MASTER THESIS SUBMITTED TO OBTAIN THE MASTER'S DEGREE IN BIOLOGY, SPECIALIZATION EVOLUTION AND BEHAVIOUR BIOLOGY

MOSS-INHABITING DIATOMS FROM CAMPBELL ISLAND (SUB-ANTARCTIC)

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Figure 1: Campbell black-browed mollymawk. Adults at empty nest. South Bull Rock, Campbell Island, January 1993. Image © Alan Tennyson

“Your assumptions are your windows on the world. Scrub them off every once in a while, or the light won’t come in.”

- Isaac Asimov (1920–1992)

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Completing your master thesis in the year 2020 is peculiar, to say the least. While writing down the final words of this thesis, the world is still fighting an invisible enemy. Apocalyptical images of hospitals filled with COVID-19 patients, empty streets around the world that are otherwise flooded with tourists, mouth masks covering the faces of friends and strangers, panicking world leaders, and wild animals winning back their territory in city centers were on our daily menu. Fortunately, none of my loved ones got sick, I had a safe lockdown and I had the opportunity to successfully complete both my studies and thesis at the University of Antwerp. The latter would not have been possible without the help and support of many people.

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ABSTRACTS

ENGLISH ABSTRACT

Diatoms (Bacillariophyta) are one of the most abundant algal groups in Polar ecosystems, both in number of specimens as in number of species. Due to their characteristic frustules and their significant responses to changes in their physical and chemical environment, they are excellent bio-indicators and are used in applied environmental, biogeographical and paleo-ecological studies. Especially in Polar regions, diatoms proved to be useful indicators of environmental and climatic changes. Contrary to the 20th century view, Polar diatom floras show a high degree of bioregionalism, together with a high endemicity. However, due to force-fitting practices, outdated species taxonomy and incorrect identifications, a revision of the Polar diatom flora is required for their conservation and further use as bio-indicators. This master thesis considers the diatom flora found in a historic moss collection, sampled on Campbell Island (sub-Antarctic) in 1969-1970 by Prof. Dr Dale Vitt. In total, 66 moss samples were retrieved from the British Antarctic Survey (BAS) herbarium in Cambridge, the United Kingdom. This historic moss collection was compared with collections of samples from other sub-Antarctic islands. Analysis of the Campbell Island diatom flora showed a well-developed and species-rich diatom composition. During the survey, a large number of currently unknown diatom species were observed that could not be identified using the available literature. Detailed analysis of light and scanning electron microscopy observations and comparisons with similar taxa worldwide led to the description of several new species. The revision of the diatom flora of Campbell Island will contribute to a better understanding of Polar diatom biodiversity.

Keywords: sub-Antarctica, Antarctic Realm, Campbell Island, new species, moss

DUTCH ABSTRACT

Diatomeeën (Bacillariophyta) zijn één van de meest voorkomende groepen van algen in polaire ecosystemen, zowel in aantal specimens als in aantal soorten. Dankzij hun kenmerkende celwanden en significante respons op veranderingen in hun fysische en chemische omgeving, zijn ze ideale bio-indicatoren en worden ze gebruikt in milieu-, biogeografische en paleo-ecologische studies. Vooral in polaire regio's bewijzen diatomeeën hun nut als indicatoren van veranderingen in het milieu en in het klimaat. In tegenstelling tot het heersende standpunt in de 20^{e} eeuw vertonen polaire diatomeeënflora's een hoge mate van endemiciteit en bioregionalisme. Om diatomeeën in de toekomst te kunnen blijven gebruiken als bio-indicatoren, is een taxonomische revisie vereist, aangezien hun taxonomie wordt gekenmerkt door een verouderde soortentaxonomie, incorrecte identificaties en force-fittingpraktijken. In deze masterthesis wordt de diatomeeënflora van een historische mos-collectie beschouwd. Deze mossen werden verzameld op het sub-Antarctische Campbell Island in 1969-1970 door Prof. Dr Dale Vitt. Zesenzestig mos-stalen werden voor dit onderzoek uit het British Antarctic Survey (BAS) herbarium in Cambridge, het Verenigd Koninkrijk, gehaald, geanalyseerd en vergeleken met stalen van andere eilanden in het sub-Antarctische gebied. De diatomeeënflora van Campbell Island blijkt sterk ontwikkeld en soortenrijk. Bovendien werd een groot aantal nog onbekende soorten geobserveerd die niet konden worden geïdentificeerd met de huidige beschikbare literatuur. Een gedetailleerde microscopische analyse (zowel licht- als elektronenmicroscoop) en een vergelijking met gelijkaardige taxa van over de hele wereld leidde tot de beschrijving van verschillende nieuwe soorten. De revisie van de diatomeeënflora van Campbell Island zal bijdragen aan een beter begrip van de polaire diatomeeëndiversiteit.

Sleutelwoorden: sub-Antarctica, Antarctica, Campbell Island, nieuwe soorten, mos

LAYMAN'S ABSTRACT

Take a deep breath. Up to 20% of the oxygen now present in your lungs was produced by diatoms, a curious group of algae. Diatoms live anywhere on Earth where water is present, and they are the only organisms known on the planet that live in self-created houses or 'cell walls' made of glass. When the environment changes, diatoms are often the first organisms that respond to that change, making them excellent bio-indicators to study climate change, for example. Some biologists focus on the immense task of identifying and naming all possible species of a group of organisms, a practice called 'taxonomy'. This is often challenging, due to the fact that there are so many species and so many conflicting opinions on how taxonomy should be applied. This study focusses on updating the taxonomy of diatoms in a very small part of the Antarctic region, on a remote but magnificent island called 'Campbell Island'. It is located in the sub-Antarctic and in 1969-1970, Prof. Dr Dale Vitt visited the island to collect various samples of moss, a habitat known to be often filled with diatoms. In this thesis, the diatoms living on those mosses are examined and compared to the diatoms on other islands in that region. Many new diatom species were discovered, and Campbell Island was found to be more unique in its diatom composition than previously thought. By studying the Campbell Island diatoms, this study hopes to contribute in making the taxonomy of diatoms a little less complex and increase our knowledge on these extraordinary organisms in Polar and other regions.

1. INTRODUCTION

1.1 GENERAL INTRODUCTION

In 1703 an Englishman peered through his microscope and observed strange rectangular shaped organisms adhering to the roots of duckweed (*Lemna*). The paper the unknown Englishman submitted to the Royal Society of London about his findings is probably the first official record of a diatom. Unfortunately, we have no idea who the author was, the paper lists only a Mr C. [1]. The rectangular shapes Mr C. observed most likely referred to *Tabellaria flocculosa*, a non-motile diatom that produces colonies by adhering to other *Tabellaria*-cells at their corners using mucilage pads [2]. Diatoms (Bacillariophyta) are single-celled eukaryotic microorganisms, occurring in almost every area or habitat on Earth where water is present, ranging from freshwater lakes and oceans to mosses and even moist soils. Their name is derived from the Greek words *dia* ('through') and *temnein* ('to cut'), since their cells are divided in two halves or box-like parts [3]. The classification of diatoms has been an ongoing debate throughout the years. Eighteenth century scientists, such as Mr C., considered diatoms as members of the plant kingdom, while 19th century biologists classified them as animals [1]. Today, we identify them as eukaryotic, microscopic, diploid, unicellular algae, characterized by a yellow-brown pigmentation and the ability to build glass (SiO_2) cell walls to protect their inner cell. Although not visible to the naked eye, diatoms can be easily recognised as the brown films on aquarium glass or rocks [3].

The hallmark of a diatom is its cell wall or *frustule,* with species-specific shapes and pore patterns [4]. Traditional classification of diatoms depends largely upon these structures. The frustule is composed of silica (SiO_2) and consists of two parts of slightly different sizes, called *valves,* and a zone or connecting band, called a *cingulum* or *girdle* [5, 6]. The frustule itself is enveloped with mucus [6]. Since the components of the frustule fit closely together, the flux of material must take place via the pores and slits in the cell wall [1]. These openings allow the cell's organic components to make contact with its environment. New wall parts are formed within the cell by the polymerization of silicic acid monomers and added via exocytosis: new valves and girdle elements are therefore smaller than older parts [1]. The outer, older valve is called *epivalve* while the inner, younger valve is called *hypovalve* [7] (see figure 2). Each diatom can be observed in two different orientations: valve view (one of the valves is seen in face view) and girdle view (valves are seen in side view). For species identifications, it is recommended to observe the cells predominantly in valve view, while girdle view is useful for identifications upon genus level [1]. Apart from light-harvesting pigments, such as chlorophyll a, chlorophyll c and fucoxanthin, diatoms have protective carotenoids as well [8].

Diatoms reproduce both by asexual cell division and sexual reproduction. Asexual reproduction is the most common and the process is well-known as the MacDonald-Pfitzer rule. One of the daughter cells receives the epitheca of the mother cell, while a new hypotheca is synthesized by the daughter cell [9]. The mother cell hypotheca functions as a new epitheca for the other daughter cell, which subsequently produces a new hypotheca [9]. The production of new frustule parts via asexual reproduction evidently leads to a decline in cell size of part of the diatom population. Cell size is restored through sexual reproduction, whereby a specialized zygotic cell, the *auxospore,* swells [1].

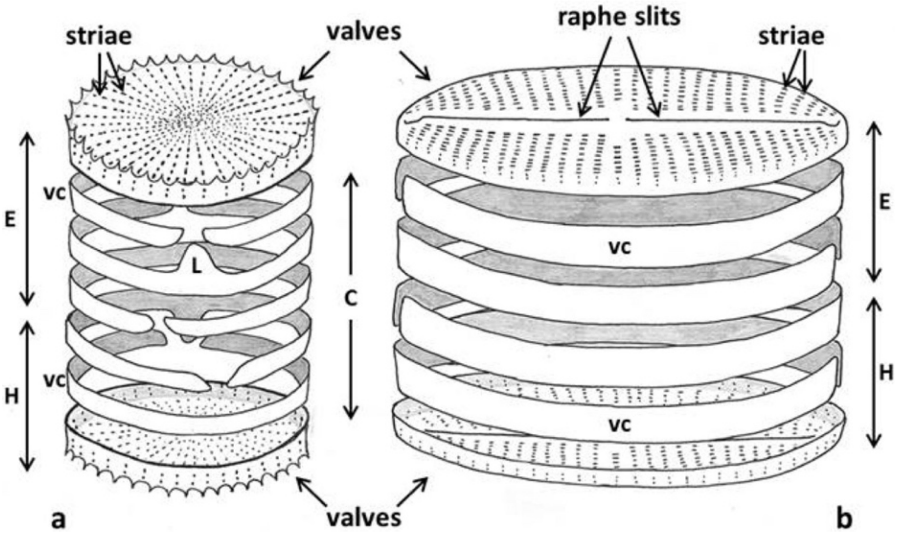

Figure 2: diagrams showing the basic structure of a diatom cell wall. (a) a radial centric and (b) a raphid pennate diatom. (c) cingulum, (e) older epitheca, (h) younger hypotheca, (l – vc) girdle bands. Image © Cox (2014) *[169]*

Diatoms are the most species-rich group of algae, with recent estimates ranging from 30,000 to 100,000 extant species [4]. To compare, there are currently 50 known dolphin species and between 8,000 and 20,000 butterfly species [6, 5]. Diatoms belong to the diverse and well-characterised Stramenopila, also known as Heterokonta [10]. The nearest extant group sharing a common ancestor with diatoms is the class Bolidophyceae.

In general, two main diatom groups can be distinguished: Coscinodiscophytina and Bacillariophytina. The former group is characterized by a circular, sometimes elliptical outline, while the valve outline of the latter is bipolar, multipolar or sometimes circular. Bacillariophytina are further subdivided into Bacillariophyceae, distinguished by a bipolar outline and slit or 'raphe' in their valve and Mediophyceae, with a bipolar, multipolar or circular valve outline, lacking a raphe [10].

Diatoms are a fairly recent group: their common ancestor evolved around 200-190 million years ago. To compare: this is approximately 60 to 70 million years later than the evolution of specialized teeth found in mammals [5]. Ancestral diatoms evolved through two subsequent rounds of endosymbiosis. What happened afterwards is still obscure. Some have proposed a pre-diatom stage, during which a naked photosynthetic cell acquired a siliceous (SiO_2) coating [11]. This was followed by an Ur-diatom stage, during which the glass coating differentiated into the complex frustule with its characteristic valves and girdle bands. Hence, the Ur-diatom was an already recognizable but extremely simple diatom [11]. Unfortunately, there is no fossil evidence of this Ur-diatom, since the fossil-bearing sediments have been destroyed through time by diagenesis. The early stages of diatom evolution are therefore hard to prove, and the available deposits that extend back to the middle Cretaceous (145-66 million years ago) contain only the record of modern diatoms [1]. There is, however, no reason to doubt that the occurrence of diatoms reaches back beyond that of the fossil record, as suggested by molecular clock analysis and sedimentary evidence [12, 13].

1.2 BIOGEOGRAPHY

Since the 18th century, biologists have thoroughly investigated the geographic distribution of plant and animal diversity but only recently, the distributions of microorganisms have been critically examined [14]. Therefore, little is known about the distribution patterns of diatoms [15]. Until recently, microorganisms were considered as ubiquitous, due to their immense population sizes, affecting their dispersal over long distances [16], and their small size, allowing passive dispersal [17]. This ubiquity idea is summarized by Baas-Becking (1932) in the central tenet '*Everything is everywhere, but the environment selects*'. However, increasing evidence is now suggesting that the geographical distribution of microorganisms ranges from global to narrow endemic and, surprisingly, that diatom communities are controlled by the same processes that operate in macro-organisms, although possibly not to the same degree [18]. Based on a global dataset of freshwater diatoms, the existence of a latitudinal gradient was recently shown in local and regional genus-richness. The gradient was highly asymmetric between the Northern and Southern hemisphere [19]. Furthermore, for dispersion over long distances, diatoms need to resist adverse environmental conditions. Both terrestrial and freshwater diatoms show a high sensitivity to abrupt heating, freezing and desiccation, which may influence their dispersal capacities over long distances and, consequently, rates of allopatric speciation [20]. Limited dispersal is in agreement with recent taxonomic revisions that show a large number of highly endemic species in isolated areas [20], for example in the genera *Humidophila* (formerly *Diadesmis*) [21], *Luticola* [22], *Muelleria* [23] and *Stauroneis* [24]. In conclusion, the ubiquity hypothesis does not appear to be very plausible for diatoms.

1.3 TAXONOMY

Diatom taxonomy faces many problems and is, as in many protist groups, notoriously messy [18]. Traditionally, the study of the frustule morphology (e.g. valve size and outline, central area shape, stria pattern and stria density, etc.) through light microscopical observations is used for taxon identification and delineation [25]. With the expansion of the application of electron microscopy observations in the 1970's, the diversity and complexity of the ultrastructure of the cell wall was revealed, expanding the range of characters available [25]. These advances, together with the increased use of molecular phylogenetic tools, are now challenging some longstanding traditional ideas, although taxonomical problems are far from solved. In the mid-20th century, many diatom species were lumped together due to the general application of a (too) broad species concept [26]. Subtle morphological variations were regarded purely as phenotypic plasticity and taxa previously seen as independent were suddenly considered conspecific [27]. The widely used European freshwater diatom floras of Hustedt (1961-1966) and Krammer & Lange-Bertalot (1986-1991) were proponents of this idea, and this had severe consequences: in non-European areas, diatom taxa were often force-fitted into European names [18]. These lumping and force-fitting practices reinforced the idea that the distribution of diatoms is cosmopolitan and that diatoms are ecological generalists [28]. Since the 1990's, species boundaries were re-evaluated, based on subtle variations in valve morphology and ultrastructure. This revealed that the minute differences in frustule characteristics often correlate with species boundaries, leaving species delimitation too coarse, hiding significant diversity [27, 29]. Due to the increased application of a more fine-grained taxonomy, it is suggested that diatom diversity may even be an order of magnitude higher than the current number of described species, with up to 200,000 extant species [29]. However, taxonomic revisions are a laborious process, and numerous diatom datasets are still waiting to be revised and updated.

1.4 ECOLOGY

Diatoms are always free-living and occur in a broad variety of environments, ranging from marine, brackish and freshwater to terrestrial. Parasitic taxa have never been observed [30]. Two principal habitats can be distinguished: moist or submerged aquatic surfaces (benthic) and open water (planktonic). The benthic community is more diverse in number and life forms, but it is more difficult to sample and study [1]. Therefore, benthic diatom species are ecologically less well understood than planktonic species. Benthic diatoms can be subdivided in motile and attached species. The motile community consists of epipelic (living on the sediment) and endopelic (living in the sediment) diatoms [1]. The division of the attached diatom community is based on their substrate: epipsammic (sand), epilithic (rock), epipelic (mud), epiphytic (plants) and epizoic (animals) [1, 9].

In spite of their tiny size (within the range of 0.01-0.2 mm), diatoms are key players in the functioning of the biosphere – the layer of our planet that harbours life [31]. It is estimated that diatoms produce up to 25% of the oxygen worldwide [27] and convert the same amount of carbon dioxide (CO_2) into organic carbon, thereby acting as an important carbon sink. This is more than all of the world's rainforests combined [32]. Diatoms fulfil an important role in the global cycling of Si as well [27]. They are also key players in the aquatic food web because of their production of high-energy lipid reserves [5]. Finally, because of their distinct habitat ranges, tolerance to environmental conditions and their silica cell walls, diatoms are excellent ecological indicators with a wide range of applications both as living organisms and fossils [9].

1.5 DIATOMS IN SUB-ANTARCTIC REGIONS

Polar non-marine diatoms are part of a unique flora that is being exposed to high gradients of solar radiation, short growing seasons, extreme temperature ranges, changing amounts of moisture, strong salinity gradients and vulnerability to climate change [23]. The first phycological studies in Polar regions stem from the 19th century and were published by J. D. Hooker, who assessed the marine Antarctic waters [33] and C. G. Ehrenberg, who observed Alaska, Spitsbergen (Svalbard), and the Antarctic Ocean [34]. Although not of primary interest, diatoms were included in these surveys [5] and Hooker described the diatoms in his observations as 'microscopic vegetables' [33]. After these early observations, studies of microbial life multiplied quickly from across the Arctic, with many publications documenting diatom floras [35, 36, 37, 38, 39, 40, 41, 42, 43]. Limited work was done in the sub-Antarctic and Antarctic [44], and the diatom flora of this region was considered as being largely composed of cosmopolitan species [45]. The number of Antarctic microscopic surveys increased during the early 20th century and varied from diatoms [46] and freshwater algae in general [47, 48, 49, 50] to marine taxa [51, 52, 53, 54]. The islands of Kerguelen and South Georgia were among the first to be

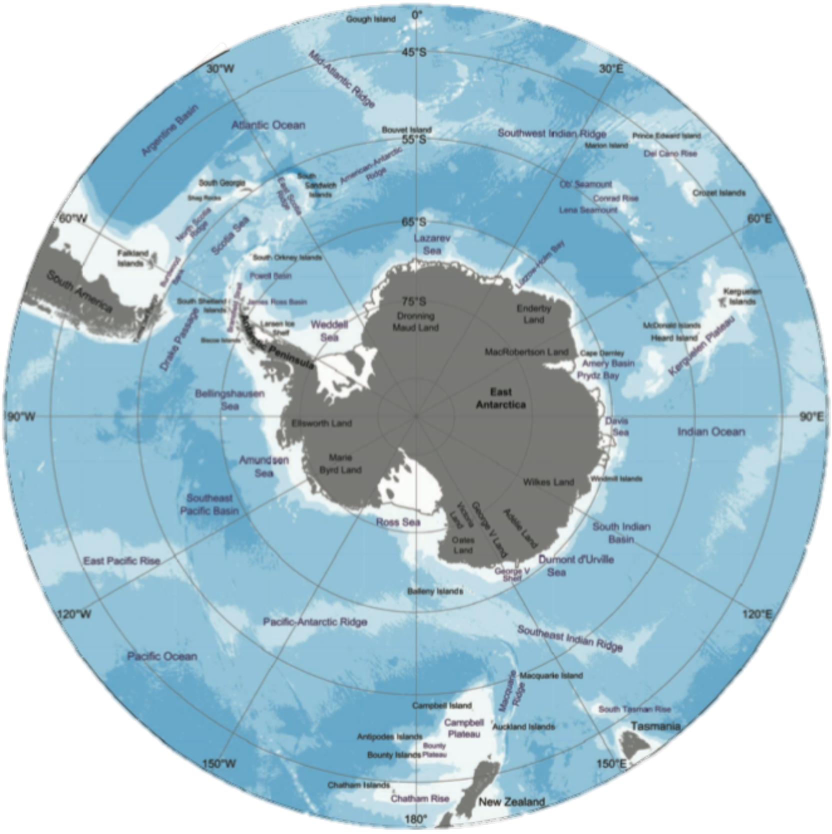

Figure 3: general map of the Southern Ocean. Image © De Broyer et al. (2014) *[168]*

investigated, due to their relative accessibility compared to other islands [23, 55, 50, 56, 57]. Kerguelen is perhaps the best investigated island in the sub-Antarctic region [45]. In 1954, Bourrelly & Manguin made an inventory of the diatom flora of Kerguelen, in which they recorded 160 species from six samples. Forty-seven of these appeared to be completely new to science [58] and many of these are still acknowledged today. Recently, a steady intensification of diatom taxonomy and biogeography research took place, with a renewed interest in the entire Antarctic and sub-Antarctic region [23]. Van de Vijver revised the flora of Iles Crozet and described 37 new taxa, many of which are still recognized as endemic to the sub-Antarctic and are never found outside of this region [59]. A large number of taxonomic revisions and descriptions of new species followed, contradicting the prevailing view of diatoms being cosmopolitan [60, 61, 24, 62, 63, 64]. The Antarctic diatom flora seems to be highly specific and even endemic, showing distinct bioregionalism [65, 66]. The genus *Luticola,* for example, was found to have one of the highest endemic rates of any diatom genus in Antarctica: of the more than 200 species of *Luticola,* almost 20% occurs in the Antarctic, with 42 of these being endemic [67]. No other genus of organisms has been observed with a similar or higher level of endemism in Antarctic limno-terrestrial environments [67]. By several researchers, an affiliation between the sub-Antarctic and South American flora was recognized [68, 69, 60, 70]. Compared to temperate and Arctic regions, species diversity of Antarctic diatoms seems to be low, probably due to the physical isolation of the continent [23]. In terrestrial sub-Antarctic ecosystems, diatoms are abundant in wet and semi-wet soils and non-aquatic moss ecosystems [5].

