However, since the distributions of the moss structural characteristics are related to moisture and habitat, it is possible that these provide additional host specific microhabitat features that may be factors in controlling diatom distributions.

CONCLUSION

This study demonstrated that well-preserved herbarium material can be an excellent tool in the ongoing revision of the non-marine diatom flora in the Antarctic Realm. Historic collections have great potential to answer taxonomic, community-related and biogeographical questions, especially given the challenges in obtaining sampling permits. The analysis of historic bryophyte material, sampled in 1969–1970 and retrieved from the British Antarctic Survey, showed that Campbell Island, a sub-Antarctic island located in the southern Pacific Ocean, has a well-developed and diverse diatom flora, characterised by the presence of several typically epiphytic genera such as *Epithemia*, *Rhopaliodia*, and *Cocconeis*, several centric genera and many taxa that could not be identified using the available literature.

An overall low taxon similarity between Campbell Island and other islands in the sub-Antarctic and Maritime Antarctic regions was found, while there was a highly comparable flora on the islands of the Indian Ocean, pointing to a specific moss diatom community in this region. The diatom flora of Campbell Island and southern South America is remarkably similar, probably due to wind dispersion via the Antarctic circumpolar current.

Three different diatom assemblages were statistically distinguished, plus one additional leftover assemblage with little or no diatoms. Moisture regime and habitat are presumably the main forces shaping the assemblages. Since the analysed samples do not yet fully represent the theoretically possible diatom flora, it is vital to analyse more (historic) samples to complete the assessment of the moss-inhabiting diatoms from Campbell Island.

SUPPLEMENTARY FILES

Supplementary file 1 – Alphabetical list of all observed taxa together with their biogeographical distribution. Codes: A = Antarctic, SA = Subantarctic Region, SA/MA = Subantarctic and Maritime Antarctic Region, SH = Southern Hemisphere, C = Cosmopolitan, U = Unknown.

https://doi.org/10.5091/plecevo.84543.supp1

Supplementary file 2 – Summary of the Chi-square goodness of fit analysis to compare all environmental and moss structural characteristics as nominal values. DA = Diatom assemblage. "*" marks significant values.

https://doi.org/10.5091/plecevo.84543.supp2

ACKNOWLEDGEMENTS

The authors wish to thank Mrs Petra Ballings and Mrs Myriam de Haan for their help with the preparation of the samples. The British Antarctic Survey is thanked for permitting the use of the Campbell Island moss collection of Dale Vitt in this study.

REFERENCES

Bishop J., Wasley J., Waterman M., et al. 2020. Diatom communities differ among Antarctic moss and lichen vegetation types. *Antarctic Science* 33(2): 1–15. https://doi.org/10.1017/S0954102020000620

Bunt J.S. 1954. Soil-inhabiting nematodes from Macquarie Island. *Australian Journal of Zoology* 2*:* 264–274. https://doi.org/10.1071/ZO9540264

Clark M.R. & Dingwall P.R. 1985. Conservation of islands in the southern ocean: a review of the protected areas of Insulantarctica. Cambridge University Press, Cambridge.

Chao A. 1984. Non-parametric estimation of the number of classes in a population. *Scandinavian Journal of Statistics* 11: 265–270. https://doi.org/10.2307/4615964

Chao A., Hwang W.-H., Chen Y.C. & Kuo C.Y. 2000. Estimating the number of shared species in two communities. *Statistica Sinica* 10(1): 227–246.

Chattová B., Lebouvier M., Syrovátka V. & Van de Vijver B. 2021. Moss-inhabiting diatom assemblages from Ile Amsterdam (TAAF, southern Indian Ocean). *Plant Ecology and Evolution* 154(1): 63–79. https://doi.org/10.5091/pleveco.2021.1767

Colwell R.K. 2013. EstimateS: statistical estimation of species richness and shared species from samples. Version 9. Available from http://viceroy.eeb.uconn.edu/estimates/ [Accessed 1 Nov. 2020].

Esposito R.M.M., Spaulding S.A., Mcknight D.M., et al. 2008. Inland diatoms from the McMurdo Dry Valleys and James Ross Island, Antarctica. *Botany* 86: 1378–1392. https://doi.org/10.1139/B08-100

Evans A.J. 1970. Some aspects of the ecology of a calenoid copepod, *Pseudoboeckella brevicaudata* Brady 1875, on a sub-Antarctic island. ANARE Scientific Reports, series B1, Zoology. Department of Supply, Antarctic Division, Melbourne.

Flower R. 2005. A taxonomic and ecological study of diatoms from freshwater habitats in the Falkland Islands, South Atlantic. *Diatom Research* 20(1): 23–96. https://doi.org/10.1080/0269249X.2005.9705620

Foged N. 1979. Diatoms in New Zealand, the North Island. *Bibliotheca Phycologica* 47: 1–224.

Gibson J.A.E., Roberts D. & Van de Vijver B. 2006. Salinity control of the distribution of diatoms in lakes of the Bunger Hills, East Antarctica. *Polar Biology* 29(8): 694–704. https://doi.org/10.1007/s00300-006-0107-8

Goeyers C. & Van de Vijver B. 2020a. Revision of the non-marine centric diatom flora (Bacillariophyta) of the sub-Antarctic Campbell Island (southern Pacific Ocean) with the descriptions of five new species. *European Journal of Taxonomy* 694: 1–30. https://doi.org/10.5852/ejt.2020.694

Goeyers C. & Van de Vijver B. 2020b. Typification and emended description of *Achnanthes muelleri* G.W.F.Carlson (*Achnanthaceae, Bacillariophyta*), a widespread Antarctic freshwater species. *Notulae algarum* 127: 1–5.

Hickman M. & Vitt D.H. 1974. The aerial epiphytic flora of moss species from sub-Antarctic Campbell Island. *Nova Hedwigia* 24: 443–458.

Hodgson D., Vyverman W. & Tyler P. 1997. Diatoms of meromictic lakes adjacent to the Gordon river, and of the Gordon river estuary in South-West Tasmania. J. Cramer, Berlin.

Jahn R., Kusber W.-H. & Romero O.E. 2009. *Cocconeis pediculus* Ehrenberg and *C. placentula* Ehrenberg var. *Placentula* (Bacillariophyta): typification and taxonomy. *Fottea* 9(2): 275–288. https://doi.org/10.5507/fot.2009.027

John J. 2016a. Diatoms from Tasmania: taxonomy and biogeography. The diatom flora of Australia. Volume 2. Koeltz Scientific Books, Königstein.

John J. 2016b. Diatoms from Stradbroke and Fraser Islands, Australia: taxonomy and biogeography. The diatom flora of Australia. Volume 1. Koeltz Scientific Books, Königstein.

Jones V.J. 1996. The diversity, distribution and ecology of diatoms from Antarctic inland waters. *Biodiversity and Conservation* 5: 1433–1449. https://doi.org/10.1007/BF00051986

Jongman R.H., ter Braak C.J.F. & Van Tongeren O.F.R. 1995. Data analysis in community and landscape ecology. Cambridge University Press, Cambridge.

Jüttner I., Wetzel C.E., Williams D.M. & Ector L. 2019. Investigations of the type materials of *Achnanthes parallela* J.R. Carter and *Achnanthes petersenii* Hustedt (Bacillariophyceae) with comments on the genus *Rossithidium* Round & Bukhtiyarova. *Botany Letters* 167(1): 57–69. https://doi.org/10.1080/23818107.2019.1668297

Kellogg T.B. & Kellogg D.E. 2001. Non-marine and littoral diatoms from Antarctic and sub-Antarctic regions: distribution and updated taxonomy. A.R.G. Gantner Verlag K.G., Rugell.

Kilroy C., Biggs B.J.F. & Vyverman W. 2007. Rules for macroorganisms applied to microorganisms: patterns of endemism in benthic freshwater diatoms. *Oikos* 116(4): 550–564. https://doi.org/10.1111/j.0030-1299.2007.15447.x

Kingston J.C. 2003. Araphid and monoraphid diatoms. Freshwater algae of North America. Ecology and classification. Academic Press, San Fransisco.