Although moss habitats represent a large proportion of the terrestrial biomass, diatoms living on them were relatively unknown until recently [5]. Early studies of the diatom flora of Macquarie Island [71] and Campbell Island [72] documented some taxa, but more recent work uncovered a well-developed and species rich diatom flora of over 250 species [73, 74, 21]. The composition and species richness of moss-inhabiting diatoms seems to be strongly influenced by moisture content [45, 21, 75]: in dry habitats, species numbers are consistently lower when compared to wet habitats and only a limited number of taxa have the capacity to thrive in xeric conditions [45]. In those taxa, valve size is directly proportional to moisture content [5]. Furthermore, the species composition of moss-inhabiting diatom communities seems to be related to habitat type, where environmental variables influencing species composition differ [5]. The composition of moss-inhabiting diatom communities on Kerguelen Island has been related to elevation, a proxy for temperature [23]. Moss diatoms with colder optima favoured higher altitudes, regardless of the moss species [23].

1.6 HISTORIC COLLECTIONS

Historic collections are cornerstones for the study of biology, providing an enormous documentation of life with numerous specimens housed in museums and academic institutes around the world. During the last two centuries, these collections served as essential components for taxonomists and systematists, and even today they provide material for studying (the loss of) biodiversity, biological invasions, global climate change, phylogenetics, biogeography, conservations and many other areas of ecology and evolutionary biology [76]. In the past twenty years, a dramatic increase in the use of historic collections took place to assess a wide variety of scientific questions and their importance has been expressed by many authors in recent literature [77, 78, 79, 76]. Major digitization initiatives are making historic specimens more accessible, leading to digital collections that enhance collaboration across disciplines and institutions. Historic collections are often used in the study of diatoms as well, for example in the description of new taxa [80, 81], the revision of existing taxa [82, 83, 84, 85], (historical) biogeography [86], conservation [87] and water quality assessment [88, 89]. This thesis underlines the importance of these historic diatom collections and highlights the necessity of these scientific archives in the study of diatom biodiversity.

1.7 OBJECTIVES

Polar ecosystems are expected to show large environmental shifts, making these regions important study areas to analyse long-term ecosystem changes [44]. Although diatoms are considered to be excellent bio-indicators, their use as indicators depends on a thorough knowledge of their diversity and taxonomy. As historical force-fitting and outdated taxonomy led to incorrect identifications in the past, a thorough revision of the Polar diatom flora is of prime importance. This master thesis investigates the moss-inhabiting diatom communities on Campbell Island. Our knowledge of the sub-Antarctic diatom flora present on the Pacific Ocean islands is very limited, making the currently existing data unsuitable for any thorough ecological and/or biogeographical analyses. As sampling possibilities on these islands are limited, historic samples are very important to increase our knowledge. This thesis is based on the analysis of 66 moss samples, collected in the austral summer of 1969-1970 by Prof. Dr Dale Vitt. Classical morphological analysis techniques such as light and scanning electron microscopy were applied to identify the diatom taxa that are present. Observed taxa were assessed using a fine-grained taxonomy and compared with similar taxa worldwide. When necessary, original type material of (often sub-Antarctic) diatom taxa was re-investigated to determine the morphological variability of the described taxa in comparison with observed specimens in the Campbell Island material. The acquired Campbell Island diatom dataset was subsequently compared with moss-inhabiting diatom communities found on the sub-Antarctic islands in the southern Atlantic and Indian Ocean using an existing, but taxonomically updated, database. This analysis will allow a better understanding of the biogeographical distributions of the sub-Antarctic Pacific diatoms.

Summarizing, the aims of this thesis are:

(1) increasing our knowledge on the non-marine diatoms of the Pacific part of the sub-Antarctic region by studying the biodiversity of the moss-inhabiting diatoms from Campbell Island
(2) updating diatom species taxonomy in general, and the sub-Antarctic diatom taxonomy more specifically, by refining identifications and reducing taxonomic instability and uncertainty
(3) increasing our knowledge on the biogeographical distribution of sub-Antarctic diatoms

2. MATERIAL & METHODS

2.1 STUDY AREA

The Antarctic Realm. The Antarctic Realm is composed of the Antarctic Continent, the Maritime Antarctic Region and the sub-Antarctic islands [90]. While 'Antarctica' generally refers to the Antarctic Continent, the Antarctic Realm has a variety of definitions [44]. In general, it refers to the area south of 60 °S or the southern limit of the high forest [91]. Another definition states that the Antarctic Realm lies south of the natural boundary formed by the Polar Frontal Zone or Antarctic Convergence [92]. This is an oceanographic boundary where cold and dense Antarctic water meets the warm and less dense waters of the Pacific, Atlantic and Indian oceans [44] and corresponds to the 10 °C February isotherm [93]. The three different parts of the Antarctic Realm all have their own, usually endemic, diatom flora and very few species are present in all three parts [94]. A large-scale investigation of 439 lakes in the Antarctic Realm found that 44% of all studied diatom taxa are endemic, with the proportion of regionally restricted taxa significantly increasing with increasing latitude, reflecting differences in air surface temperature and the degree of geographical isolation [95]. The genus *Luticola* was already mentioned in the introduction and has one of the highest endemic rates of any diatom genus in Antarctica. However, of the 42 endemic taxa, 38 are found in one single region only (23 endemics out of 28 taxa in total in Maritime Antarctica, 9 endemics out of 14 taxa in Continental Antarctica and 6 endemics out of 8 taxa in sub-Antarctica) [67].

Sub-Antarctica. Sub-Antarctica is located between the Antarctic and Subtropical Convergence. The region has no larger landmasses and consists merely of some islands in the southern Atlantic (South Georgia), southern Indian (Prince Edward Islands, Iles Crozet, Iles Kerguelen, Heard Island) and southern Pacific Ocean (see below). The islands have an oceanic climate, with temperatures never dropping below 0°C, no permafrost and the average precipitation exceeding 1,000 mm. Water is never limited, which results in countless lakes and pools. The vegetation on most of the islands is composed of several, usually endemic, vascular plants, a well-developed moss carpet and numerous lichen species. Compared to the Atlantic and Indian Ocean sectors, the islands in the southern Pacific Ocean are very small [96], i.e. Auckland Islands (626 km^2), Campbell Island (113 km^2), Macquarie Island (128 km^2), Antipodes Island (21 km^2), Snares Island (3.3 km^2), and Bounty Island (1.35 km^2) [97]. Apart from Macquarie Island, governed by Australia, all islands belong to New Zealand and are only very infrequently visited.

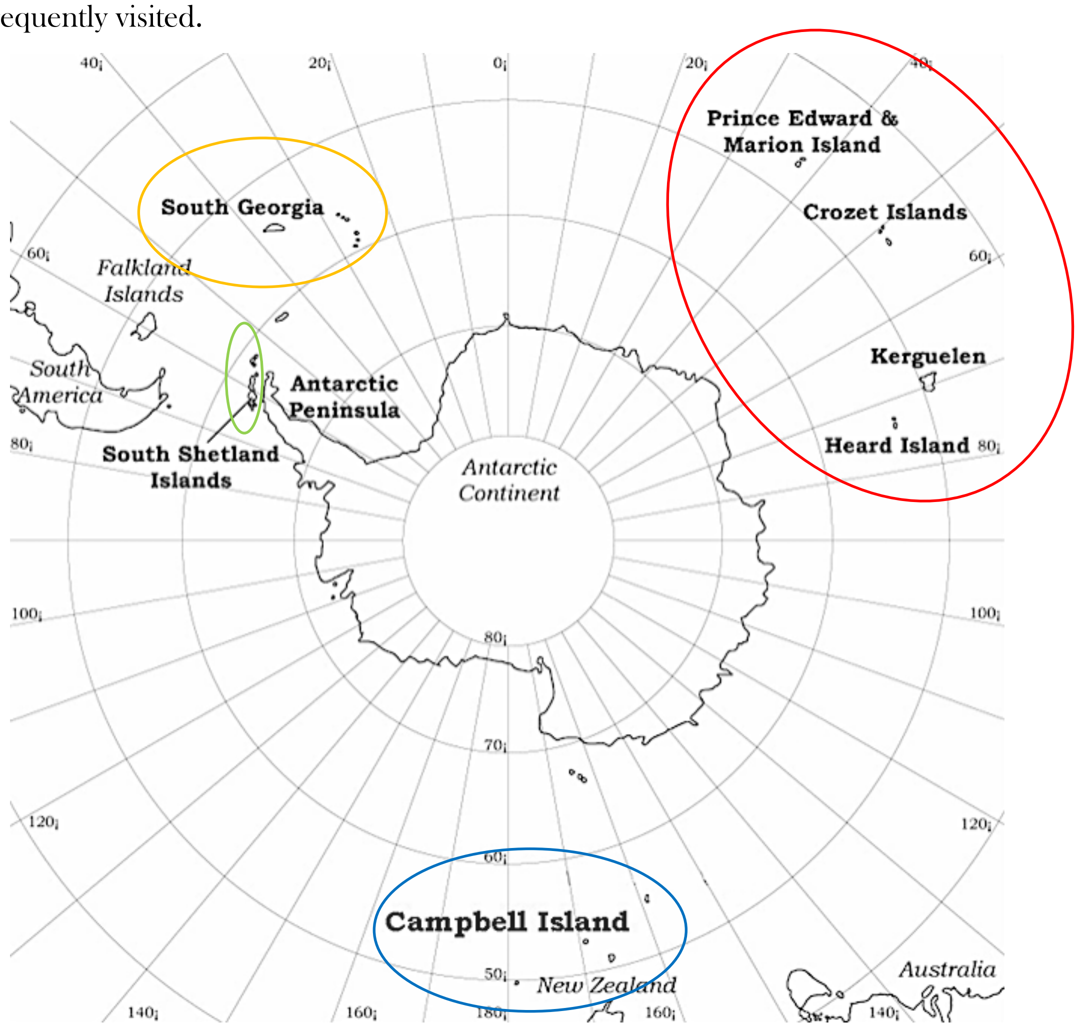

Figure 4: Map and colour-coded legend of islands in the Antarctic Realm.

Indian Ocean	Pacific Ocean	Atlantic Ocean	Maritime Antarctica
Prince Edward Islands Iles Crozet Iles Kerguelen Heard Island	Campbell Island Auckland Islands Antipodes Island Snares Island Bounty Island Macquarie Island	South Georgia	South Shetland Islands

Campbell Island. Campbell Island (52°33.7'S, 169°09'E) is situated 700 km south of the New Zealand mainland [98]. The island is an eroded remnant of extensive Oligocene to Miocene basaltic volcanism [99] and is covered with large peat deposits, up to 10 m thick [96]. A cloudy, moist and cool climate prevails with minimal sunshine [100]. Extreme winds from a predominantly western direction, cloudiness, high humidity, uniform cool temperatures and soil fertility patterns establish the environmental gradients that influence vegetation patterns [101, 102]. Altitude ranges from sea level to 558 m (Mount Honey), which corresponds to mean January air temperatures of 9.3°C and 5.5°C [103]. A large part of the island is covered with deep peat soils up to 10 m thick that started to accumulate after the Last Glaciation (circa 13,000 BP) [104, 105]. Today, shrub, grassland, rushes and large-leaved forb vegetation grow on the peat cover [104]. A well-developed moss carpet is present, offering a suitable environment for several diatom communities [45]. The vegetation has been heavily modified due to grazing by domestic sheep and cattle and burning during farming [100, 101]. Progressive elimination of grazing animals took place between 1970 and 1990 [106]. The history of farming and natural disturbances resulted in a complex mosaic of vegetation-soil systems of varying maturity [101]. The lakes and ponds of Campbell Island are mostly oligohaline and acidic and the nutrient status ranges from oligotrophic to hyper-eutrophic [107], the latter mainly due to the presence of colonies of marine birds and mammals near the waterbodies. According to a study from 2014 that assessed the aquatic diatom flora on Campbell island, the diatom composition differs markedly from the diatom communities on the nearby Macquarie Island, suggesting that the island may be part of a biogeographical province that is different from the rest of the sub-Antarctic [107]. This might, however, also be the result of insufficient (and often incorrect) taxonomic knowledge of the diatom flora in the Pacific sector of the sub-Antarctic region.

2.2 SAMPLING AND PREPARATION OF THE SLIDES

Sampling. During December 1969 and January 1970, an expedition was conducted to Campbell Island, with the support of the National Science Foundation (USA) [72]. Thirty-five days were spent on the island (from the 21st of December 1969 to the 24th of January 1970) and approximately 1,100 specimens of moss were collected [72]. A large number of these moss samples are stored at the moss herbarium of the British Antarctic Survey collection (Cambridge, UK). During a short visit to the collection in 2018, 66 historic Campbell island moss samples were subsampled for diatom analysis. The original sample label was photographed (see appendix D, figures D9-10) to ensure optimal documentation of the available information. For each sample, the name of the moss species, location of the sample and a short description of the sampling locality are available. Unfortunately, field notes, other than mentioned on the sample labels or in the paper by Hickman & Vitt (1974) [108], were not available (Prof. Dr Dale Vitt, pers.

comment). A full list of the Campbell Island moss samples and the sampling locations is added in Appendix C: figure C1 and table C1.

Preparation of samples. Diatom samples for light microscopic observations were prepared following the method described in van der Werff [109]. Small subsamples of the dry mosses were cleaned in a glass beaker by adding 37% H_2O_2 and heated to 80 °C for at least one hour. Distilled water was added to prevent the samples from boiling dry. The reaction was completed with the addition of saturated $KMnO_4$. After digestion and centrifugation (3 × 10 minutes at 3,700g), the resulting cleaned material was diluted with distilled water to avoid excessive concentrations of diatom valves on the slides. Cleaned diatom valves were mounted in Naphrax©, a mounting medium with refraction index 1.73. For electron microscopic observations, 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 aluminum specimen (Agar) stubs dressed 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).

Sample analysis. The light microscopy slides were analyzed at 1,000x magnification using an Olympus BX53 microscope, equipped with Differential Interference Contrast (Nomarski) optics and the UC30 camera connected to the Cell Sense Standard program. All taxa found during analysis of the slides were photographed multiple times, to obtain an overview of the morphological variability of the encountered taxa. A photographic voucher flora representing all encountered diatom taxa per sample was assembled using Adobe Photoshop CS4. In each slide, 400 diatom valves were counted and identified in random transects, yielding a representative idea of the species richness and composition in the samples. Raphid diatoms were only counted when the entire central area (both central raphe endings visible) was present. Araphid and centric diatoms were only counted when more than half of the valve was present. After the 400 valves were counted, slides were subsequently scanned in order to find rare species that were not observed during the counts. Scanning electron microscopy observations were performed at Meise Botanic Garden (Belgium) using a JEOL JSM-7100FLV Field Emission SEM (at 1 kV and working distance of 3.5-6.0 mm) and at the National History Museum in London, UK, using a ZEISS ULTRA SEM Microscope (at 3 kV and working distance of 3.5-4.0 mm). Detailed photographs were taken to facilitate species identifications. All unmounted material, microscopic slides and stubs are stored in Meise Botanic Garden. Taxa were identified based on the morphological species concept, using distinct morphological features visible in the light microscope. Electron microscopy was used for a more detailed analysis of the taxa when light microscopy was not or insufficiently informative. The most recent taxonomic literature was used to identify the taxa. Appendix A lists all taxonomic papers and monographs used in this thesis. A large-scale dataset containing almost 750 diatom counts from moss samples collected on various sub-Antarctic and Maritime Antarctic localities was used for the biogeographical analysis performed in this study (Van de Vijver, unpublished results). This dataset was assembled based on published data [74, 110, 111, 112, 113]. To ensure taxonomic uniformity, the dataset had already been made taxonomically consistent by Bart Van de Vijver prior to this thesis and was therefore ready to use.

Data analysis. Shannon-Wiener diversity index ($\log_{10}$-based) and Hill's evenness index were calculated using the statistical package MVSP 3.2 [114]. Per sample, the total number of taxa (taxon = species, varieties and formas including valves identified on higher taxonomic levels such as genus level) was expressed as all taxa observed during the 400 valve counts. To evaluate the extent to which the sampling effort in this thesis represented the complete diatom flora of Campbell island, the mean Chao2 richness estimator [115] was calculated using the EstimateS program 9.1 [116]. This technique estimates the theoretical maximum number of taxa that a given sample-set can contain, and is therefore a good estimation on how well the sample-set represents the species diversity of a certain region based on the collected material. The Sørensen-similarity index [117] was used for a pairwise comparison between the moss-inhabiting diatom flora of Campbell Island with that of other sub-Antarctic localities (Maritime Antarctica including Livingston and James Ross Island, Iles Kerguelen, Iles Crozet, Heard Island, the Prince Edward Islands and South Georgia). The index uses presence/absence data and therefore does not evaluate the abundance of the taxa. The result is expressed as percentage. The formula of the index is:

$$S = \frac{2C}{A + B + 2C}$$

with **A** representing the number of taxa exclusively observed in sample A, **B** the number of taxa exclusively observed in sample B and **C** the number of taxa observed in both sample A and B. To allow a better evaluation of the resulting similarity values, pairwise comparisons between the other islands and archipelagos was likewise performed. Ordination and clustering techniques were used to detect the principal patterns in species composition in the moss samples of Campbell Island. A square root transformation was applied to the species abundance data. To prevent excessive noise in the dataset, only taxa with a total abundance of 2% in at least one sample were included, removing very rare taxa from further statistical analysis. The Campbell Island moss samples were assigned to groups using both cluster analysis (based on Minimum Variance Strategy and with Squared Euclidian Distance as dissimilarity index) in MVSP and ordination statistics performed in CANOCO version 4.5 [118]. To assess whether linear or unimodal ordination techniques should be applied, an initial detrended correspondence analysis (DCA) was performed to estimate the gradient length in standard deviation (SD) units. For gradients smaller than 2 SD, linear species response curves could be expected whereas larger gradient lengths point to unimodal models [118]. As the resulting total gradient length was 15.569, unimodal techniques should be applied to elucidate the principal patters in the species abundance data. All statistical techniques used in this thesis are described in full detail in Jongman *et al.* [119].

3. RESULTS

Additional results, tables and figures are attached in the Appendix and are referred to as such in the results section. The following abbreviations were used throughout the identifications:

1. cf. (confer): taxon resembles species but due to the lack of visible details or insufficient observations the final identification is uncertain;
2. s.l. (sensu lato): 'in a broad sense', definition of taxon is broader than originally defined or accepted;
3. sp.: taxon could only be identified to genus level, refers to single species (in contrast to spp., referring to a group of related species);
4. incertae sedis: identification upon genus level not possible with currently available literature.

3.1 TAXON COMPOSITION ANALYSIS

A total of 66 historic moss samples from Campbell Island have been prepared and analysed for this thesis. Of these, 34 did not contain sufficient diatom valves and were removed from the dataset. All further results are therefore obtained from the analysis of the remaining 32 samples. A total of 141 taxa (including species, varieties and formas) belonging to 45 genera has been observed during the microscopic counts and the total number of counted valves was 12,800. An additional 13 taxa were detected in the samples after scanning the slides outside the counts. The complete list of all diatom taxa encountered in this study and their relative abundances is added in Appendix B (table B1). Out of the 141 taxa, 64 were identified up to species, subspecies or variety level (45.4% of the total number of taxa). Fifty taxa could only be identified upon genus level (35.5% of total). These are referred to by their genus name, combined with 'sp.', a number or letter when the genus contained more than one unidentified taxon and '-CA', to indicate that the sample is from Campbell Island. The identification of another 25 taxa (17.7% of total) was uncertain, but these showed some resemblance to already described species. This is indicated in the taxon list by adding 'cf.' between the genus and species name. Two taxa could not be identified upon genus level and were classified as 'incertae sedis' (1.4% of total).

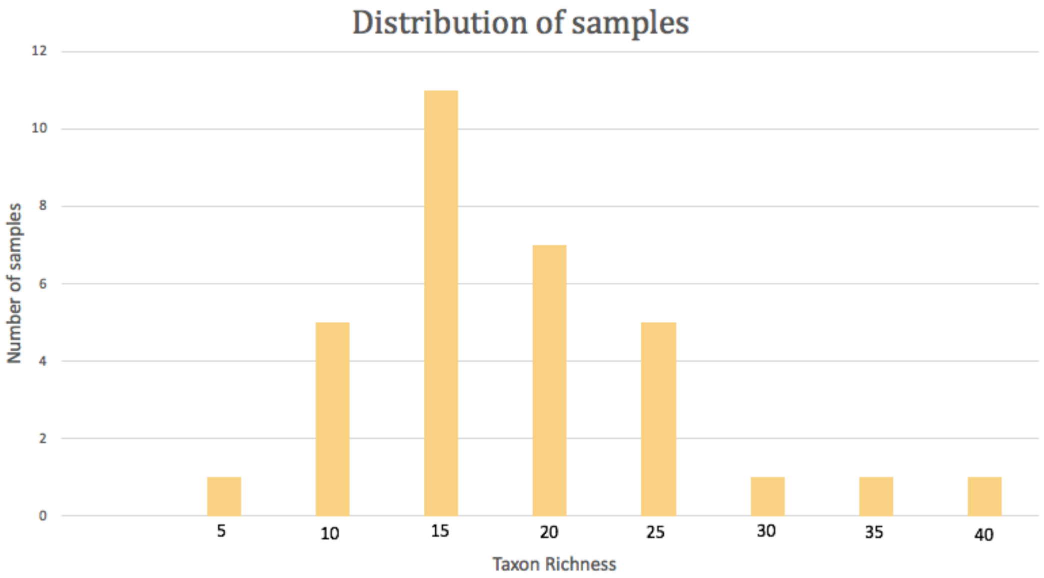

Figure 5: Distribution of samples based on taxon richness, expressed as number of taxa (e.g. 20 indicates number of samples between 16 and 20).

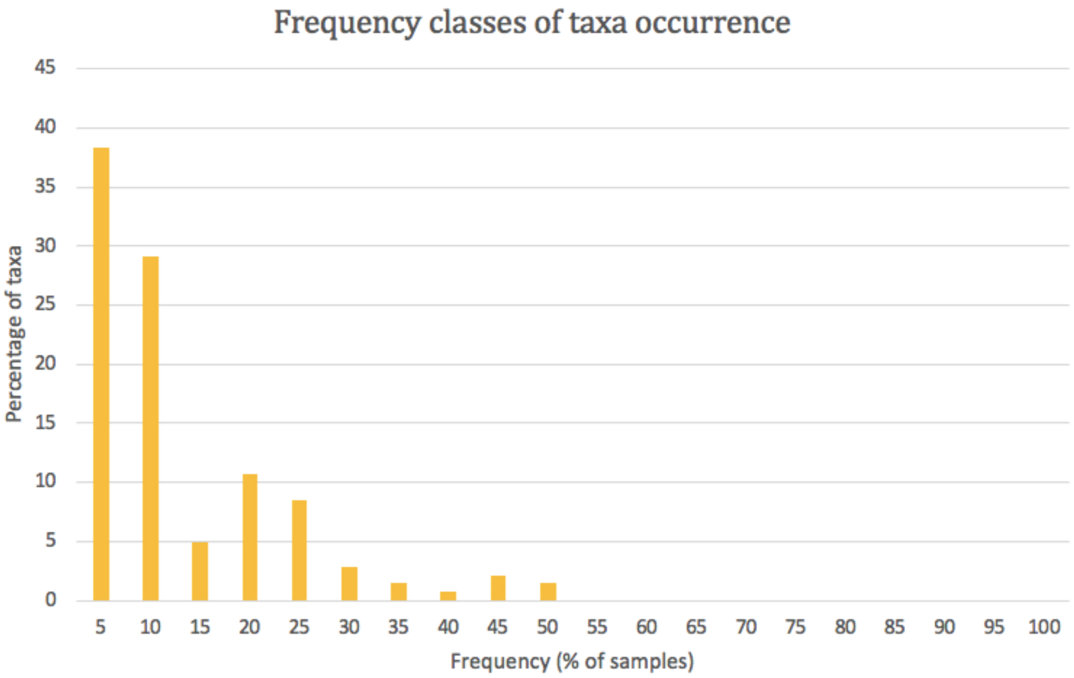

Figure 6: Frequency classes of taxa occurrence in the analyzed samples (e.g. 10 indicates 6-10% of all samples).

Taxon richness per sample, based solely on the valve counts, varied from 3 to 37 taxa, with a median value of 15 taxa per sample. Sample CA-256 had the highest number of taxa whereas sample CA-296 only yielded three taxa and was almost entirely dominated by *Angusticopula cosmica* Goeyers & Van de Vijver. Figure 5 clearly shows that most samples contained less than 20 taxa. More diverse samples with more than 25 taxa were rather scarce. As can be seen in figure 6, a large number of taxa was restricted to only a limited number of samples. Almost 38% of all taxa occurred in less than 5% of the samples, 29% of taxa occurred in 6-10%, etc. Additionally, very few taxa (1%) occurred

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 & Bukhtiyarova	19.2
Humidophila (Lange-Bertalot & Werum) R.L.Lowe *et al.*	15.2
Psammothidium Bukhtiyarova & Round	13.0
Pinnularia Ehrenberg	5.5
Angusticopula Houk *et al.*	5.3
Ferocia Van de Vijver & Houk	4.5
Eunotia Ehrenberg	4.3
Cocconeis Ehrenberg	3.7
Diatomella Greville	3.5
Fragilaria Lyngbye	2.7
Other	23.2

Table 2: summary of the genera and their frequency (%). Frequency refers to the percentage of samples that contain the genus.

Genera Campbell Island	Frequency (%)
Humidophila (Lange-Bertalot & Werum) R.L.Lowe *et al.*	75
Pinnularia Ehrenberg	71.9
Psammothidium Bukhtiyarova & Round	68.8
Angusticopula Houk *et al.*	59.4
Planothidium Round & Bukhtiyarova	59.4
Diatomella Greville	50
Frustulia Rabenhorst	40.6
Adlafia Gert Moser *et al.*	37.5
Gomphonema Ehrenberg	37.5
Nupela Vyverman & Compere	37.5

in 50% or more of all samples. The most taxon-rich genera were *Pinnularia* Ehrenberg (17 taxa or 12.1% of all taxa in total), *Psammothidium* Bukhtiyarova & Round (10 taxa or 7.1%) and *Humidophila* R.L.Lowe et al. (9 taxa or 6.4 %), respectively.

In terms of abundance, *Planothidium* Round & Bukhtiyarova (19.2% of all counted valves), *Humidophila* (15.2%), *Psammothidium* (13.0%), *Pinnularia* (5.5%), *Angusticopula* Houk, Klee & H.Tanaka (5.3%), *Ferocia* Van de Vijver & Houk (4.5%) and *Eunotia* Ehrenberg (4.3%) were the most important genera in this study (see table 1). Together, these 7 genera represented 67% of all counted valves, although the remaining 38 genera represented 61% of all observed taxa in the Campbell Island samples. 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 (2.8% and 2.1% of the total number of taxa, respectively). In terms of frequency, *Humidophila* (75%), *Pinnularia* (71.9%), *Psammothidium* (68.8%), *Angusticopula* (59.4%), *Planothidium* (59.4%), *Diatomella* (50%) and *Frustulia* (40.6%) were the most important genera in this study.

The most common taxa encountered in this thesis were *Planothidium renei* (Lange-Bertalot & Rol.Schmidt) Van de Vijver (15.2% of total counted valves), *Humidophila costei* (Le Cohu & Van de Vijver) R.L.Lowe et al. (4.8%), *Ferocia houkiana* Goeyers & Van de Vijver (4.5%), *Psammothidium cf. confusiforme* Van de Vijver & Beyens (3.7%), *Cocconeis placentula s.l.* Ehrenberg (3.7%), *Diatomella balfouriana* Greville (3.5%) and *Psammothidium cf. confusum* (Manguin) Van de Vijver (3.4%). *Planothidium renei* represented more than 15% of all counted valves and was also observed in 50% of the samples. Similarily, *Diatomella balfouriana* was present in 50% of the samples, but represented only 3.5% of all counted valves. None of the taxa occurred in all of the samples. Together, the seven most common taxa represented 39% of all counted diatom valves. On the other extreme of the abundance range, 45 taxa (almost one third of all observed taxa) together accounted for only 1% of all counted diatom valves.

Table 3: summary of the 20 most abundant taxa observed during this study.

Taxon name	**% of counted valves**
Planothidium renei (Lange-Bertalot & Rol.Schmidt) Van de Vijver	15.2
Humidophila costei (Le Cohu & Van de Vijver) R.L.Lowe *et al.*	4.8
Ferocia houkiana Goeyers & Van de Vijver	4.5
Psammothidium cf. confusiforme Van de Vijver & Beyens	3.7
Cocconeis placentula s.l. Ehrenberg	3.7
Diatomella balfouriana Greville	3.5
Psammothidium cf. confusum (Manguin) Van de Vijver	3.4
Fragilaria spA-CA	2.7
Rossithidium sp1-CA	2.6
Planothidium subantarcticum Van de Vijver & C.E.Wetzel	2.3
Psammothidium cf. incognitum (Krasske) Van de Vijver	1.7
Angusticopula chilensis Houk *et al.*	1.6
Nupela sp1-CA	1.5
Humidophila nienta (J.R.Carter) R.L.Lowe *et al.*	1.4
Psammothidium manguinii (Hustedt) Van de Vijver	1.0
Humidophila biceps (Grunow in Van Heurck) Furey *et al.*	0.8
Planothidium aueri (Krasske) Lange-Bertalot	0.7
Pinnularia carteri Krammer	0.6
Diploneis subovalis Cleve	0.4
Psammothidium antarcticum B. Van de Vijver	0.4

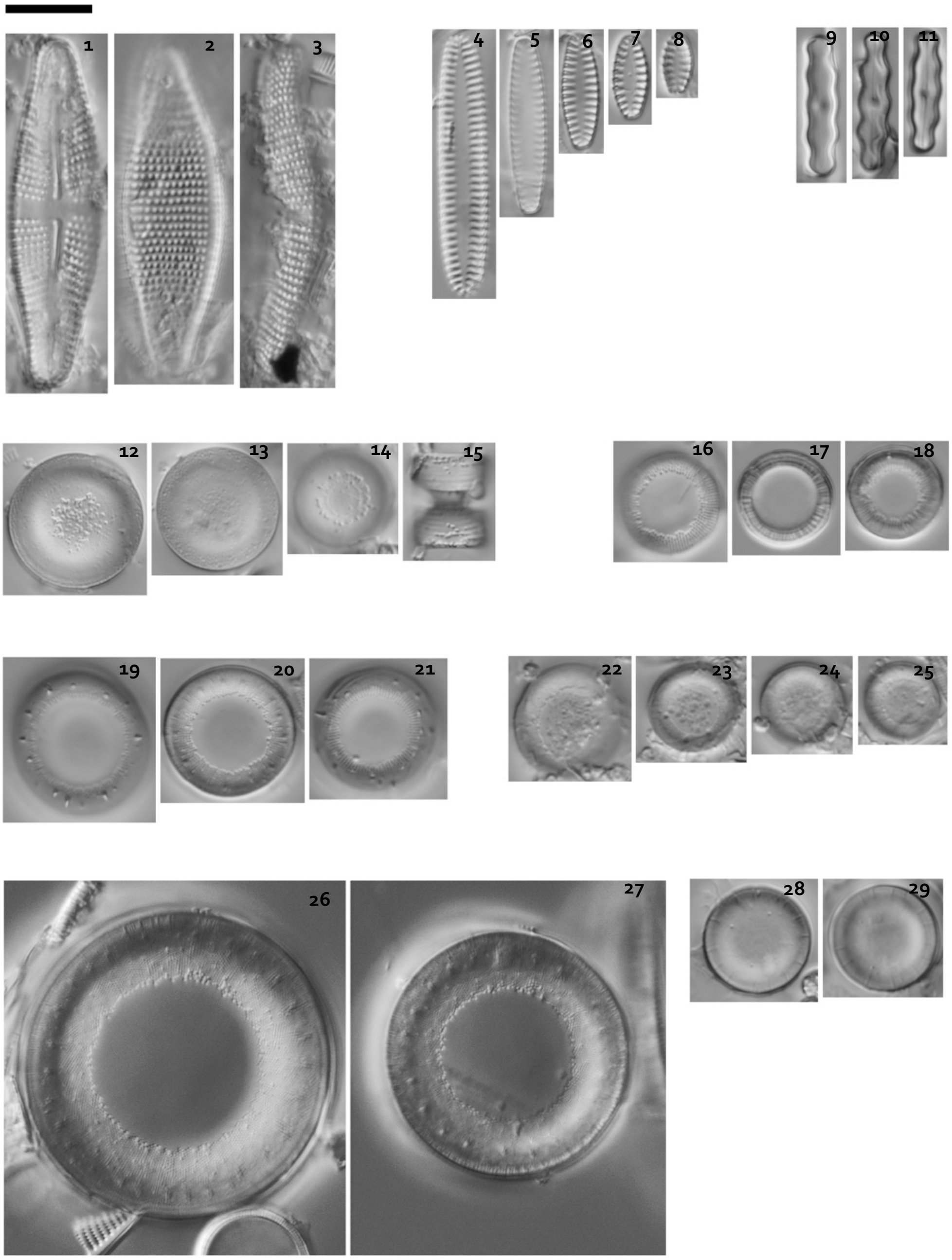

Figure 7: overview of the taxa that could not be identified using the available literature. (1-3) *Achnanthes muelleri*, (4-8) *Frankophila dalevittii,* (9-11) *Adlafia tenuis,* (12-15) *Ferocia houkiana,* (16-18) *Arcanodiscus indistinctus,* (19-21) *Arcanodiscus crawfordianus,* (22-25) *Arcanodiscus saundersianus,* (26-27) *Angusticopula cosmica,* (28-29) *Angusticopula chilensis.* Scale bar = 10 µm.

During the course of this thesis, a large number of taxa were found that could not be identified using the currently available literature. Even after detailed taxonomic analysis, scanning electron microscopic observations and comparison with similar taxa, an identification was not possible. The majority of these taxa can be considered new to science, but the procedure to describe them formally is time-consuming and labour-intensive, due to the often obscure literature that needs to be updated and verified.

Nevertheless, some of these unknown taxa were analysed in more detail. Based on the results, they were successfully described within the framework of this thesis following all the rules of the International Code for Botanical Nomenclature. The publications in which these new taxa appeared can be found in the Appendix (Appendix H). Figure 7 gives an overview of the different species using LM-images. One new taxon, the araphid *Frankophila dalevittii* Van de Vijver & Goeyers, was described in the small genus *Frankophila,* and was named in honour of Prof. Dr Dale Vitt (see Appendix H3). Prof. Dr Vitt collected the moss-samples on Campbell Island in 1969-1970 and was most helpful during the course of this thesis [120]. Five other taxa were described in centric genera that are typically observed in terrestrial samples: *Angusticopula cosmica*, *Arcanodiscus crawfordianus* Goeyers & Van de Vijver, *A. indistinctus* Goeyers & Van de Vijver, *A. saundersianus* Goeyers & Van de Vijver and *Ferocia houkiana.*

Several other already described taxa required further taxonomic treatment: *Angusticopula chilensis* (Grunow) Houk et al. and *Achnanthes muelleri* G.W.F.Carlson were only known from a handful of light microscopic illustrations (*A. chilensis*) or a line drawing (*A. muelleri*), since the original material was lost. As large populations of these species were observed in the material from Campbell Island, they could be illustrated for the first time using SEM. This allowed a refinement of their description, an emendation of the original description of *Achnanthes muelleri*, and a formal epitypification, which is a ‘supportive type’ that greatly improves our taxonomic knowledge of that taxon [121]. Finally, *Navicula tenuis* Krasske*,* was morphologically analysed in combination with the analysis of the original type material (slide and material kept in the Krasske collection in Kassel, Germany). The results showed that the taxon should be placed in a different genus and thus a formal transfer was made to the genus *Adlafia.* As the original name, *Navicula tenuis,* had already been used before by another author, this ‘taxonomic mistake’ by Krasske had to be corrected in the paper.

3.2 BIOGEOGRAPHY OF THE MOSS-INHABITING DIATOM FLORAS

Table 4: Overview of the number of samples, the number of observed taxa, the estimated number of species based on CHAO2 Species estimator, the % of theoretically maximum number of taxa and the minimum and maximum observed taxa.

Locality	Nr of samples	Nr of observed taxa	CHAO2 calculated taxa	%	Min-max
Campbell Island	32	141	188	75.0	3-37
Prince Edward Islands	219	162	171	94.7	4-58
Iles Crozet	101	137	146	93.8	9-48
Iles Kerguelen	172	165	170	97.1	6-62
Heard Island	139	156	169	92.3	7-56
South Georgia	36	76	91	83.5	5-29
Maritime Antarctica	79	85	86	98.8	7-40

Table 5: results of the similarity analysis based on the Sørensen Community Index. Numbers are in %.

	CI	MA	KE	CR	HE	PE	SG
CI		13	13	36	33	32	19
MA			16	17	14	14	16
KE				81	86	81	51
CR					76	71	49
HE						79	52
PE							49

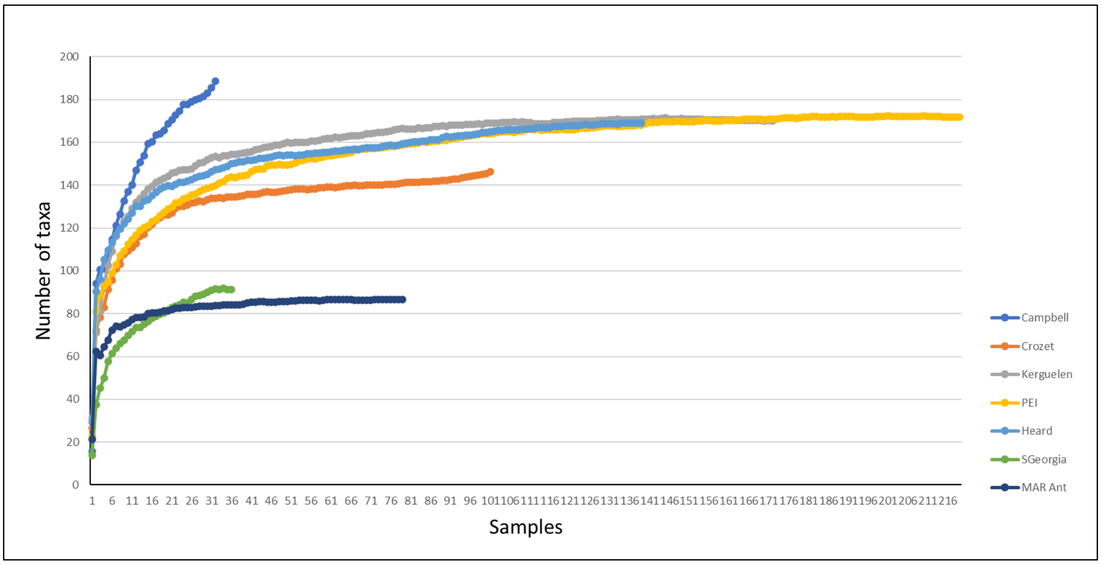

Figure 8: species accumulation curves for all investigated Antarctic localities

To assess whether the moss-inhabiting diatom flora from Campbell Island has a unique composition compared to the rest of the sub-Antarctic and Maritime Antarctic region, the floras from several localities were compared using a simple biogeographical analysis. Prior to this analysis, it was necessary to verify whether the observed flora in the analysed samples sufficiently represented the actual flora that is theoretically present on the islands. A theoretical estimation was done using the program EstimateS [116]. The estimation is based on the maximum number of taxa that could be found when an endless number of samples would be theoretically analysed. The results show that only 75% of the theoretical maximum number of taxa was observed during the study of the Campbell Island samples. This is clearly lower than the other sub-Antarctic localities (83.5-98.8%) (see Table 4 for an overview of all localities).

The similarity analysis shows that the moss-inhabiting diatom flora from Campbell Island has a very low similarity with the other sub-Antarctic and Maritime Antarctic localities (see Table 5). The similarity with Maritime Antarctica is the lowest (13%), whereas the highest similarity is reached with Iles Crozet (36%). On the other hand, the islands in the southern Indian Ocean (Iles Crozet, the Prince Edward Islands, Iles Kerguelen and Heard Island) show very high similarities between them. The highest similarity is found between Iles Kerguelen and Heard Island (86% similarity), Iles Crozet (81%) and the Prince Edward Islands (81%). Heard Island and the Prince Edward Islands (79%), Iles Crozet and Heard Island (76%) and Iles Crozet and the Prince Edward Islands (71%) share a high number of taxa as well. Furthermore, South Georgia, located in the southern Atlantic Ocean, shares less taxa with the islands of the southern Indian Ocean, resulting in lower similarity values (0.49-0.51). The island also has a low similarity with Campbell Island.

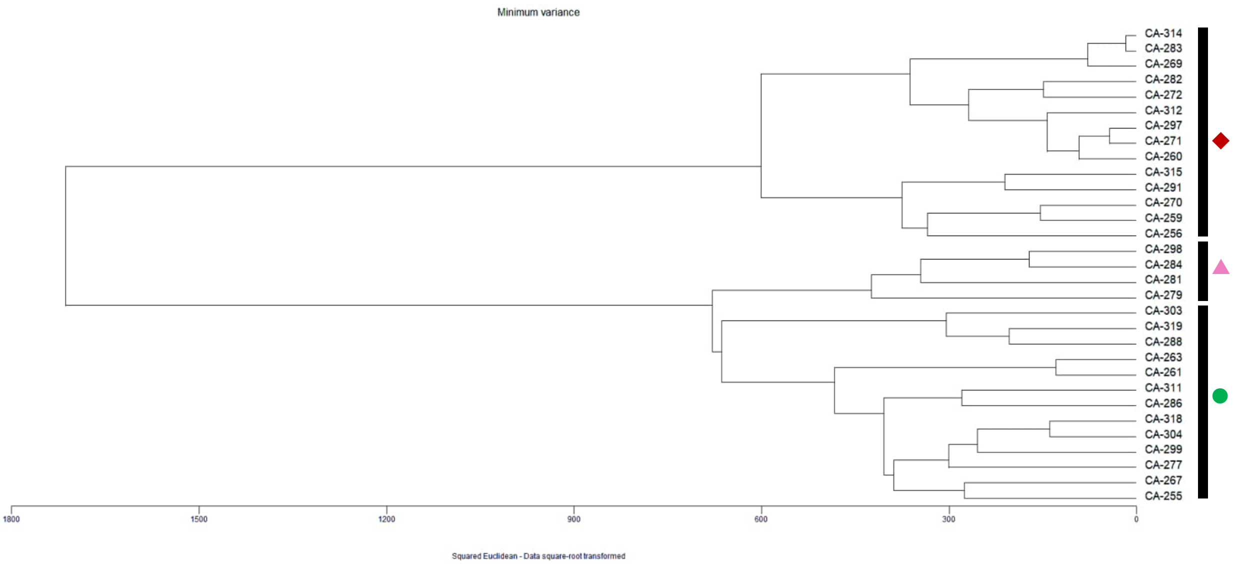

Figure 9: cluster diagram of the Campbell Island moss samples, performed with MVSP. Three main diatom assemblages can be distinguished (Group I = ◆, samples CA-314-256; Group II = ●, samples CA-303-255; Group III = ▲, samples CA-298-279). Sample CA-296 was identified as outlier and was subsequently removed. A bigger version of this image can be found in the Appendix.