Kopalová K., Ochyra R., Nedbalová L. & Van de Vijver B. 2014. Moss-inhabiting diatoms from two contrasting Maritime Antarctic islands. *Plant Ecology and Evolution* 147(1): 67–84. https://doi.org/10.5091/plecevo.2014.896

Kovach W.L. 1993. MVSP - A MultiVariate Statistical Package for Windows, ver. 3.2. Kovach Computing Services, Pentraeth.

Krammer K. 2000. Diatoms of Europe. Vol. 1. The genus *Pinnularia*. A.R.G. Gantner Verlag. Kommanditgesellschaft, Königstein.

Kulikovskiy M., Andreeva S.A., Gusev E.S., Kuznetsova I.V. & Annenkova N.V. 2016. Molecular phylogeny of monoraphid diatoms and raphe significance in evolution and taxonomy. *Biology Bulletin* 43: 398–407. https://doi.org/10.1134/S1062359016050046

Lange-Bertalot H. 1996. Iconographia Diatomologica. Annotated Diatom Micrographs. Volume 2. Koeltz Scientific Books, Köningstein.

Lange-Bertalot H. 2001. *Navicula sensu stricto*, 10 genera separated from *Navicula* sensu lato, *Frustulia.* In: Lange-Bertalot H. (ed.) Diatoms of Europe. Volume 2: Diatoms of the European inland waters and comparable habitats: 177–526. A.R.G. Gantner Verlag, Königstein.

Lange-Bertalot H. & Moser G. 1994. *Brachysira.* Monographie der Gattung und *Naviculadicta* nov. gen. *Bibliotheca Diatomologica* 29. J. Cramer, Berlin.

Lange-Bertalot H., Hofmann G., Werum M. & Cantonati M. 2017. Freshwater benthic diatoms of Central Europe: over 800 common species used in ecological assessment. Koeltz Botanical Books, Königstein.

Lowe R.L., Kociolek P., Johansen J.R., Van de Vijver B., Lange-Bertalot H. & Kopalová K. 2014. *Humidophila* gen. nov., a new genus for a group of diatoms (Bacillariophyta) formerly within the genus *Diadesmis:* species from Hawaiï, including one new species. *Diatom Research* 29(4): 351–360. https://doi.org/10.1080/0269249X.2014.889039

Malcolm B. & Malcolm N. 2006. Mosses and other bryophytes: an illustrated glossary. Second Edition. Micro-Optics Press, Nelson.

McBride T.P. 2009. Freshwater diatoms on sub-Antarctic Macquarie Island: an ecological survey of 14 lakes. *Papers and Proceedings of the Royal Society of Tasmania* 143(2): 73–82. https://doi.org/10.26749/rstpp.143.2.73

McBride T.P. & Selkirk J.M. 1999. Palaeolake diatoms on sub-Antarctic Macquarie Island: possible markers of climate change. In: John J. (ed.) Proceedings of the 15th International Diatom Symposium (Perth, Australia, 28 September–2 October 1998): 227–236. Gantner Verlag, Liechtenstein.

McBride T.P., Selkirk P.M. & Adamson D.A. 1999. Present and past diatom communities on sub-Antarctic Macquarie Island. In: Mayama S., Idei M. & Koizumi I. (eds) Proceedings of the 14th International Diatom Symposium (Tokyo, Japan, 2–8 September 1996): 353–365. Koeltz Scientific Books, Königstein.

Pienitz R., Douglas M.S.V. & Smol J.P. 2004. Long-term environmental change in Arctic and Antarctic lakes. Springer, Dordrecht.

Pinseel E., Van de Vijver B., Kavan J., Verleyen E. & Kopalová K. 2016. Diversity, ecology and community structure of the freshwater littoral diatom flora from Petuniabukta (Spitsbergen). *Polar Biology* 40(3): 533–551. https://doi.org/10.1007/s00300-016-1976-0

Quilty P.G. 2007. Origin and evolution of the sub-Antarctic islands: the foundation. *Papers and Proceedings of the Royal Society of Tasmania* 141: 35–58. https://doi.org/10.26749/rstpp.141.1.35

Rainsley E., Turney C.S.M., Golledge N.R., et al. 2019. Pleistocene glacial history of the New Zealand sub-Antarctic islands. *Climate of the Past* 15(2): 423–448. https://doi.org/10.5194/cp-15-423-2019

R Development Core Team 2020. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. Available from https://www.R-project.org [Accessed 1 Nov. 2020].

Romero O.E. & Van de Vijver B. 2011. *Cocconeis crozetensis*, a new monoraphid diatom from sub-Antarctic freshwater and moss habitats. *Diatom Research* 26(1): 89–98. https://doi.org/10.1080/0269249X.2011.575118

Sabbe K., Verleyen E., Hodgson D.A., Vanhoutte K. & Vyverman W. 2003. Benthic diatom flora of freshwater and saline lakes in the Larsemann Hills and Rauer Islands, East Antarctica. *Antarctic Science* 15(2): 227–248. https://doi.org/10.1017/S095410200300124X

Sainsbury G.O.K. 1955. A handbook of the New Zealand mosses. *Royal Society of New Zealand Bulletin* 5: 1–490.

Saunders K.M., Hodgson D.A. & McMinn A. 2009. Quantitative relationships between benthic diatom assemblages and water chemistry in Macquarie Island lakes and their potential for reconstructing past environmental changes. *Antarctic Science* 21(1): 35–39. https://doi.org/10.1017/S0954102008001442

Saunders K.M., Hodgson D.A., McMurtrie S. & Grosjean M. 2015. A diatom-conductivity transfer function for reconstructing past changes in the Southern Hemisphere westerly winds over the Southern Ocean. *Journal of Quaternary Science* 30(5): 464–477. https://doi.org/10.1002/jqs.2788

Sørensen T. 1948. A method of establishing groups of equal amplitudes in plant sociology based on similarity of species content and its application to analyses of the vegetation on Danish commons. *Biologiske Skrifter* 5: 1–34.

Souffreau C., Vanormelingen P., Verleyen E., Sabbe K. & Vyverman W. 2010. Tolerance of benthic diatoms from temperate aquatic and terrestrial habitats to experimental desiccation and temperature stress. *Phycologia* 49(4): 309–324. https://doi.org/10.2216/09-30.1

Sterken M., Verleyen E., Jones V.J., et al. 2015. An illustrated and annotated checklist of freshwater diatoms (Bacillariophyta) from the Maritime Antarctic Region. *Plant Ecology and Evolution* 148: 431–455. https://doi.org/10.5091/plecevo.2015.1103

ter Braak C.J.F. & Prentice I.C. 1988. A theory of gradient analysis. *Advances in Ecological Research* 18: 271–313.

ter Braak C.J.F. & Šmilauer P. 1998. CANOCO Release 4. Reference Manual and Users Guide to CANOCO for Windows: Software for Canonical Community Ordination. Microcomputer Power, Ithaca, USA.

Thorn V.C. 2008. New Zealand sub-Antarctic phytoliths and their potential for past vegetation reconstruction. *Antarctic Science* 20(1): 21–32. https://doi.org/10.1017/S0954102007000727

Tyler P.A. 1996. Endemisms in Freshwater Algae, With Special Reference to the Australian Region. *Hydrobiologia* 336: 127–135. https://doi.org/10.1007/978-94-017-0908-8_12

Van de Vijver B. 2019. Revision of the *Psammothidium manguinii* complex (Bacillariophyta) in the sub–Antarctic Region with the description of four new taxa. *Fottea* 19(1): 90–106. https://doi.org/10.5507/fot.2019.001

Van de Vijver B. & Beyens L. 1997a. Freshwater diatoms from some islands in the maritime Antarctic region. *Antarctic Science* 9(4): 418–425. https://doi.org/10.1017/S0954102097000540

Van de Vijver B. & Beyens L. 1997b. The epiphytic diatom flora of mosses from Stromness Bay area, South Georgia. *Polar Biology* 17(6): 492–501. https://doi.org/10.1007/s003000050148

Van de Vijver B. & Beyens L. 1999a. Moss diatom communities from Ile de la Possession (Crozet, sub-Antarctica) and their relationship with moisture. *Polar Biology* 22: 232–240. https://doi.org/10.1007/s003000050414