3.3 MOSS-INHABITING DIATOM COMMUNITIES FROM CAMPBELL ISLAND

The cluster analysis and DCA ordination statistics separated the Campbell Island moss samples into three distinct diatom groups (see Figures 9-10). One sample, CA-296, was entirely dominated by one taxon and therefore proved to be an outlier. It was subsequently removed from further analysis. The first two DCA axes (eigenvalues λ_1 = 0.695, λ_2 = 0.470) explained 16.3% of the variation in the diatom composition with an additional 6.3% explained on the next two axes (see Table 6). Table 7 gives an overview of the dominating taxa in each of these three sample groups, whereas table 8 gives an overview of the numeric sample characteristics.

Table 6: summary of the ordination results of the DCA analysis

DCA Campbell Island moss samples	**Axis 1**	**Axis 2**	**Axis 3**	**Axis 4**
Eigenvalues	0.695	0.470	0.261	0.188
Lengths of gradient (SD units)	5.100	4.476	3.217	2.776
Cumulative % variance of species	9.7	16.3	19.9	22.6

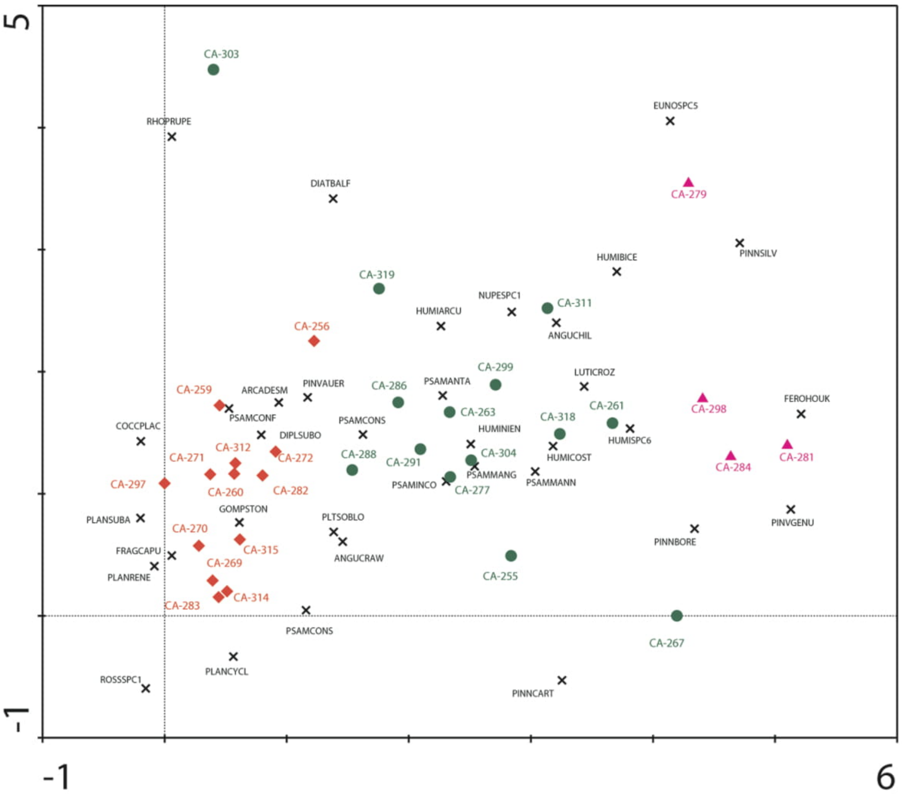

Figure 10: DCA-analysis showing the Campbell Island samples plotted on the first two axes. 1 outlier (CA-296) was removed. Separation of the groups was based on cluster analysis, performed in MVSP. ◆ = group I, ● = group II, ▲= group III. Black crosses indicate taxa that determine the position of the samples in the DCA-diagram. Full names of these taxa can be found in the Appendix (table B1).

The first group (Group I = ◆) is located on the far lower left of the DCA-diagram and contains moss samples collected from wet, submerged and rocky areas, for example wet cliffs nearby waterfalls, boggy soil streams, seepy limestone bluffs and wet rocks. The group is dominated by taxa in the genera *Planothidium* (41.6% of total counted valves), *Psammothidium* (13.3%) and *Cocconeis* Ehrenberg (8.3%), with *Planothidium renei* (34.4%) as dominating taxon and *Cocconeis placentula s.l.* (8.3%), *Psammothidium cf. confusum* (6.9%), *Fragilaria sp.A* (6%) and *Rossithidium sp.1* (6%) as sub-dominant taxa. The second group (Group II = ●) is located in the middle of the DCA-diagram. Moss samples in this group were collected on cliffs, overhangs and wet rocks and is dominated by the genera *Humidophila* (31.8%), *Psammothidium* (17.5%), *Diatomella* (7.9%) and *Eunotia* (5.2%). This second assemblage show a high abundance of *Humidophila costei* (11.6%), *Humidophila sp.6* (8.8%), *Diatomella balfouriana* (7.8%), *Humidophila arcuata* (5.6%) and *Psammothidium mannensianum* (4.3%). The third group (Group III = ▲) is located on the right side of the diagram. The moss samples of this assemblage were collected in terrestrial habitats in dry or saline localities, such as dried up seal wallows and rocks above the ocean. The genera *Ferocia* (33%), *Pinnularia* (29.6%), *Eunotia* (13%) and *Humidophila* (12.8%) showed the highest abundance in this assemblage, while *Ferocia houkiana* (33%) was the dominant taxon. *Pinnularia austroshetlandica* (14.4%), *Eunotia sp.1* (12.5%), *Humidophila sp.B* (11%) and *Pinnunavis genustriata* (5.9%) were sub-dominant.

Table 7: summary of the most abundant taxa in the three main 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%.

		Group I	Group II	Group III
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	**PINNGENU**	•	•	☐

In table 8, an overview is given of the numeric sample characteristics for each of the three diatom assemblages. Group I has a mean taxon richness of 18 and an evenness of 0.6. The Shannon-Wiener diversity index is 1.8. The number of observed taxa per sample in this assemblage ranges from 8-37, with a median value of 15 taxa per sample. Group II is characterized by a taxon richness of 17 and an evenness of 0.7. The Shannon-Wiener diversity index is the highest of the three assemblages with 1.9. The number of observed taxa per sample ranges from 6-27, with a median value of 16 taxa per sample. Group III has a mean taxon richness of 11 and an evenness of 0.5. The Shannon-Wiener diversity index is 1.2. The number of observed taxa per sample varies from 6-15, with a median value of 12 taxa per sample.

Table 8: overview of the mean taxon richness, mean evenness, mean diversity, range (max-min of taxa per sample) and median of taxa per sample in each of the three assemblages.

	Group I	**Group II**	**Group III**
Mean richness	17.8 ± 8.7	16.8 ± 6	11 ± 3.7
Mean evenness	0.6 ± 0.1	0.7 ± 0.1	0.5 ± 0.1
Mean diversity	1.8 ± 0.6	1.9 ± 0.4	1.2 ± 0.5
Max	37	27	15
Min	8	6	6
Median	15	16	12

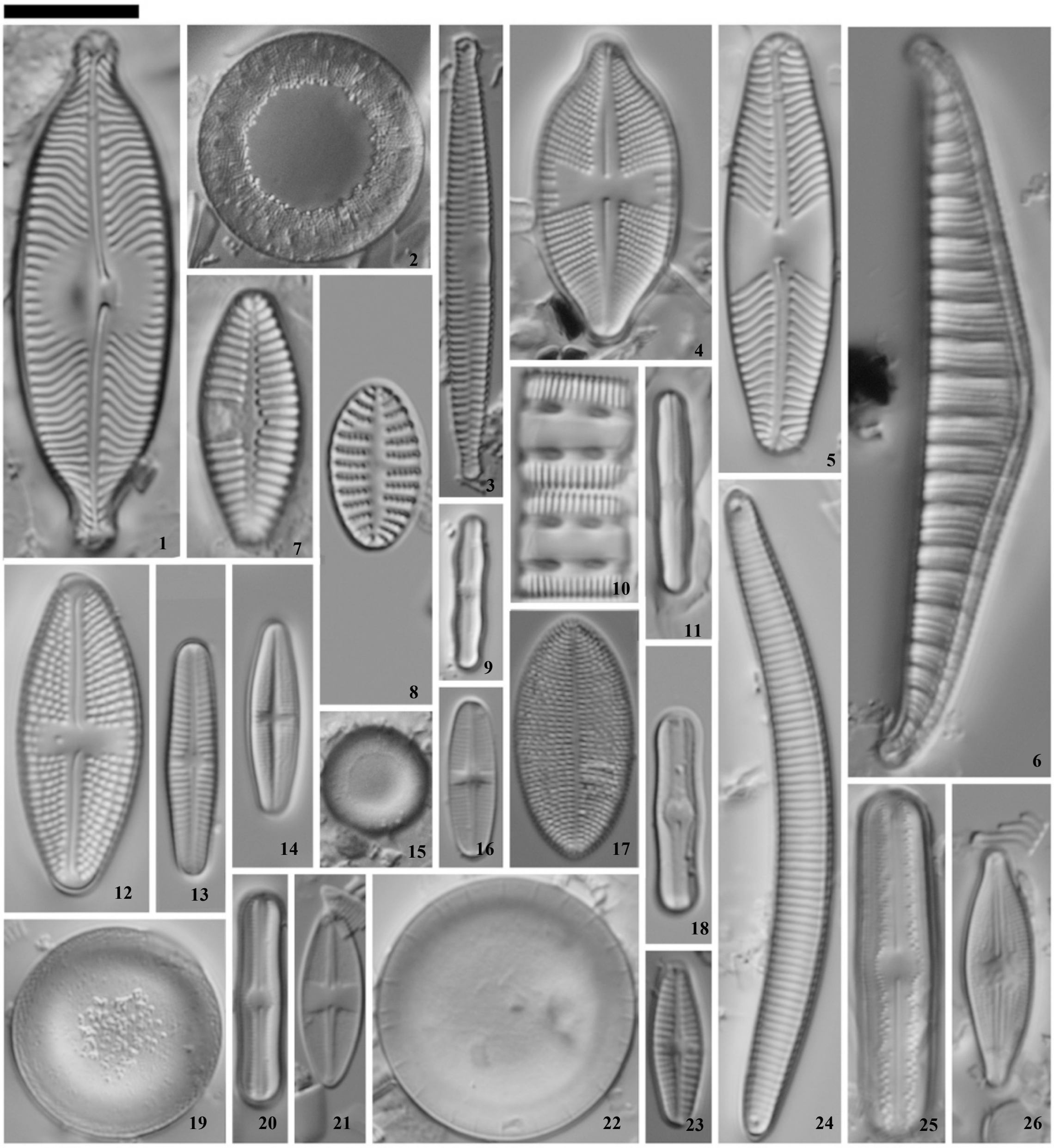

Figure 11: 26 most abundant diatom taxa (based on valve counts). (1) *Pinnunavis genustriata,* (2) *Angusticopula cosmica,* (3) *Fragilaria sp. A*, (4) *Psammothidium mannensianum,* (5) *Pinnularia austroshetlandica,* (6) *Rhopalodia cf. rupestris,* (7) *Planothidium subantarcticum,* (8) *Platessa oblongella,* (9) *Humidophila nienta,* (10) *Diatomella balfouriana,* (11) *Humidophila sp. B,* (12) *Luticola crozetensis,* (13) *Rossithidium sp. 1,* (14) *Psammothidium cf. confusum,* (15) *Arcanodiscus desmetianus,* (16) *Psammothidium cf. confusiforme,* (17) *Cocconeis placentula s.l.,* (18) *Humidophila sp. 6,* (19) *Ferocia houkiana,* (20) *Humidophila costei,* (21) *Psammothidium cf. incognitum,* (22) *Angusticopula chilensis,* (23) *Planothidium renei,* (24) *Eunotia sp. 1,* (25) *Humidophila arcuata,* (26) *Nupela sp. 1.* Scale bar = 10 µm.

4. DISCUSSION

4.1 SPECIES DIVERSITY

Of the 66 historic moss samples that were collected from Campbell Island and that were analysed in this thesis, 34 did not contain sufficient diatom valves. Most of these samples were obtained from mosses collected in relatively dry, purely terrestrial environments. The moisture content of the mosses plays a fundamental role in the shaping of moss-inhabiting diatom communities: desiccation is not tolerated by diatoms [122]. This moisture-dependence can be an explanation for why samples from these areas contained very few diatom valves. A similar observation was made in several other studies dealing with moss-inhabiting diatoms in the sub-Antarctic region [74, 111, 112, 113, 123]. All of these studies identified moisture as one of the prime factors determining the diatom composition living on mosses. Only a handful of species, e.g. *Pinnularia borealis*, seems to be able to survive in dry habitats [123].

Only 32 samples were analysed in this 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 vs. 32 samples). The same observation can be made for the other islands in the southern Indian Ocean. One of the reasons for this difference is the fact that sampling campaigns on the southern Indian Ocean islands were entirely set up for diatom analysis (Van de Vijver, pers. comm.), whereas on Campbell Island, mosses were sampled for a moss-based study. This means that on the other islands, there was less focus on collecting a lot of different moss taxa, but rather to sample many typical diatom habitats. Unfortunately, sampling on the islands in the southern Pacific Ocean is not easy to organise and bound to a lot of regulations and permit restrictions, making a new expedition solely focused on diatom sampling in the near future very unlikely. A second explanation for this low number is the way the samples were selected prior to this thesis in 2018. The Campbell Island moss herbarium initially contained more than 1,000 samples collected during the field campaign, of which only a fraction ended up in the moss herbarium of the British Antarctic Survey (<200 according to the BAS specimen catalogue). Of this fraction, only 66 were selected. The selection was merely based on the description on the labels or on the availability of sufficient moss material to subsample. Mostly samples showing an indication of the presence of moisture (such as neighbouring waterfalls) were chosen. A more thorough sampling of this historic moss collection will yield more interesting samples that can be used for further diatom analysis.

In this study, a high number of taxa (50 taxa or 35.5% of taxa in total) could only be identified upon genus level, with an additional 25 taxa (17.7%) that were identified upon species level but with a high degree of uncertainty. Two taxa (1.4%) could not even be identified upon genus level. It is possible that the latter two either belong to marine species (for which our taxonomic knowledge is almost zero) or even to unknown, at present undescribed, genera. This lack of species-level identifications is not uncommon in Antarctic diatom studies, especially when a more critical, fine-grained taxonomy is applied. To illustrate, in the study of the diatom communities from the Prince Edward Islands conducted by Van de Vijver *et al.* (2008) [112], a total of 26 taxa (12% of total) could only be identified upon genus level, while the identity of two (0.9%) was uncertain. Some of these taxa later proved to be new to science and were described as such [62]. The difference in uncertain identifications between Campbell Island and the Prince Edward Islands is easily explained, given the tremendous taxonomic effort that was done in the southern Indian Ocean prior to 2005, whereby lots of new taxa have been described [59]. A similar taxonomic analysis for the southern Pacific Ocean is lacking. This was demonstrated by the description of several new taxa that were published the past two years, including two papers that were written during the course of this thesis [120, 124, 125]. Taxonomic efforts will have to be increased to reach the same level of taxonomic accuracy as on the Indian Ocean islands.

Although only 32 samples containing sufficient diatoms were analysed, it is clear that the Campbell Island moss diatom flora is highly diverse and well-developed. At present, only one study dealing with moss-inhabiting diatoms was carried out on Campbell Island. Hickman & Vitt (1974) [108] reported 59 epiphytic diatom taxa in only five moss samples. Unfortunately, it is not possible to compare the species list in their paper since our taxonomic knowledge of the sub-Antarctic diatom flora has been drastically updated the past 40 years. Hickman & Vitt illustrated their paper with line drawings and only a few LM pictures. The only taxon that was certainly found in common is *Diatomella balfouriana*, based on the LM pictures in Hickman & Vitt. The line drawings, however, were very hard to identify, although it appears that the majority of the names are most likely not correct anymore when using the currently available and up-to-date taxonomy. This is a common problem with old literature of the sub-Antarctic region and was already noticed when Van de Vijver and co-workers revised the sub-Antarctic flora from the Indian Ocean islands [59]. Van de Vijver *et al.* [126] revised all records of the genus *Navicula* in the Antarctic realm, based on the list in Kellogg & Kellogg (2002) [127]. The initial >250 records were brought back to less than 10, most of which had to be described as new species [126]. The observations in this thesis highlight once more the need for a thorough analysis of all Antarctic data to obtain a better idea of the biogeographical distribution of diatoms worldwide. This problem is not unique for the sub-Antarctic region, and was recently detected as well in the northern hemisphere, where force-fitting and a too broad interpretation of species descriptions led to identifications errors [128].

In 2015, Saunders *et al.* [107] identified 140 diatom taxa in a large survey of the aquatic diatom flora in ponds and lakes on Campbell Island. These samples were sent to Meise Botanic Garden and have been briefly checked (Van de Vijver, unpubl. res.). It was clear that the identifications need to be updated and corrected before a comparison with the moss diatom flora can be made. The original authors found a high number of cosmopolitan taxa and taxa that are confined to the sub-Antarctic islands in the Indian Ocean, mainly because only taxonomic information from these islands was available and the observed Campbell island flora was force-fitted into Indian island taxa (Van de Vijver, unpubl. res.). Moreover, the aquatic diatom flora can differ markedly from the moss-inhabiting flora. The moss diatom flora was dominated by typical aerophilic genera such as *Pinnularia*, *Eunotia*, *Humidophila*, *Diatomella* and several centric genera known to prefer aerial habitats [21]. On the other hand, typical aquatic genera, such as *Navicula*, *Nitzschia*, *Stauroneis* and *Gomphonema,* were less frequently observed and when present, only occurred in minor abundances. A similar observation was made for instance by Kopalová *et al.* (2014) [113] who found significant differences between the terrestrial diatom flora and the aquatic flora of the same area, whereas no differences could be detected between the aquatic moss diatom flora (=diatoms living on submerged mosses) and the aquatic benthic diatom flora. The moss samples analysed for this thesis were all entirely terrestrial. Submerged mosses were not present in the sample collection. It is possible that purely aquatic moss samples would have resulted in a higher proportion of more aquatic genera, although this remains highly speculative.

4.2 CAMPBELL ISLAND DIATOM BIOGEOGRAPHY

The biogeographical analysis of the moss-inhabiting diatom floras on the sub-Antarctic and Maritime Antarctic localities showed that the number of taxa on Campbell Island was comparable to that on the other localities. The highest numbers were found on Iles Kerguelen (165 taxa in 172 samples) and the Prince Edward Islands (162 taxa in 219 samples), although these high numbers were reached after the analysis of a much larger number of samples. Additionally, the samples were most likely also collected in a higher number of different habitats, including aquatic mosses that were lacking in the Campbell Island moss dataset. Only on South Georgia the number was much lower (76 taxa in 36 samples), which is most likely more an effect of underreporting than a reflection of the real diversity. The South Georgia study was performed in 1997, well before an elaborate taxonomic revision, and the samples have never been reanalysed, other than updating name changes (Van de Vijver, pers. comm.) It is highly probable that this number will increase in the future.

The species richness on the sub-Antarctic Islands is in clear contrast with the lower richness observed on the more southerly situated Maritime Antarctica. Kopalová *et al.* (2014) [113] observed only 130 taxa in the diatom moss flora on Livingston and James Ross Island. Both islands are located close to the Antarctic peninsula and have a lower number of different moss habitats (Van de Vijver, pers. comm.), even though aquatic mosses were included as well in the study. The difference in richness becomes even more striking when considering the moss diatom flora on the Antarctic Continent. To date, no published records exist on moss diatoms from the Antarctic Continent. One study by Bishop *et al.*, currently under revision, (Jordan Bishop is a PhD student of B. Van de Vijver and I was able to have a look at his data) reported the presence of only 49 taxa, several of which are most likely from marine origin, blown onto the mosses by wind and seaspray. Sabbe *et al.* (2003) [61] described a total of 31 diatom taxa from freshwater and saline lakes and pools in Eastern Antarctica, while Gibson *et al.* (2006) [129] reported 29 diatom taxa from various lakes, again in Eastern Antarctica. Both studies, however, dealt with aquatic diatom floras, a totally different habitat than moss. The observed trend of decreasing species richness, moving southwards, has been attributed to the harshness of the environment, geographic isolation and factors related to latitude, e.g. period of ice cover and light intensity [61, 130]. Furthermore, for comparison, the diatom flora on New Caledonia is composed of more than 750 taxa [131] and in Sweden, more than 1,500 taxa were recorded (Van de Vijver, unpubl. data). This puts the diatom richness on the sub-Antarctic islands in a different perspective. The most obvious reasons for this extreme difference include the remoteness of the Antarctic localities, their geological origin, being oceanic islands, and the higher diversity in potential diatom habitats in tropical and more temperate areas.

The species accumulation curves show that for almost every investigated Antarctic locality, a plateau was more or less reached. Moreover, the calculations show that for almost every locality, more than 90% of the theoretically possible flora was recorded. This means that the analysis of additional samples would barely increase the maximum number of taxa (see Figure 7 in the results section). For Campbell Island, on the contrary, the analysed samples do not fully represent the theoretically possible diatom flora. Therefore, it will be necessary to analyse more samples to complete the assessment of the moss-inhabiting diatom flora from Campbell Island. The choice of new samples should also better reflect the possible microhabitats on Campbell Island. As stated before, typical aquatic (submerged) mosses were barely or not included in this study, simply because they were not available.

As mentioned in the introduction, past taxonomic practices still have an enormous influence on the perception of diatom biodiversity and distribution. Due to historical force-fitting of European names to diatoms of other localities and the application of different species concepts, it is challenging to compare the results of different studies with each other. Moreover, these past practices led to the conclusion that diatom floras are cosmopolitan and show no endemism. This study hopes to contribute to the changing of this view. It has already been shown that both the Arctic and Antarctic regions differ markedly in their diatom flora. For example, when the presence of the genus *Stauroneis* was compered in both Polar regions, it appeared that only a handful of taxa were shared [65]. Furthermore, the genus *Eunotia* has a very high diversity in the northern hemisphere with more than 150 different taxa [132] whereas in the sub-Antarctic region, less than 20 taxa occurred [66]. Within the Antarctic Realm, diatom floras differ as well. The first suggestion for a biogeographical zonation of the Southern Ocean based on diatom floras was made by Hirano in 1965 [133] and later, three biogeographical regions were distinguished, based on a similarity analysis of the diatom composition of various localities [45]. A decrease in species richness was found moving southward: the islands near the Antarctic Convergence (e.g. Iles Crozet, Iles Kerguelen, Macquarie Island) have a high species richness, while areas around the Antarctic Peninsula (e.g. South Shetland Islands) have lower species numbers [45, 130]. As mentioned before, the Antarctic Continent forms a separate entity when the diatom flora is considered.

The diatom flora of the different islands in the sub-Antarctic and Maritime Antarctic region were compared in this study, to investigate possible biogeographical patterns in the distribution of diatoms. The similarity analysis shows that the islands in the southern Indian Ocean share a large number of taxa. This may point to the presence of a specific moss diatom flora on the sub-Antarctic islands of the Indian Ocean. This flora seems to be different from what was observed for South Georgia, although the flora on this island is in serious need of revision and the results need to be interpreted with care. However, the similarity with the moss diatom flora from Campbell Island, which was analysed with the most up-to-date literature, is also rather low and limited to species that are generally accepted to be more or less cosmopolitan worldwide (e.g. *Navicula gregaria*) or only widespread in the entire sub-Antarctic region (e.g. several *Psammothidium* taxa).

Campbell Island is unique in many aspects. Several genera that are known to be typically epiphytic, such as *Epithemia*, *Rhopalodia* and *Cocconeis*, are almost absent on the other sub-Antarctic islands, but present in often large populations on Campbell Island. Several genera, such as *Frustulia*, *Sellaphora*, *Psammothidium* and some centric genera, seem to have known a higher degree of speciation on Campbell Island. The fact that most of these taxa could at present not be identified using the currently available literature, confirms this possible higher level of speciation. It is unclear why and when this speciation took place. Molecular phylogenetic analysis may be helpful in solving this question, but for this, new sampling will be necessary. The uniqueness of the Campbell Island diatom flora can be explained in various ways. Campbell Island is an oceanic island and therefore all botanical organisms that are today present 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 so-called circum-Antarctic current and diatoms could easily disperse from the southern Indian Ocean islands. The fact that several of the at present unidentified taxa showed 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 species, except being triple in size [64]. An extra 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 wind patterns 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 [134, 135]. Moreover, Campbell Island is located nearby New Zealand and Tasmania. Unfortunately, the diatom flora of these larger land masses is barely known. Published literature [136, 137] is far from complete and filled with taxonomic mistakes. Nevertheless, several taxa from the genera *Stauroneis* and *Actinella* were found to be present on Tasmania as well. 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.

To complete the biogeographical discussion of the Campbell Island flora, it should be noted that the Maritime Antarctic flora is quite different, which is expressed in the rather low similarity value. This observation holds true for all other sub-Antarctic islands as well and is not surprising, as the Maritime Antarctic region shows large differences in climate and geology, both having a severe impact on the different diatom microhabitats [113, 138]

4.3 CAMPBELL ISLAND DIATOM COMMUNITIES

The samples in this thesis were collected during a sampling campaign in 1969-1970 by Prof. Dr Dale Vitt. The campaign was organized for the sampling of mosses, liverworts and lichens [108]. Detailed ecological information necessary for a thorough diatom analysis, other than mentioned on the sample labels or in the paper of Hickman & Vitt (1974) [108], was unfortunately not available. Measurements that could be explanatory for the separation of the diatom assemblages, such as temperature, pH, salinity, water level fluctuation, etc. are lacking, although in previous studies, these parameters could not explain the observed distinctions between clusters [111]. The exact factors that determine these main diatom groups are not known and it is therefore plausible that the following explanation is insufficient and will have to be updated in the future. Nevertheless, three assemblages could be distinguished in this study, based on the community analysis.

Moisture content of mosses plays a pivotal role in the composition of moss-inhabiting diatom communities. It is therefore suggested that in this study, moisture content is most likely also the main determining factor in shaping the three diatom assemblages. This is reflected in the sampling locations of the groups. Samples from Group I were collected in predominantly wet areas, such as rocks in waterfalls, boggy soil streams, wet cliffs and wet limestone. This first assemblage showed the highest mean taxon richness and the highest number of taxa observed in a single sample. *Planothidium* and *Psammothidium* are the most important genera. Both genera show an often-restricted biogeographical distribution in the (sub-)Antarctic Region [64]. *Psammothidium* is often found in epilithic (= growing on stones or stonelike material) environments, which can be confirmed by their abundance in this group. *Psammothidium cf. confusum* for example, 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 [74, 110]. *Planothidium renei,* another diatom with a restricted sub-Antarctic distribution, was the dominating taxon in this group, found in almost all samples of Group I, some samples of Group II and never in Group III. *Cocconeis placentula s.l.* was regularly present in this assemblage as well. It is one of the most common taxa found in freshwater bodies and its distribution seems to be cosmopolitan [139], considering *C. placentula* was first described 170 years ago by

Ehrenberg from freshwater localities in Berlin. It was found in three samples from Group II but never in Group III. Furthermore, unidentified representatives of *Fragilaria* and *Rossithidium* have been observed in this assemblage 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 Group I and was only found in one sample of Group II (and never in Group III), this study carefully 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 the diatom communities in running water bodies such as rivers; waterfalls and brooks [45, 112]. 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 [140, 141, 142]. 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 samples grouped in the second assemblage were mainly collected in moist and rocky areas, often with restricted light conditions, e.g. on wet rocks, under overhangs, on cliff faces, in crevices and dark wet recesses. This group 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 in this second group, with *H. costei* being the most dominant. Only *H. costei* was found in the other assemblages, however only scarcely. As the name of the genus already suggests, most taxa belonging to *Humidophila* are often found in moist, humid and aerophilous habitats [143], which can be confirmed by the observations 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 communities [112]. On Amsterdam Island, shaded areas had high abundances of several *Humidophila* taxa (although not the same taxa as on Campbell Island were found) (B. Chattová, unpubl. data). *Diatomella* had only one representative taxon with *Diatomella balfouriana.* This diatom genus has a typical biogeographical distribution in Polar and mountainous regions, while *Diatomella balfouriana* is its most reported and widespread taxon [144]. Although *D. balfouriana* was very dominant in the second assemblage, it was frequently observed as well in Group I and never in Group III. This can be explained by the often dry and saline areas in which samples from Group III were collected. *Psammothidium mannensianum* was also abundant in this second assemblage and the previous observation that *P. mannensianum* often co-occurs with *P. manguinii* [64] can be confirmed here*. Psammothidium mannensianum* was never found in the other assemblages, although *P. manguinii* was observed in one sample from Group I. Species of the *P. manguinii* complex are often found in dry, terrestrial areas [64]. On Ile de la Possession, the main island of the Iles Crozet, *P. manguinii* of mainly observed in bare soils in caves and on fellfields [59].

The third group was composed of moss samples collected from terrestrial habitats in dry or saline localities, such as dried up seal wallows and rocks above the ocean. 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 Group I. In Group II, *F. houkiana* was observed in samples that were collected in crevices, while in Group III, it was most abundant in samples collected on rocks and recesses. This could suggest a tolerance for drier environments*. Pinnularia austroshetlandica* is very dominant as well in this assemblage, 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 communities living on rocks nearby and above oceans are often influenced by salty sea-spray. *Pinnunavis genustriata,* another sub-dominant taxon in Group III, was found as well in this sample 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 Group II and III, in samples collected on rock ledges, cliff ledges and a recess nearby 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 [145]. 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.

5. CONCLUSION

Diatoms are one of the most abundant groups of algae on Earth's Polar regions and function as excellent bio-indicators for environmental changes. The principal goal of this thesis was to update diatom taxonomy in the sub-Antarctic region, to enable the further use of diatoms as bio-indicators and to increase our understanding of their biogeographical distribution. The moss-inhabiting diatom flora of Campbell Island, retrieved from a historic moss collection, was analysed and compared with the floras of other islands of the sub-Antarctic and Maritime Antarctic region. Although a high number of samples could not be analysed due to the presence of insufficient diatoms, a well-developed flora of 141 different taxa belonging to 45 genera was revealed. A high number of taxa could only be described upon genus level, which is common for diatom studies in the Antarctic region and highlights the need for future (fine-grained) taxonomic studies in this region. Six new taxa were formally described: *Frankophila dalevittii*, *Angusticopula cosmica*, *Arcanodiscus crawfordianus*, *A. indistinctus*, *A. saundersianus* and *Ferocia houkiana*. *Angusticopula chilensis* and *Achnanthes muelleri* were subjected to further taxonomic treatment and *Navicula tenuis* was formally transferred to the genus *Adlafia*. The biogeographical analysis showed that the number of taxa on Campbell Island was comparable to that on the other localities, although the analysed samples do not fully represent the theoretically possible diatom flora. Therefore, it is vital to analyse more samples in the future to complete the assessment of the moss-inhabiting diatoms from Campbell Island. New samples should also better reflect possible microhabitats on the island. The similarity analysis of this study showed a highly comparable flora on the islands of the Indian Ocean, pointing to a specific moss diatom community in this region. The similarity of these islands and Campbell Island was low, and Campbell Island seems to be unique in many aspects, e.g. several typically epiphytical genera are present (while absent on other islands) and some genera seem to have known a higher degree of speciation. This is confirmed by the many taxa that could not be identified. Moreover, many Campbell Island taxa are shared with South America, and a possible similarity with New Zealand and Tasmania still needs to be confirmed, although taxonomy in these localities needs to be updated as well. The flora of Maritime Antarctica seems to be quite different, expressed by the low similarity value. Furthermore, three Campbell Island diatom assemblages were distinguished, in which moisture level could be the main determining factor shaping the diatom communities.

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APPENDIX

Figure 12: view of Campbell Island with its characteristic and native Campbell Island daisies (*Pleurophyllum speciosum*). Image © Young Adventurers

APPENDIX A: LITERATURE USED FOR IDENTIFICATIONS

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APPENDIX B. LIST OF DIATOM TAXA

Table B1: List of diatom taxa and DCA-codes of the Campbell Island moss samples. Relative abundances (RA; given in %) refer to the percentage of all counted valves for each taxon.

Taxon	Code	RA (%)
Achnanthes muelleri G.W.F.Carlson	**ACHNMUEL**	0,2
Achnanthidium cf. sieminskae Witkowski *et al.*	**ACHMSIEM**	0,0
Achnanthidium modestiforme (Lange-Bertalot) Van de Vijver	**ACHMMODE**	0,1
Achnanthidium sp1-CA	**ACHMSPC1**	0,0
Actinella parva Vanhoutte & Sabbe	**ACTIPARV**	0,3
Adlafia bryophila (J.B.Petersen) Moser *et al.*	**ADLABRYA**	0,2
Adlafia cf. bryophiloides (Manguin) Van de Vijver	**ADLACFBR**	0,0
Adlafia sp1-CA	**ADLASPC1**	0,9
Adlafia sp2-CA	**ADLASPC2**	0,2
Adlafia sp5-CA	**ADLASPC5**	0,0
Adlafia tenuis Van de Vijver & Goeyers	**ADLATENU**	0,0
Angusticopula chilensis Houk et al.	**ANGUCHIL**	1,6
Angusticopula cosmica Goeyers & Van de Vijver	**ANGUCOSM**	3,1
Arcanodiscus crawfordianus Goeyers & Van de Vijver	**ARCACRAW**	0,6
Arcanodiscus desmetianus Van de Vijver	**ARCADESM**	2,4
Brachysira cf. neoexilis Lange-Bertalot	**BRACNEOE**	0,1
Caloneis marnieri Manguin	**CALOMARN**	0,0
Cavinula heterostauron var. rostrata (H.Germain) B. van de Vijver	**CAVIHERO**	0,0
Chamaepinnularia australomediocris (Lange-Bertalot & Rol.Schmidt) Van de Vijver	**CHAMAUST**	0,1
Chamaepinnularia soehrensis var. muscicola (J.B.Petersen) Lange-Bertalot & Krammer	**CHAMSOEH**	0,0
Chamaepinnularia sp2-CA	**CHAMSPC2**	0,0
Chamaepinnularia sp3-CA	**CHAMSPC3**	0,2
Cocconeis placentula s.l. Ehrenberg	**COCCPLAC**	3,7
Delicata cf. delicatula (Kützing) Krammer	**DELIDELI**	0,0
Diatomella balfouriana Greville	**DIATBALF**	3,5
Diploneis subovalis Cleve	**DIPLSUBO**	0,4
Encyonema neogracile Krammer	**ENCYNEOG**	0,0
Encyonema sp1-CA	**ENCYSPC1**	0,0
Encyonema sp14-CA	**ENCYSP14**	0,0
Encyonema sp15-CA	**ENCYSP15**	0,0
Encyonema sp2-CA	**ENCYSPC2**	0,1
Encyonopsis sp1-CA	**ENCSSPC1**	0,0
Encyonopsis sp3-CA	**ENCSSPC3**	0,0
Encyonopsis sp6-CA	**ENCSSPC6**	0,0
Epithemia cf. adnata (Kützing) Brébisson	**EPITADNA**	0,1
Eunotia cf. bidens Ehrenberg	**EUNOBIDE**	0,1
Eunotia cf. papilio (Ehrenberg) Grunow	**EUNOPAPI**	0,0
Eunotia sp1-CA	**EUNOSPC1**	0,0
Eunotia sp2-CA	**EUNOSPC2**	0,8
Eunotia sp12-CA	**EUNOSP12**	0,1
Ferocia houkiana Goeyers & Van de Vijver	**FEROHOUK**	4,5
Fragilaria spA-CA	**FRAGCAPU**	2,7
Frankophila dalevittii Van de Vijver & Goeyers	**FRANDALE**	0,9
Frustulia cf. crassinervia (Brébisson ex W.Smith) Lange-Bertalot & Krammer	**FRUSCRAS**	0,1
Frustulia cf. saxonica Rabenhorst	**FRUSSAXO**	0,4
Frustulia sp1-CA	**FRUSSPC1**	0,0
Frustulia sp4-CA	**FRUSSPC4**	0,1
Frustulia sp6-CA	**FRUSSPC6**	0,1
Frustulia sp7-CA	**FRUSSPC7**	0,0
Geissleria sp1-CA	**GEISSPC1**	0,0
Gomphonema sp13-CA	**GOMPSP13**	0,0
Gomphonema sp3-CA	**GOMPSP3**	0,1
Gomphonema sp6-CA	**GOMPSP6**	0,3
Gomphonema sp8-CA	**GOMPSP8**	0,5
Gomphonema stonei E.Reichardt	**GOMPSTON**	0,6
Hantschia sp1-CA	**HANZSPC1**	0,1
Hantschia sp2-CA	**HANZSPC2**	0,4

Table B1: continued

Hantzschia amphioxys (Ehrenberg) Grunow	**HANZAMPH**	0,1
Humidophila arcuata (Lange-Bertalot) R.L.Lowe *et al.*	**HUMIARCU**	2,3
Humidophila biceps (Grunow in Van Heurck) Furey *et al.*	**HUMIBICEP**	0,8
Humidophila costei (Le Cohu & Van de Vijver) R.L.Lowe *et al.*	**HUMICOST**	4,8
Humidophila crozetikerguelensis (Le Cohu & Van de Vijver) R.L.Lowe *et al.*	**HUMICROZ**	0,1
Humidophila ingeae (Van de Vijver) R.L.Lowe *et al.*	**HUMIINGE**	0,3
Humidophila nienta (J.R.Carter) R.L.Lowe *et al.*	**HUMINIEN**	1,4
Humidophila sp6-CA	**HUMISPC6**	3,6
Humidophila spA-CA	**HUMISPCA**	0,5
Humidophila spB-CA	**HUMISPCB**	1,5
Incertae sedis 1-CA	**INCESPC1**	0,0
Incertae sedis 2-CA	**INCESPC2**	0,0
Kobayasiella cf. subantarctica Van de Vijver & Vanhoutte	**KOBASUBA**	0,2
Lecohuia geniculata (H.Germain) Lange-Bertalot & U.Rumrich	**LECOGENI**	0,4
Luticola crozetensis Van de Vijver *et al.*	**LUTICROZ**	1,5
Luticola muticopsis (Van Heurck) D.G.Mann	**LUTIMUTI**	0,0
Luticola sp4-CA	**LUTISPC4**	0,2
Luticola sp5-CA	**LUTISPC5**	0,1
Luticola sp6-CA	**LUTISPC6**	0,0
Navicula bicephala Hustedt	**NAVIBICE**	0,0
Navicula gregaria Donkin	**NAVIGREG**	0,1
Navicula sp1-CA	**NAVISPC1**	0,0
Navicula sp10-CA	**NAVISP10**	0,0
Navicula sp11-CA	**NAVISP11**	0,0
Navicula sp2-CA	**NAVISPC2**	0,0
Navicula sp4-CA	**NAVISPC4**	0,0
Naviculadicta elorantana Lange-Bertalot	**NAVDELOR**	0,1
Nitzschia acidoclinata Lange-Bertalot	**NITZACID**	0,2
Nitzschia archibaldii Lange-Bertalot	**NITZARCH**	0,0
Nitzschia communis Rabenhorst	**NITZCOMM**	0,0
Nitzschia gracilis Hantzsch	**NITZGRAC**	0,0
Nitzschia palustris Hustedt	**NITZPALU**	0,0
Nitzschia spA-CA	**NITZSPCA**	0,0
Nitzschia tubicola Grunow	**NITZTUBI**	0,0
Nupela cf. chilensis (Krasske) Lange-Bertalot	**NUPECHIL**	0,3
Nupela sp1-CA	**NUPESPC1**	1,5
Pinnularia acidicola Van de Vijver & Le Cohu	**PINNACID**	0,1
Pinnularia amae Van de Vijver *et al.*	**PINNAMAE**	0,0
Pinnularia austroshetlandica (G.W.F.Carlson) A.Cleve	**PINNAUST**	1,8
Pinnularia carteri Krammer	**PINNCART**	0,6
Pinnularia cf. borealis Ehrenberg	**PINNBORE**	0,8
Pinnularia cf. lindanedbalovae Van de Vijver & Moravcová	**PINNLIND**	0,5
Pinnularia cf. microstauron (Ehrenberg) Cleve	**PINNMICR**	0,1
Pinnularia cf. silvatica J.B.Petersen	**PINNSILV**	0,6
Pinnularia microstauron var. rostrata Krammer	**PINNMIRO**	0,4
Pinnularia peracuminata Krammer	**PINNPERA**	0,0
Pinnularia sp1-CA	**PINNSPC1**	0,1
Pinnularia sp8-CA	**PINNSP8**	0,0
Pinnularia sp7-CA	**PINNSP7**	0,1
Pinnularia sp4-CA	**PINNSPC4**	0,0
Pinnularia spA-CA	**PINNSPCA**	0,1
Pinnularia subantarctica var. elongate (Manguin) Van de Vijver & Le Cohu	**PINNSUEL**	0,0
Pinnularia viridiformis Krammer	**PINNVIRI**	0,2
Pinnunavis elegans (W.Smith) Okuno	**PINVELEG**	0,6
Pinnunavis genustriata (Hustedt) Lange-Bertalot & Krammer	**PINVGENU**	1,2
Planothidium aueri (Krasske) Lange-Bertalot	**PLANAUER**	0,7
Planothidium cf. cyclophorum (Heiden) Van de Vijver	**PLANCYCL**	0,9
Planothidium renei (Lange-Bertalot & Rol.Schmidt) Van de Vijver	**PLANRENE**	15,2
Planothidium subantarcticum Van de Vijver & C.E.Wetzel	**PLANSUBA**	2,3
Platessa oblongella (Østrup) C.E.Wetzel *et al.*	**PLTSOBLO**	1,1
Psammothidium abundans (Manguin) Bukhtiyarova & Round	**PSAMABUN**	0,2
Psammothidium antarcticum Van de Vijver	**PSAMANTA**	0,4
Psammothidium cf. confusiforme Van de Vijver & Beyens	**PSAMCOFF**	3,7