Van de Vijver B. & Beyens L. 1999b. Biogeography and ecology of freshwater diatoms in sub-Antarctica: a review. *Journal of Biogeography* 26(5): 993–1000. https://doi.org/10.1046/j.1365-2699.1999.00358.x

Van de Vijver B. & Gremmen N. 2006. Three new moss-inhabiting diatom species from sub-Antarctic Marion Island. *Diatom Research* 21(2): 427–439. https://doi.org/10.1080/0269249X.2006.9705680

Van de Vijver B. & Le Cohu R. 2017. *Diatomella colonialis*, a new diatom species (Bacillariophyta) from the Sub-Antarctic Region. *Phytotaxa* 306(4): 281–286. https://doi.org/10.11646/phytotaxa.306.4.4

Van de Vijver B., Ledeganck P. & Beyens L. 2001. Habitat preferences in freshwater diatom assemblages from Sub-Antarctic Îles Kerguelen. *Antarctic Science* 13:28–36. https://doi.org/10.1017/S0954102001000050

Van de Vijver B., Ledeganck P. & Beyens L. 2002a. Three new species of *Diadesmis* from soils of Ile de la Possession (Crozet Archipelago, Sub-Antarctic). *Cryptogamie, Algologie* 23: 333–341.

Van de Vijver B., Frenot Y. & Beyens L. 2002b. Freshwater diatoms from Ile de la Possession (Crozet Archipelago, sub-Antarctica). *Bibliotheca Diatomologica* 46: 1–412.

Van de Vijver B., Beyens L., Vincke S. & Gremmen N.J.M. 2004. Moss-inhabiting diatom communities from Heard Island, sub-Antarctic. *Polar Biology* 27(9): 532–543. https://doi.org/10.1007/s00300-004-0629-x

Van de Vijver B., Gremmen N. & Smith V. 2008. Diatom communities from the sub-Antarctic Prince Edward Islands: diversity and distribution patterns. *Polar Biology* 31(7): 795–808. https://doi.org/10.1007/s00300-008-0418-z

Van de Vijver B., Zidarova R., Sterken M., et al. 2011. Revision of the genus *Navicula* s.s. (Bacillariophyceae) in inland waters of the Sub-Antarctic and Antarctic with the description of five new species. *Phycologia* 50(3): 281297. https://doi.org/10.2216/10-49.1

Van de Vijver B., Ector L. & Cox E.J. 2012. Ultrastructure of *Diatomella balfouriana* with a discussion of septum-like structures in diatom genera. *Diatom Research* 27(4): 213–221. https://doi.org/10.1080/0269249X.2012.720612

Van de Vijver B., Wetzel C., Kopalová K., Zidarova R. & Ector L. 2013. Analysis of the type material of *Achnanthidium lanceolatum* Brebisson ex Kützing (Bacillariophyta) with the description of two new *Planothidium* species from the Antarctic region. *Fottea* 13(2): 105–117. https://doi.org/10.5507/fot.2013.010

Van de Vijver B., de Haan M. & Lange-Bertalot H. 2014a. Revision of the genus *Eunotia* (Bacillariophyceae) in the Antarctic Region. *Plant Ecology and Evolution* 147: 256–284. https://doi.org/10.5091/plecevo.2014.930

Van de Vijver B., Kopalová K., Zidarova R. & Levkov Z. 2014b. Revision of the genus *Halamphora* (Bacillariophyta) in the Antarctic Region. *Plant Ecology and Evolution* 147(3): 374–391. https://doi.org/10.5091/plecevo.2014.979

Van de Vijver B., Kopalová K. & Zidarova R. 2016. Revision of the *Psammothidium germainii* complex (Bacillariophyta) in the Maritime Antarctic Region. *Fottea* 16: 145–156. https://doi.org/10.5507/fot.2016.008

Van de Vijver B., Chattová B., Lebouvier M. & Houk V. 2017a. *Ferocia* gen. nov., a new centric diatom genus (Bacillariophyceae) from the sub-Antarctic region. *Phytotaxa* 332(1): 22–30. https://doi.org/10.11646/phytotaxa.332.1.2

Van de Vijver B., Lange-Bertalot H., Wetzel C.E. & Ector L. 2017b. *Michelcostea*, a new diatom genus (Bacillariophyta) from the sub-Antarctic Region. *Nova Hedwigia* 146: 125–136.