Table B1: continued

Psammothidium cf. confusum (Manguin) Van de Vijver	**PSAMCONF**	3,4
Psammothidium cf. incognitum (Krasske) Van de Vijver	**PSAMINCO**	1,7
Psammothidium confusoneglectum Kopalová *et al.*	**PSAMCNEG**	0,2
Psammothidium germainii (Manguin) Sabbe	**PSAMGERM**	0,0
Psammothidium manguinii Van de Vijver	**PSAMMANG**	1,0
Psammothidium mannensianum Van de Vijver	**PSAMMANN**	1,8
Psammothidium subatomoides (Hustedt) Bukhtiyarova & Round	**PSAMSUBA**	0,5
Rhopalodia cf. gibba (Ehrenberg) O.Müller	**RHOPGIBB**	0,3
Rhopalodia cf. rupestris (W.Smith) Krammer	**RHOPRUPE**	2,0
Rossithidium sp1-CA	**ROSSSPC1**	2,6
Sellaphora cf. bacillum (Ehrenberg) D.G.Mann	**SELLBACI**	0,1
Sellaphora cf. saugeresii (Desmazières) C.E.Wetzel & D.G.Mann	**SELLSAUG**	0,0
Sellaphora sp1-CA	**SELLSPC1**	0,0
Sellaphora sp5-CA	**SELLSPC5**	0,0
Sellaphora spC-CA	**SELLSPCC**	0,0
Sellaphora subantactica Van de Vijver & Beyens	**SELLSUBA**	0,5
Sellaphora tumida Van de Vijver & Beyens	**SELLTUMI**	0,0
Stauroforma exiquiformis (Lange-Bertalot) Flower	**STAUEXIG**	0,0
Stauroneis cf. frauenfeldiana (Grunow) Heiden	**STNEFRAU**	0,0
Stauroneis kriegeri R.M.Patrick	**STNEKRIE**	0,1
Stauroneis pseudomuriella Van de Vijver & Lange-Bertalot	**STNEPSEU**	0,0
Surirella sp1-CA	**SURISPC1**	0,1
Surirella sp2-CA	**SURISPC2**	0,1

Table B2: Campbell Island genera and their frequency in %

Genera Campbell Island	**Frequency (%)**
Humidophila (Lange-Bertalot & Werum) R.L.Lowe *et al.*	75
Pinnunavis Okuno	71,875
Rhopalodia O.Müller	68,75
Angusticopula Houk *et al.*	59,375
Platessa Lange-Bertalot	59,375
Diatomella Greville	50
Frustulia Rabenhorst	40,625
Adlafia Gert Moser *et al.*	37,5
Gomphonema Ehrenberg	37,5
Pinnularia Ehrenberg	37,5
Cocconeis Ehrenberg	34,375
Eunotia Ehrenberg	31,25
Navicula Bory	31,25
Naviculadicta Lange-Bertalot	31,25
Fragilaria Lyngbye	28,125
Sellaphora Mereschkowsky	28,125
Surirella Turpin	25
Diploneis (Ehrenberg) Cleve	21,875
Ferocia Van de Vijver & Houk	21,875
Planothidium Round & Bukhtiyarova	21,875
Psammothidium Bukhtiyarova & Round	21,875
Encyonopsis Krammer	18,75
Stauroforma Flower *et al.*	18,75
Achnanthidium Kützing	15,625
Encyonema Kützing	15,625
Nupela Vyverman & Compere	15,625
Arcanodiscus Maidana & E.Morales	12,5
Frankophila Lange-Bertalot	12,5
Rossithidium Bukhtiyarova & Round	12,5
Incertae	12,5
Actinella F.W.Lewis	9,375
Brachysira Kützing	9,375
Chamaepinnularia Lange-Bertalot & Krammer	9,375
Epithemia Kützing	9,375
Hantzschia Grunow	9,375
Kobayasiella Lange-Bertalot	9,375
Luticola D.G.Mann	9,375

Achnanthes Bory	6,25
Nitzschia Hassall	6,25
Caloneis Cleve	3,125
Cavinula D.G.Mann & Stickle	3,125
Delicata Krammer	3,125
Geissleria Lange-Bertalot & Metzeltin	3,125
Lecohuia Lange-Bertalot	3,125
Stauroneis Ehrenberg	3,125

Table B3: Campbell Island genera and their relative abundance in %

Genera Campbell Island	**RA (%)**
Planothidium Round and Bukhtiyarova	19,20
Humidophila (Lange-Bertalot & Werum) R.L.Lowe *et al.*	15,20
Psammothidium Bukhtiyarova & Round	13,00
Pinnularia Ehrenberg	5,50
Angusticopula Houk *et al.*	5,30
Ferocia Van de Vijver & Houk	4,50
Eunotia Ehrenberg	4,30
Cocconeis Ehrenberg	3,70
Diatomella Greville	3,50
Fragilaria Lyngbye	2,70
Rossithidium Bukhtiyarova & Round	2,60
Arcanodiscus Maidana & E.Morales	2,40
Rhopalodia O.Müller	2,30
Luticola D.G.Mann	1,80
Nupela Vyverman & Compere	1,80
Pinnunavis Okuno	1,80
Gomphonema Ehrenberg	1,50
Adlafia Gert Moser *et al.*	1,40
Platessa Lange-Bertalot	1,10
Frankophila Lange-Bertalot	0,90
Frustulia Rabenhorst	0,80
Sellaphora Mereschkowsky	0,80
Hantzschia Grunow	0,50
Diploneis (Ehrenberg) Cleve	0,40
Lecohuia Lange-Bertalot	0,40
Nitzschia Hassall	0,40
Actinella F.W.Lewis	0,30
Chamaepinnularia Lange-Bertalot & Krammer	0,30
Navicula Bory	0,30
Achnanthes Bory	0,20
Encyonema Kützing	0,20
Kobayasiella Lange-Bertalot	0,20
Stauroneis Ehrenberg	0,20
Achnanthidium Kützing	0,10
Brachysira Kützing	0,10
Encyonopsis Krammer	0,10
Epithemia Kützing	0,10
Naviculadicta Lange-Bertalot	0,10
Surirella Turpin	0,10
Caloneis Cleve	0,00
Cavinula D.G.Mann & Stickle	0,00
Delicata Krammer	0,00
Geissleria Lange-Bertalot & Metzeltin	0,00
Stauroforma Flower *et al.*	0,00
Incertae sedis	0,00

APPENDIX C. LIST OF CAMPBELL ISLAND SAMPLES AND SAMPLING LOCATIONS

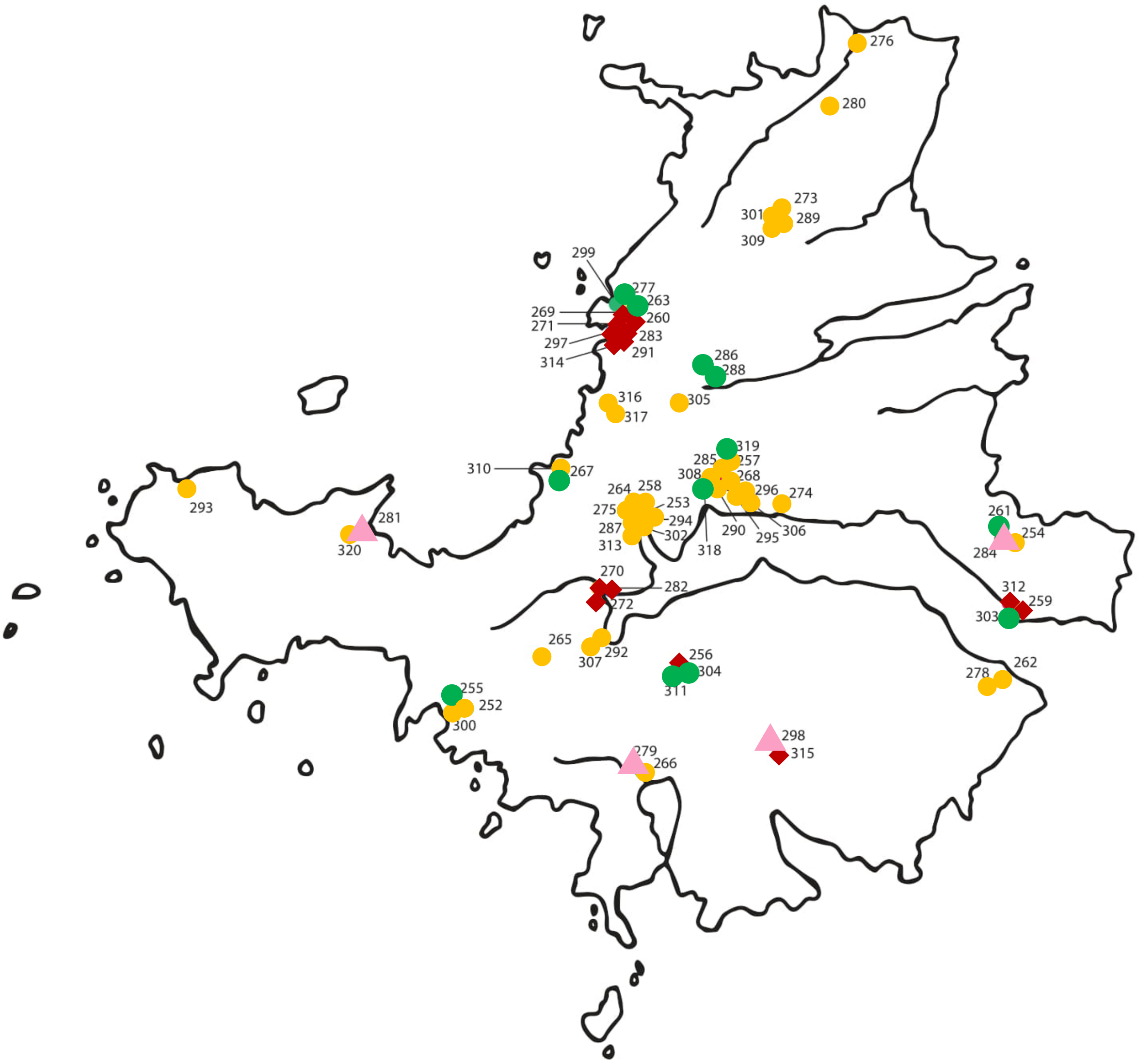


Figure C1: sampling locations on Campbell Island. Legend: ● = not used in dataset, ◆ = group I, ● = group II, ▲ = group III. Illustration © Charlotte Goeyers

Table C1: list of all moss samples from Campbell Island. BAS-number (in bold), Dale Vitt-number (next to BAS-number), sampling location and sampling date are described. Legend: 🟡 = not used in dataset, ◆ = group I, 🟢 = group II, ▲= group III.

🟡 **252** (2469)
Acanthocladium extenuatum
Wet rock surface
Nth slope Mt. Dumas (1300-1500 ft.)
2 January 1970

🟡 **253** (2050)
Acrocladium auriculatum
Moist channel *Dracophyllum* shrub
Near old Tucker Cove Station (200 ft.)
22 December 1969

🟡 **254** (2722)
Brachythecium rutabulum
Moubray Hill (818 ft.)
12 January 1970

🟢 **255** (2473)
Breutelia 59longate
On soil, base of cliff
Nth slope Mt. Dumas (1300-1500 ft.)
2 January 1970

◆ **256** (2340)
Breutelia pendula
On boggy soil in stream
NW slope of Mt. Honey (1700-1800 ft.)
31 December 1969

🟡 **257** (2869)
Breutelia pendula
On boulder
Ledges at summit of Lyall ridge (1300 ft.)
14 January 1970

🟡 **258** (2066)
Bryum billardieri
In crotch of *Dracophyllum*
Near Old Tucker Cove Station (200 ft.)
22 December 1969

◆ **259** (2702)
Bryum blandum
On rocks along shore
Nth Perseverance Harbour (E of Moubray Hill)
12 January 1970

◆ **260** (2998)
Bryum laevigatum + B. blandum
Wet rock in waterfall
N-NE slope Mt. Azimuth (1300 ft.)
19 January 1970

🟢 **261** (2737)
Camptochaete aciphylla + Macromitrium longirostre
In crevice (Moubray Hill) (818 ft.)
12 January 1970

🟡 **262** (2946)
Camptochaete arbuscula
Base of *Dracophyllum* branch
Dense *Dracophyllum* scrub (Sth Perseverance Harbour)
16 January 1970

🟢 **263** (2491)
Camptochaete ramulosa
Wet cliff next to waterfall
W slope Azimuth-Faye ridge
8 January 1970

🟡 **264** (2967)
Campylopus clavatus
On boulder, Beeman Hill
17 January 1970

🟡 **278** (2930)

🟡 **265** (2247)
Campylopus introflexus
Peaty bank
N-NE Mt. Dumas
28 December 1969

🟡 **266** (2132)
Campylopus pallidus
Rotten stump at edge low wet area
NW Six Foot Lake (junction with stream)
23 December 1969

🟢 **267** (2972)
Conostomum pentastichum
Cliff ledge
SE slope Ct. Col ridge (700-800 ft.)
18 January 1970

🟡 **268** (2167)
Conostomum pentastichum
Soil over rock
S Slope Lyall ridge (across from Shoal Point)
24 December 1969

◆ **269** (2501)
Cratoneuropsis relaxa
Rock in waterfall
W slope Azimuth-Faye ridge
8 January 1970

◆ **270** (2198)
Cratoneuropsis relaxa
Wet rocks above water level (stream near ocean)
Camp Cove
26 December 1969

◆ **271** (3034)
Cratoneuropsis relaxa
Wet cliff face
N-NE slope Mt. Azimuth (1300 ft.)
19 January 1970

◆ **272** (2202)
Cratoneuropsis relaxa
Wet dripping shaded bluff limestone (near ocean)
Camp Cove
26 December 1969

🟡 **273** (2578)
Dicranoloma billardieri
Peat in tussock grassland
Lower E slope Mt. Faye
7 January 1970

🟡 **274** (2600)
Dicranoloma billardieri
Humus covered bank below waterfall
Waterfall + dripping cliffs S-E Mt. Lyall
9 January 1970

🟡 **275** (2081)
Dicranoloma robustum
Wet humus in *Dracophyllum* scrub
Near old Tucker Cove Station (200 ft.)
22 December 1969

🟡 **276** (2561)
Dicranoloma robustum var. setosum
Peat in tussocks
N-running stream, west of Bull Rock
6 January 1970

🟢 **277** (2523)
Dicranoweisia antarctica
Rock ledge, W slope Azimuth-Faye ridge
8 January 1970

◆ **291** (2496)

Table C1: continued.

Distichophyllum pulchellum
Humus, *Dracophyllum* scrub on Sth side
Perseverance Harbour (east of Shoal Point)
16 January 1970

▲ **279** (2125)
Drepanocladus fluitans
Dried up seal wallow
NW side Six Foot Lake (junction with stream)
23 December 1969

🟡 **280** (2543)
Drepanocladus fluitans
Peat in seepage
Faye-Sorenson ridge
8 January 1970

▲ **281** (2790)
Eriopus apiculatus
Rocks above ocean
Limestone shore Middle Bay (NW Bay)
13 January 1970

◆ **282** (2090)
Fissidens leptocladus
Seepy limestone bluff
Camp Cove
23 December 1969

◆ **283** (2504)
Fissidens rigidulus
Rock in waterfall
W slope Azimuth-Faye ridge
8 January 1970

▲ **284** (2740)
Holomitrium perichaetiale
On rock
Moubray Hill (818 ft.)
12 January 1970

🟡 **285** (2864)
Hypnum chrysogaster
Humus covered boulder
Ledges at summit Lyall ridge (1300 ft.)
14 January 1970

🟢 286 (3131)
Hypopterygium novae-seelandiae
Dark wet recess
Bluff on Sth side Mt. Fizeau
22 January 1970

🟡 **287** (2383)
Isopterygium pulchellum + Macromitrium caducipilum
Trunk *Dracophyllum*
Along stream, N-NE of old Tucker Cove Station
3 January 1970

🟢 **288** (3128)
Isopterygium limatum
Cliff face
Bluff on Sth side Mt. Fizeau
22 January 1970

🟡 **289** (2539)
Leptostomum inclinans
Boulders
Faye-Sorenson ridge
8 January 1970

🟡 **290** (2887)
Lepyrodon lagurus
Cliff face
Ledges at summit Lyall ridge (1300 ft.)
14 January 1970

Blindia contecta
Wet cliff next to waterfall
West facing slope Azimuth-Faye ridge
8 January 1970

🟡 **292** (2902)
Macromitrium caducipilum
Dracophyllum trunk
Garden Cove
15 January 1970

🟡 **293** (2631)
Macromitrium longirostre
Rocks on bluffs
Penguin Bay, NE of Yvon Villarceau Peak
11 January 1970

🟡 **294** (2035)
Macromitrium longirostre
Sth side of Beeman Hill (Nth of Beeman Station)
21 December 1969

🟡 **295** (2316)
Muelleriella crassifolia
Boulders near tideline
Nth side Perseverance Harbour, across from Shoal Point
30 December 1969

🟡 **296** (2315)
Orthodontium lineare
Soil overhang cliff
Nth side Perseverance Harbour, across from Shoal Point
30 December 1969

◆ **297** (3031)
Philonotis pyriformis
Rock in waterfall
N-NE slope Mt. Azimuth (1300 ft.)
19 January 1070

▲ **298** (3069)
Philonotis scabrifolia
In recess at large waterfall
St of Mt. Honey on stream flowing to SE Harbour
21 January 1970

🟢 **299** (2492)
Philonotis scabrifolia + Thamnobryum pandum
Wet cliff next to waterfall
W slope Azimuth-Faye ridge
8 January 1970

🟡 **300** (2252)
Polytrichadelphus magellanicus
Soil at stream bank
NW Mt. Dumas
28 December 1969

🟡 **301** (2579)
Ptychomnium aciculare
Peat in tussock grassland
Lower E slopes Mt. Faye
7 January 1970

🟡 **302** (2970)
Rhacomitrium crispulum
On boulders
Beeman Hill
17 January 1970

🟢 303 (2668)
Racopilum strumiferum
Wet rock under large overhang, cave next to sea
Shore Nth side Perseverance Harbour (E Moubray Hill)
12 January 1970

Table C1: continued

🟢 **304** (2433)
Rhacocarpus purpurascens
N-NW slope Mt. Honey near summit (1700-1800 ft.)
31 December 1969

🟡 **305** (2421)
Rhaphidorrhynchium amoenum
Wet rock
Weathered basalt outcrop, west of Lyall ridge
4 January 1970

🟡 **306** (2153)
Rhizogonium novae-hollandiae
Swiftrunning stream at Sth base Lyall ridge, across from Shoal Point
24 December 1969

🟡 **307** (3053)
Rhizogonium pennatum
Peat bank
Near creek in *Dracophyllum,* Sth of Garden Cove
20 January 1970

🟡 **308** (2860)
Schlotheimia campbelliana
Wet rock under overhang
Ledges at summit Lyall ridge (1300 ft.)
14 January 1970

🟡 **309** (2544)
Sphagnum australe
Peat in seepage
Faye-Sorenson ridge
8 January 1970

🟡 **310** (2973)
Tayloria octoblepharum
Old albatross nest
SE slope St. Col ridge (700-800 ft.)
18 January 1970

🟢 **311** (2333)
Thamnobryum pandum
Rock beneath overhang
N-NW slope Mt. Honey near summit (1700-1800 ft.)
31 December 1969

♦ **312** (2701)
Thuidium furfurosum
On rocks, along shore Nth side Perseverance Harbour
E of Moubray Hill
12 January 1970

🟡 **313** (2063)
Thuidium furfurosum
Open wet peaty soil
Near old Tucker Cove Station (200 ft.)
22 December 1969

♦ **314** (2498)
Thuidium furfurosum var. sparsum
Wet cliff next to waterfall
W facing slope Azimuth-Faye ridge
8 January 1970

♦ **315** (3077)
Tridontium tasmanicum + Cratoneuropsis relaxa
Submerged on edge waterfall
Mt. Honey on stream flowing into SE Harbour
21 January 1970

🟡 **316** (2971)
Weymouthia cochlearifolia
Humus at base Bulbinella
SE slope St. Col ridge (700-800 ft.)
18 January 1970

🟡 **317** (2971)
Weymouthia cochlearifolia
Humus at base Bulbinella
SE slope St. Col ridge (700-800 ft.)
18 January 1970

🟢 **318** (2278)
Weymouthia cochlearifolia
Crevice of cliff
Summit Lyall ridge (1300 ft.)
29 December 1969

🟡 **319** (2845)
Zygodon intermedius
Under overhang, ledges at summit Lyall ridge (1300 ft.)
14 January 1970

🟡 **320** (2806)
Zygodon menziesii
On rock, limestone shore of Middle Bay
13 January 1970