Van de Vijver B., de Haan M. & Goeyers C. 2019a. Analysis of the type material of *Navicula tenuis* Krasske (Bacillariophyta) and its transfer to the genus Adlafia. *Notulae algarum* 115: 1–3.

Van de Vijver B., Scholberg P. & Lebouvier M. 2019b. *Pinnularia schoelynckiana*, a new limnoterrestrial diatom species (Bacillariophyta) from the sub- Antarctic Iles Kerguelen (southern Indian Ocean). *Botany Letters* 167(1): 42–49. https://doi.org/10.1080/23818107.2019.1675185

Van de Vijver B., Ballings P. & Goeyers C. 2020a. *Frankophila dalevittii*, a new freshwater diatom (Bacillariophyta) from Campbell Island. *Phytotaxa* 429(1): 57–64. https://doi.org/10.11646/phytotaxa.429.1.4

Van de Vijver B., Ector L. & Williams D. 2020b. Observations on and typification of *Gomphonema auritum* A.Braun ex Kützing (Gomphonemataceae, Bacillariophyta). *Notulae algarum.* 148: 1–6.

van der Werff A. 1955. A new method of concentrating and cleaning diatoms and other organisms. *SIL Proceedings* 12(1): 276–277. https://doi.org/10.1080/03680770.1950.11895297

Verleyen E., Van de Vijver B., Tytgat B., et al. 2021. Diatoms define a novel freshwater biogeography of the Antarctic. *Ecography* 44: 1–13. https://doi.org/10.1111/ecog.05374S

Vitt D.H. 1971. New species of mosses from Campbell Island, New Zealand. *The Bryologist* 74(4): 464–472.

Vitt D.H. 1974. A key and synopsis of the mosses of Campbell Island, New Zealand. *New Zealand Journal of Botany* 12(2): 185–210.

Vitt D.H. 1979. The moss flora of the Auckland Islands, New Zealand, with a consideration of habitats, origins and adaptations. *Canadian Journal of Botany* 57: 2226–2263. https://doi.org/10.1139/b79-272

Vitt D.H. 1991. Distribution patterns, adaptive strategies, and morphological changes of mosses along elevational and latitudinal gradients on South Pacific Islands. In: Nimis P.-L. & Crovello T.J. (eds) Quantitative approaches to phytogeography: 205–231. Kluwer Academic Publishers, Dordrecht. https://doi.org/10.1007/978-94-009-2063-7_7

Vitt D.H., Crandall-Stotler B. & Wood A. 2014. Survival in a dry world through avoidance and tolerance. In: Rajakaruna N., Boyd R. & Harris T. (eds) Plant ecology and evolution in harsh environments: 267–295. Nova Publishers, Hauppauge.

Vyverman W., Vyverman R., Hodgson D. & Tyler P. 1995. Diatoms from Tasmanian mountain lakes: a reference data-set (TASDIAT) for environmental reconstruction and a systematic and autoecological study. *Bibliotheca diatomologica* 33: 1–198.

Vyverman W., Verleyen E., Sabbe K., et al. 2007. Historical processes contrain patterns in global diatom diversity. *Ecology* 88(8): 1924–1931. https://doi.org/10.1890/06-1564.1

Werum M. & Lange-Bertalot H. 2004. Diatoms in springs from Central Europe and elsewhere under the influence of hydrology and anthropogenic impacts. *Iconographia Diatomologica* 13: 1–417.

Zidarova R., Kopalová K., Van de Vijver B. & Lange-Bertalot H. 2016. Diatoms from the Antarctic Region, Maritime Antarctica. *Iconographia Diatomologica* 24: 1–509.

Communicating editor: Brecht Verstraete.

Submission date: 6 Aug. 2021

Acceptance date: 29 Nov. 2021

Publication date: 30 Mar. 2022