APPENDIX D. IMAGES & GRAPHS

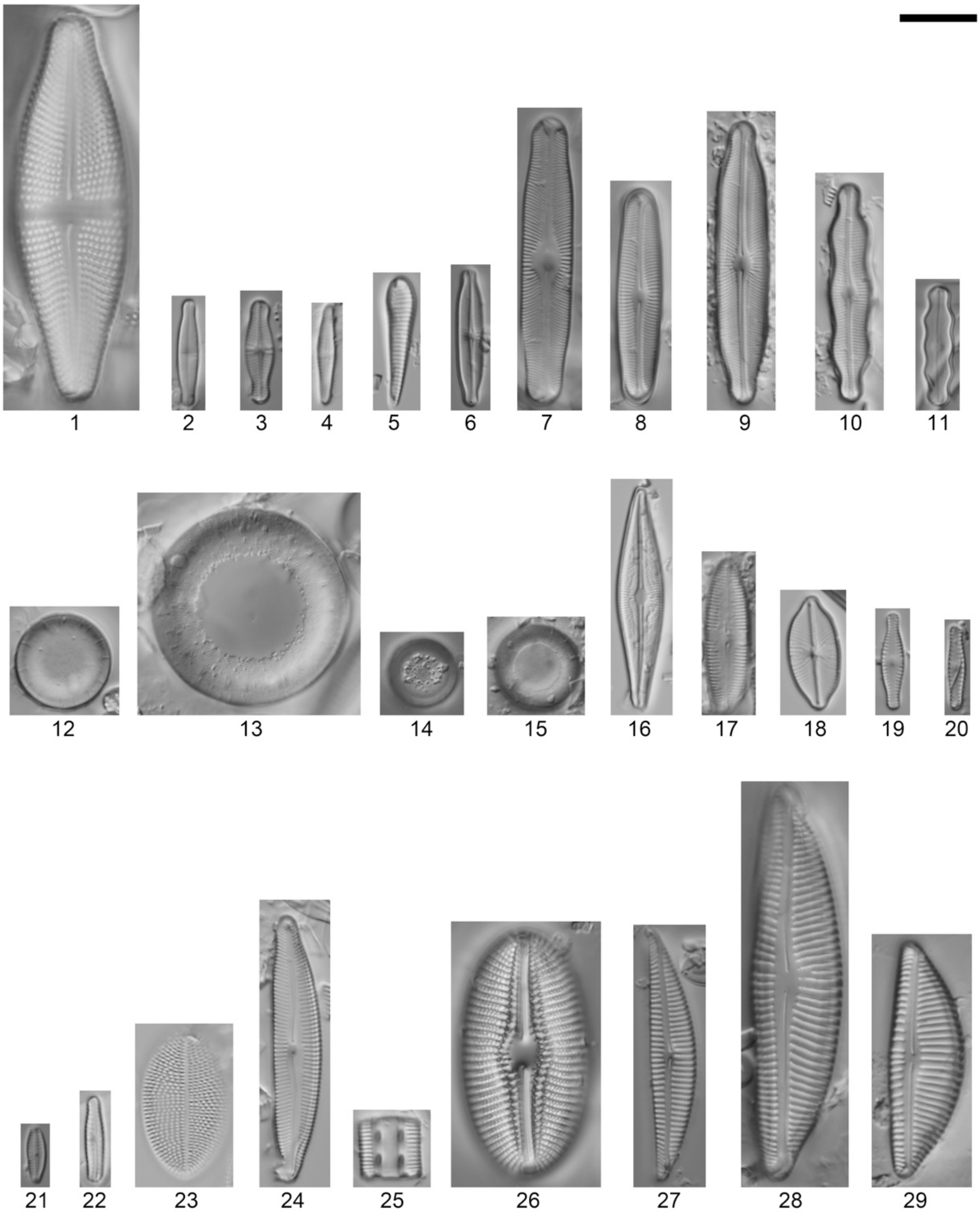


Figure D1: LM images of all observed taxa in this study (1000x). (1) *Achnanthes muelleri,* (2) *Achnanthidium cf. sieminskae,* (3) *Achnanthidium modestiforme,* (4) *Achnanthidium sp.1,* (5) *Actinella parva,* (6) *Adlafia bryophila,* (7) *Adlafia cf. bryophiloides,* (8) *Adlafia sp.1,* (9) *Adlafia sp.2,* (10) *Adlafia sp.5,* (11) *Adlafia tenuis,* (12) *Angusticopula chilensis,* (13) *Angusticopula cosmica,* (14) *Arcanodiscus crawfordianus,* (15) *Arcanodiscus desmetianus,* (16) *Brachysira cf. neoexilis,* (17) *Caloneis marnieri,* (18) *Cavinula heterostauron rostrata,* (19), *Chamaepinnularia australomediocris,* (20) *Chamaepinnularia soehrensis var. muscicola,* (21) *Chamaepinnularia sp.2,* (22) *Chamaepinnularia sp.3,* (23) *Cocconeis placentula s.l.,* (24) *Delicata cf. delicatula,* (25) *Diatomella balfouriana,* (26) *Diploneis subovalis,* (27) *Encyonema neogracile,* (28) *Encyonema sp.1,* (29) *Encyonema sp.2.* Scale bar = 10 µm

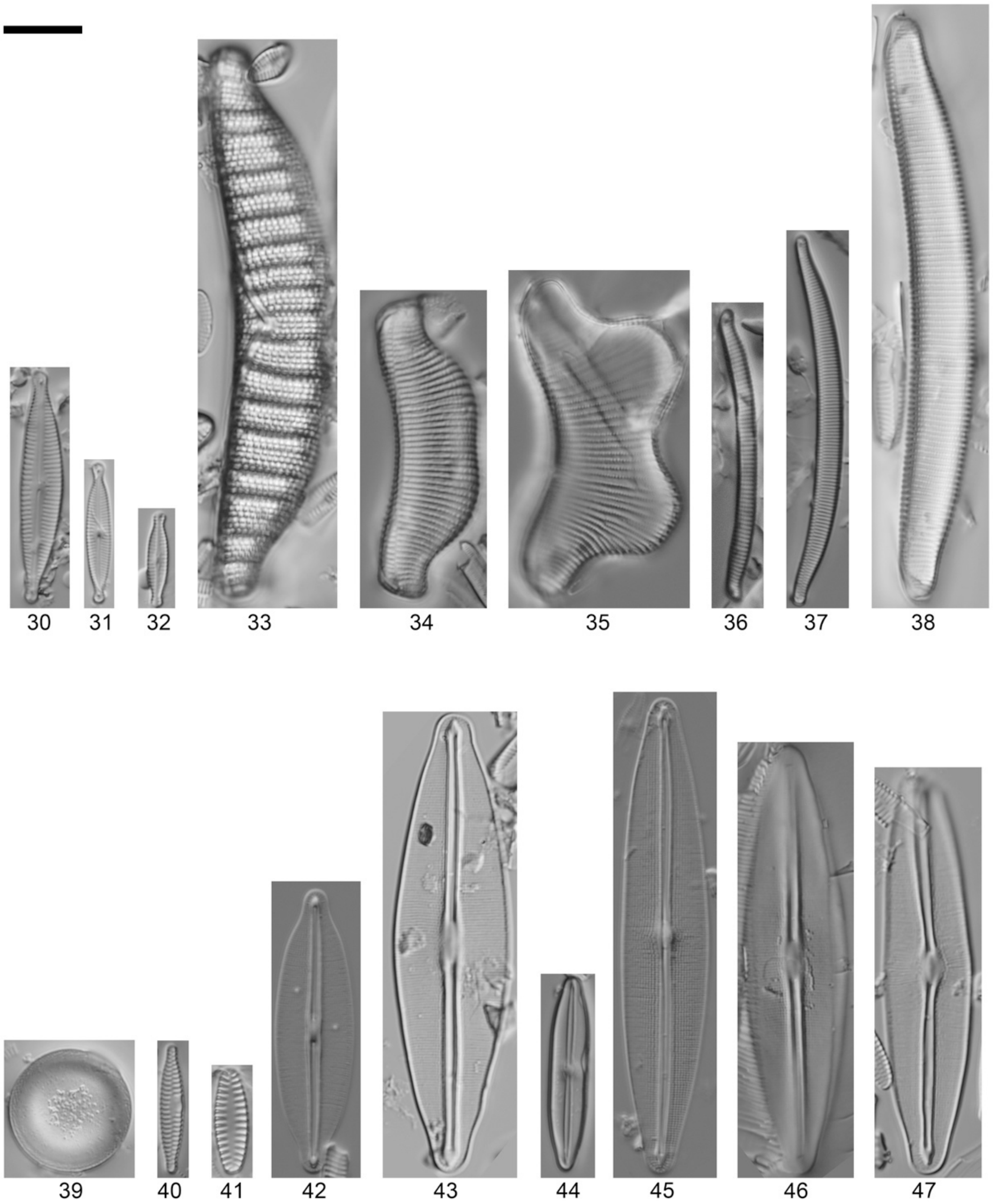


Figure D2: LM images (1000x). (30) *Encyonema sp.14,* (31) *Encyonopsis sp.1,* (32) *Encyonopsis sp.3,* (33) *Epithemia cf. adnata,* (34) *Eunotia cf. bidens,* (35) *Eunotia cf. papilio,* (36) *Eunotia sp.1,* (37) *Eunotia sp.2,* (38) *Eunotia sp.12,* (39) *Ferocia houkiana,* (40) *Fragilaria sp.A,* (41) *Frankophila dalevittii,* (42) *Frustulia cf. crassinervia,* (43) *Frustulia cf. saxonica,* (44) *Frustulia sp.1,* (45) *Frustulia sp.4,* (46) *Frustulia sp.6,* (47) *Frustulia sp.7.* Scale bar = 10 µm

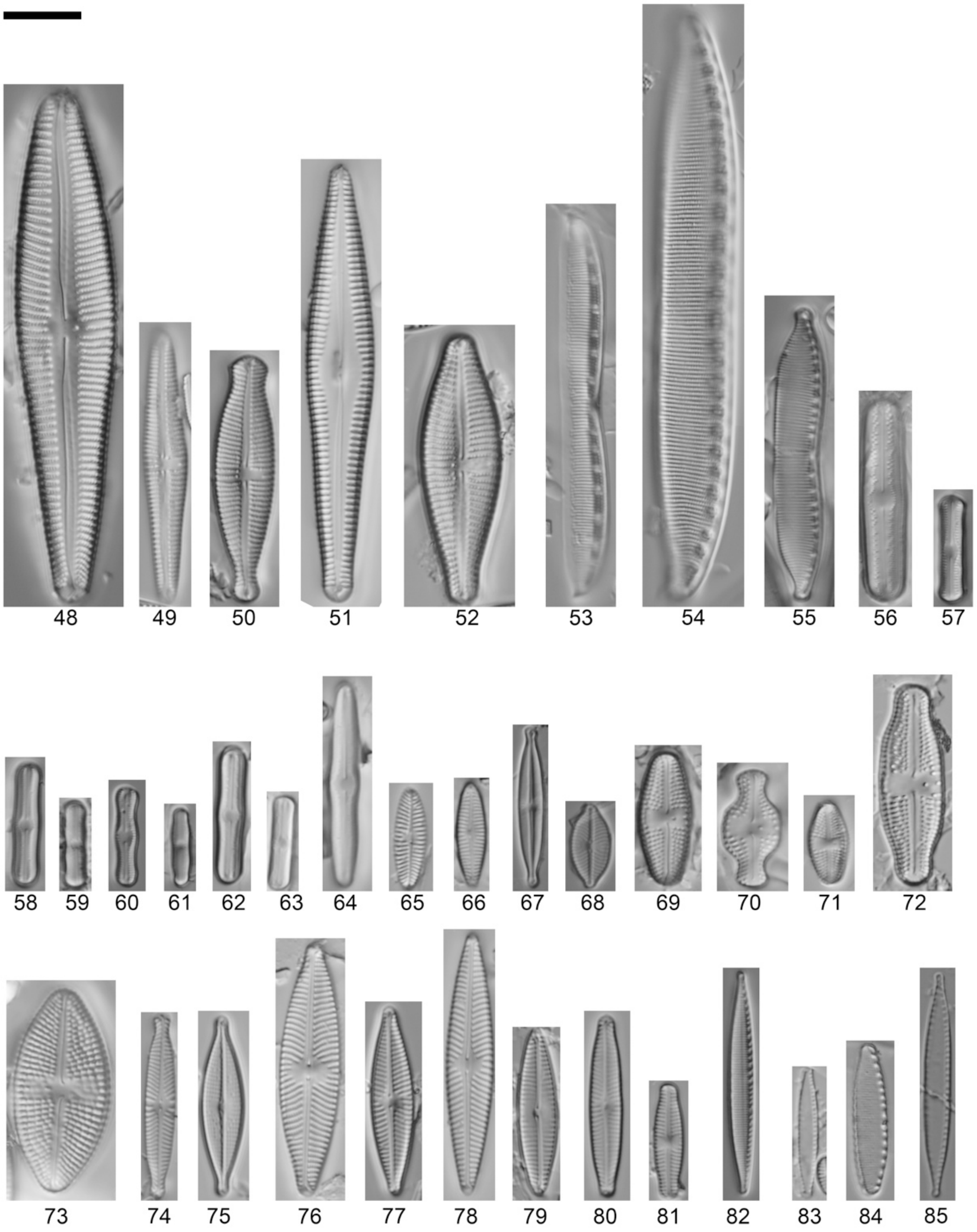


Figure D3: LM images (1000x). (48) *Gomphonema sp.3,* (49) *Gomphonema sp.6,* (50) *Gomphonema sp.8,* (51) *Gomphonema sp.13,* (52) *Gomphonema stonei,* (53) *Hantzschia sp.1,* (54) *Hantzschia sp.2,* (55) *Hatzschia amphioxys,* (56)*Humidophila arcuata,* (57) *Humidophila biceps,* (58) *Humidophila costei,* (59) *Humidophila crozetikerguelensis,* (60) *Humidophila ingeae,* (61) *Humidophila nienta,* (62) *Humidophila sp.6,* (63) *Humidophila sp.A,* (64) *Humidophila sp.B,* (65) *Incertae sedis 1,* (66) *Incertae sedis 2,* (67) *Kobayasiella cf. subantarctica,* (68) *Lecohuia geniculata,* (69) *Luticola crozetensis,* (70) *Luticola muticopsis,* (71) *Luticola sp.4,* (72) *Luticola sp.5,* (73) *Luticola sp.6,* (74) *Navicula bicephala,* (75) *Navicula gregaria,* (76) *Navicula sp.1,* (77) *Navicula sp.2,* (78) *Navicula sp.4,* (79) *Navicula sp.10,* (80) *Navicula sp.11,* (81) *Naviculadicta elorantana,* (82) *Nitzschia acidoclinata,* (83) *Nitzschia archibaldii,* (84) *Nitzschia communis,* (85) *Nitzschia gracilis.* Scale bar = 10 µm

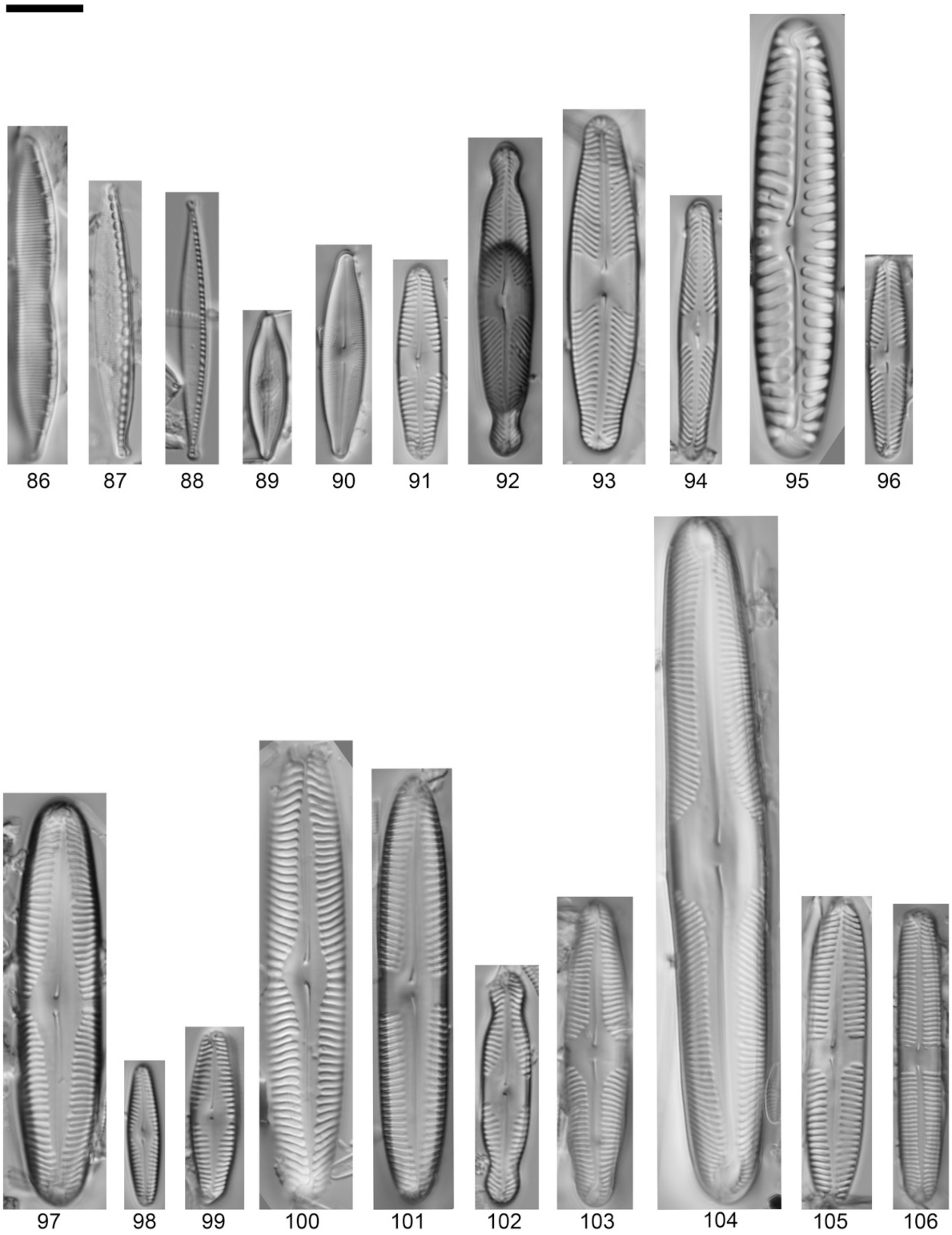


Figure D4: LM images (1000x). (86) *Nitzschia palustris,* (87) *Nitzschia sp.A,* (88) *Nitzschia tubicola*, (89) *Nupela cf. chilensis*, (90) *Nupela sp.1*, (91) *Pinnularia acidicola*, (92) *Pinnularia amae*, (93) *Pinnularia austroshetlandica*, (94) *Pinnularia carteri*, (95) *Pinnularia cf. borealis*, (96) *Pinnularia cf. lindanedbalovae*, (97) *Pinnularia cf. microstauron*, (98) *Pinnularia cf. silvatica*, (99) *Pinnularia microstauron rostrata*, (100) *Pinnularia peracuminata,* (101) *Pinnularia sp.1,* (102) *Pinnularia sp.A,* (103) *Pinnularia sp.4,* (104) *Pinnularia sp.7,* (105) *Pinnularia sp.8,* (106) *Pinnularia subantarctica var. elongata.* Scale bar = 10 µm

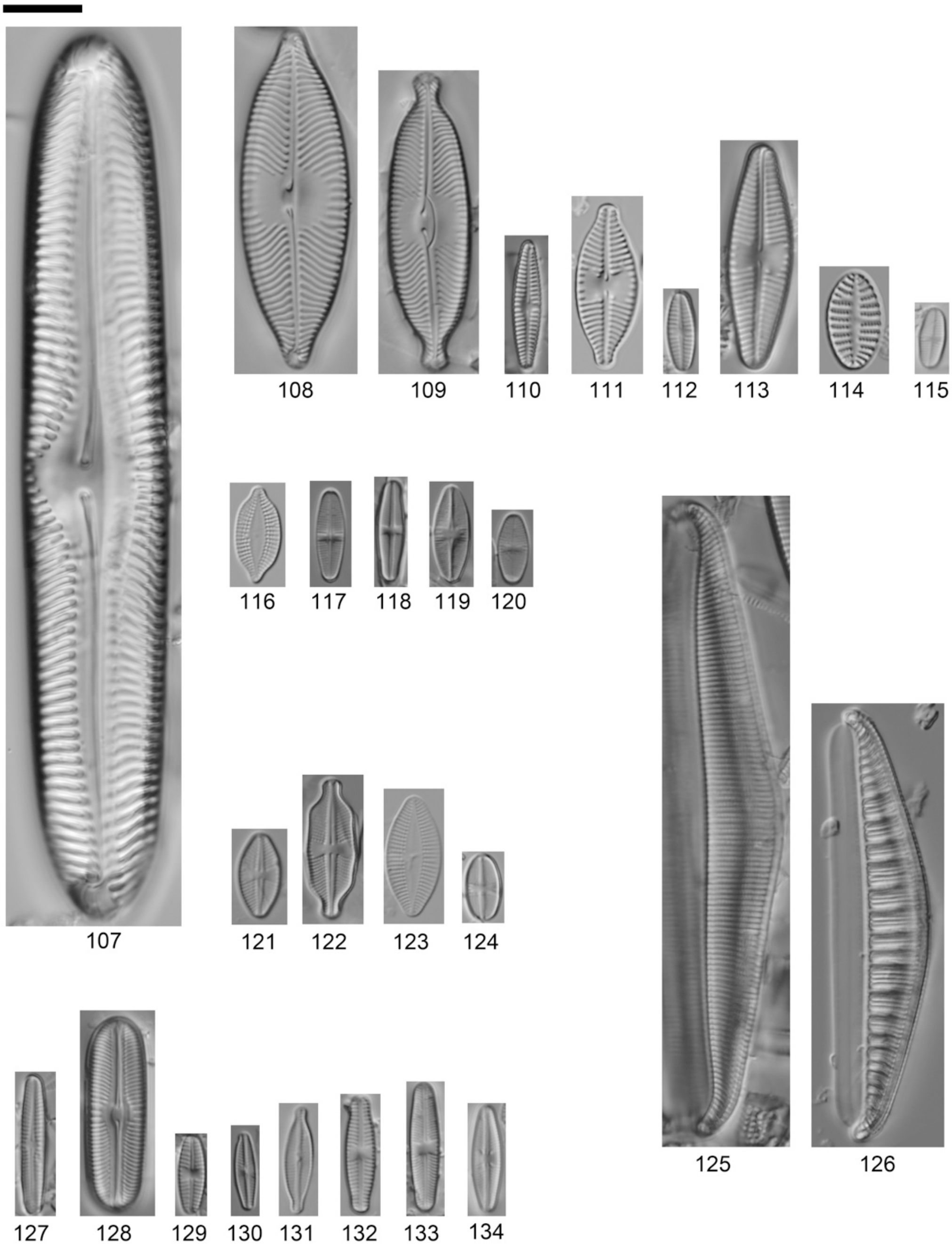


Figure D5: LM images (1000x). (107) *Pinnularia viridiformis,* (108) *Pinnunavis elegans,* (109) *Pinnunavis genustriata,* (110) *Planothidium aueri,* (111) *Planothidium cf. cyclophorum,* (112) *Planothidium renei,* (113) *Planothidium subantarcticum,* (114) *Platessa oblongella,* (115) *Psammothidium abundans,* (116) *Psammothidium antarcticum,* (117) *Psammothidium cf. confusiforme,* (118) *Psammothidium cf. confusum,* (119) *Psammothidium cf. incognitum,* (120) *Psammothidium confusuneglectum,* (121) *Psammothidium germainii,* (122) *Psammothidium manguinii,* (123) *Psammothidium mannensianum,* (124) *Psammothidium subatomoides,* (125) *Rhopalodia cf. gibba,* (126) *Rhopalodia cf. rupestris,* (127) *Rossithidium sp.1,* (128) *Sellaphora cf. bacillum,* (129) *Sellaphora cf. saugeresii,* (130) *Sellaphora sp.1,* (131) *Sellaphora sp.5,* (132) *Sellaphora sp.C,* (133) *Sellaphora subantarctica,* (134) *Sellaphora tumida.* Scale bar = 10 µm

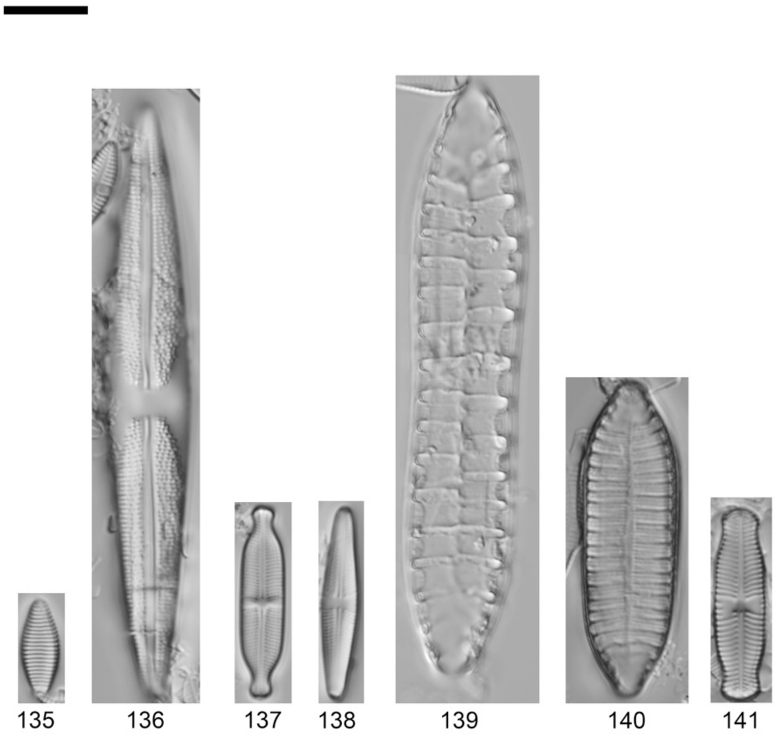


Figure D6: LM images (1000x). (135) *Stauroforma exiquiformis,* (136) *Stauroneis cf. frauenfeldiana,* (137) *Stauroneis kriegeri,* (138) *Stauroneis pseudomuriella,* (139) *Surirella sp.1,* (140) *Surirella sp.2,* (141) *Geissleria sp.1.* Scale bar = 10 µm

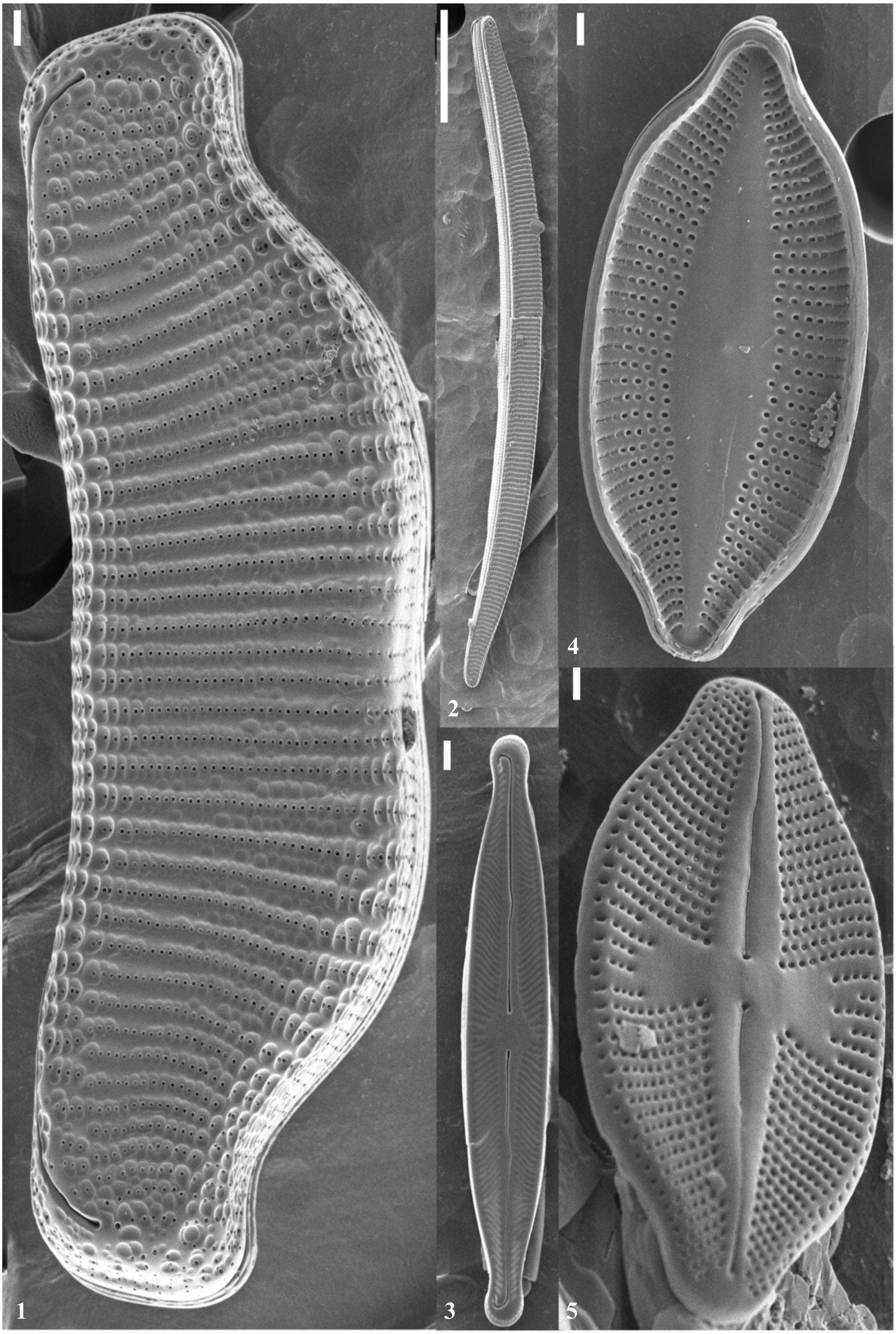


Figure D7: SEM images. (1) *Eunotia cf. bidens* (Scale bar = 1μm), (2) *Eunotia sp.2* (Scale bar = 10μm), (3) *Kobayasiella subantarctica* (Scale bar = 1μm), (4-5) *Psammothidium manneniasianum* (Scale bar = 1μm)

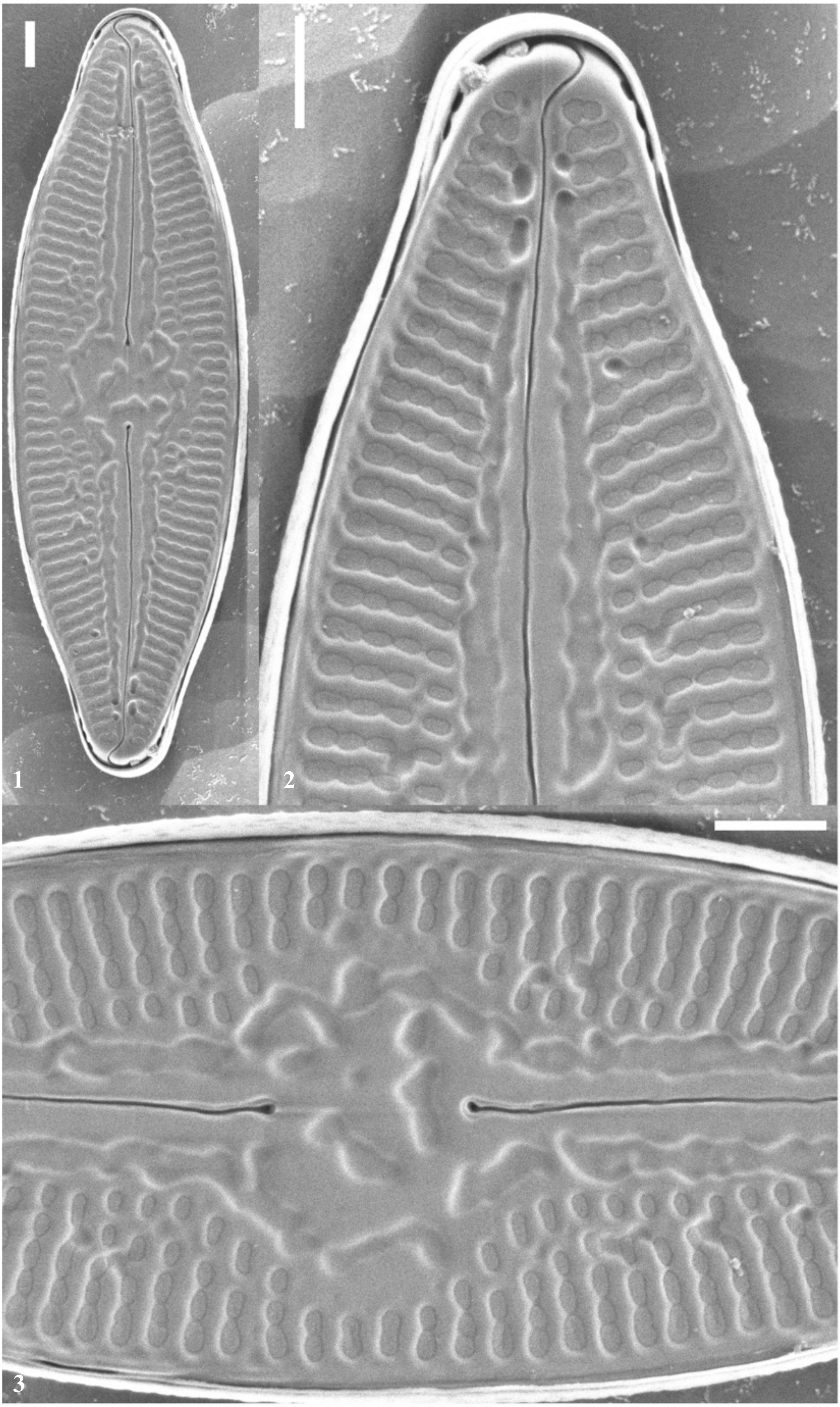
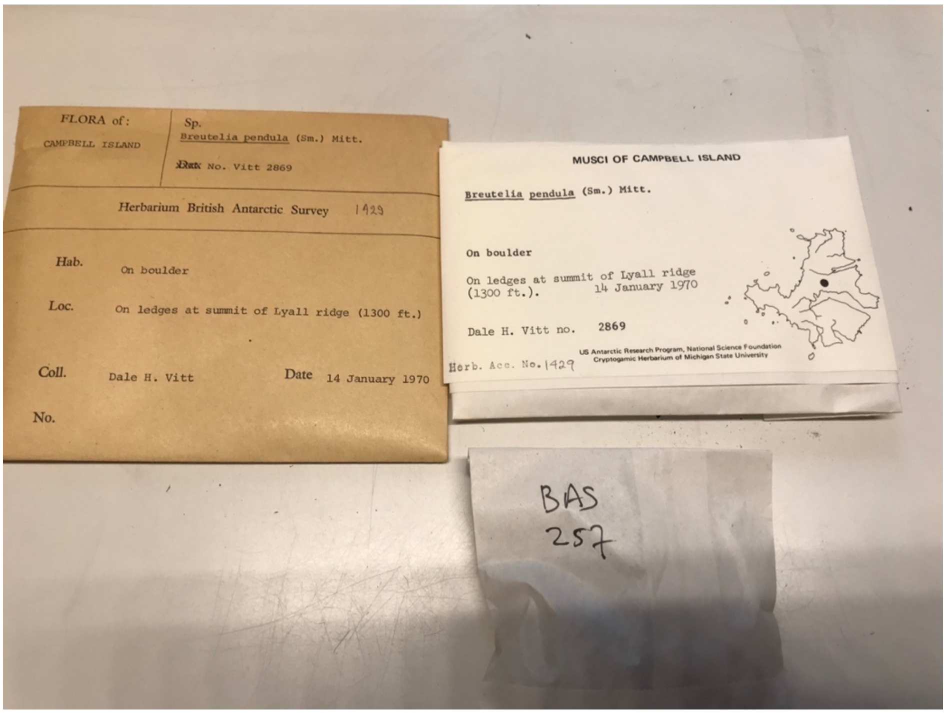


Figure D8: SEM images. (1-3) *Nupela* cf. *chilensis.* Scale bar = 1 µm



FLORA of:
CAMPBELL ISLAND

Sp.
Breutelia pendula (Sm.) Mitt.

~~Det~~ No. Vitt 2869

Herbarium British Antarctic Survey 1429

Hab. On boulder

Loc. On ledges at summit of Lyall ridge (1300 ft.)

Coll. Dale H. Vitt Date 14 January 1970

No.

MUSCI OF CAMPBELL ISLAND

Breutelia pendula (Sm.) Mitt.

On boulder

On ledges at summit of Lyall ridge
(1300 ft.). 14 January 1970

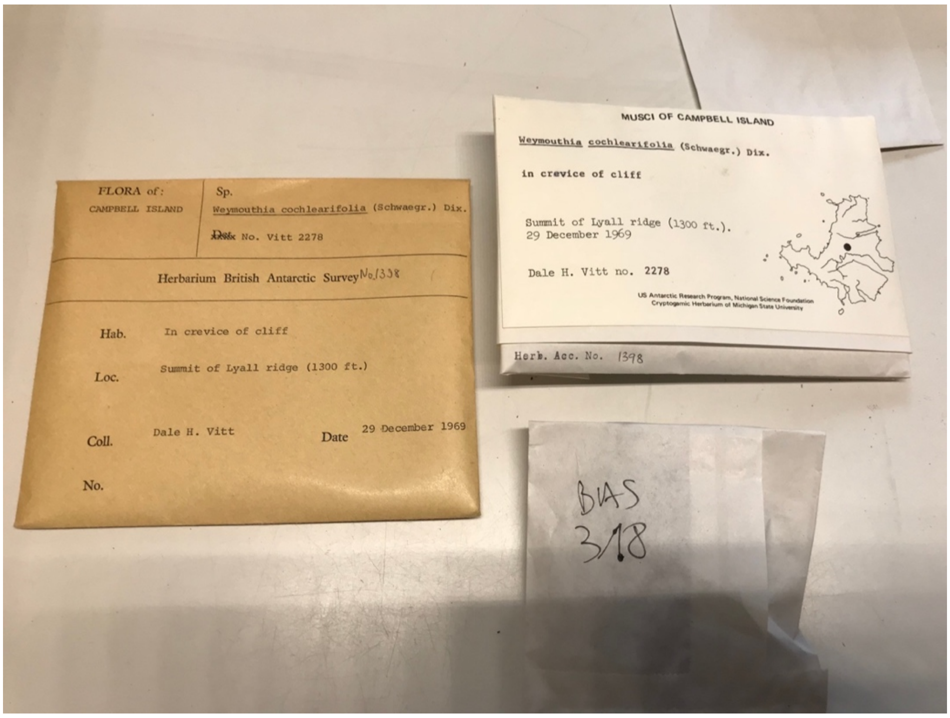
Dale H. Vitt no. 2869

US Antarctic Research Program, National Science Foundation
Cryptogamic Herbarium of Michigan State University

Herb. Acc. No. 1429

BAS
257

Figure D9: image of the BAS-samples retrieved from the moss herbarium of the British Antarctic Survey collection (Cambridge, UK)



FLORA of:
CAMPBELL ISLAND

Sp.
Weymouthia cochlearifolia (Schwaegr.) Dix.

~~Det~~ No. Vitt 2278

Herbarium British Antarctic Survey No.1398

Hab. In crevice of cliff

Loc. Summit of Lyall ridge (1300 ft.)

Coll. Dale H. Vitt Date 29 December 1969

No.

MUSCI OF CAMPBELL ISLAND

Weymouthia cochlearifolia (Schwaegr.) Dix.

in crevice of cliff

Summit of Lyall ridge (1300 ft.).
29 December 1969

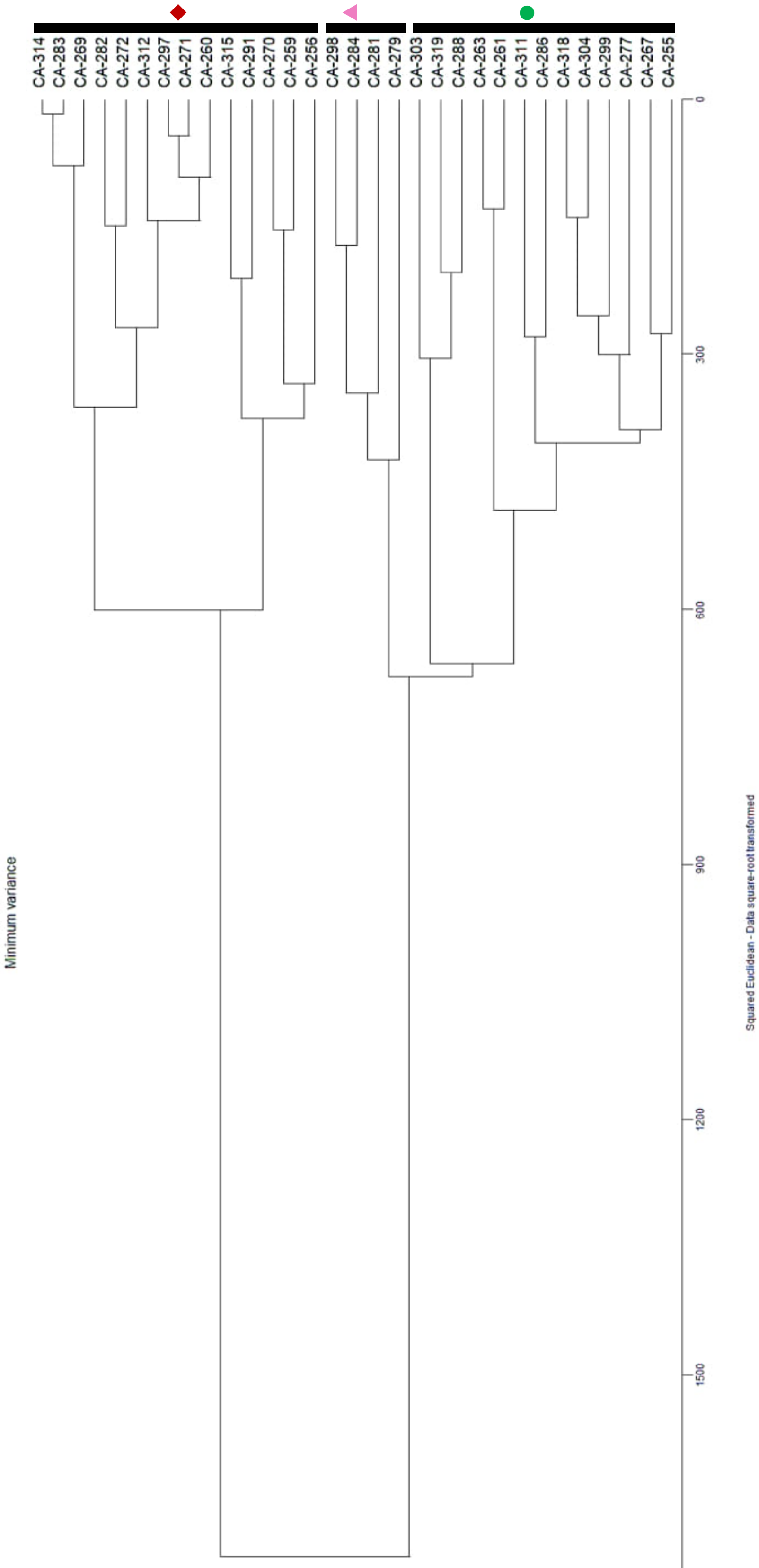
Dale H. Vitt no. 2278

US Antarctic Research Program, National Science Foundation
Cryptogamic Herbarium of Michigan State University

Herb. Acc. No. 1398

BAS
318

Figure D10: image of the BAS-samples retrieved from the moss herbarium of the British Antarctic Survey collection (Cambridge, UK)


CA-314
CA-283
CA-269
CA-282
CA-272
CA-312
CA-297
CA-271
CA-260
CA-315
CA-291
CA-270
CA-259
CA-256
CA-298
CA-284
CA-281
CA-279
CA-303
CA-319
CA-288
CA-263
CA-261
CA-311
CA-286
CA-318
CA-304
CA-299
CA-277
CA-267
CA-255
0
300
600
900
1200
1500
1800
Squared Euclidean - Data square-root transformed
Minimum variance

APPENDIX E. COUNTS

Table E1: number of counted valves per taxon for all 32 Campbell Island moss samples. A total of 400 valves were counted per sample.

	255	256	259	260	261	263	267	269	270	271	272	277	279	281	282	283	284	286	288	291	296	297	298	299	303	304	311	312	314	315	318	319
ACHNMUEL				2		2				4												2		18								
ACHMSIEM		2																														
ACHMMODE		11																														
ACHMSPC1														2																		
ACTIPARV	1											24								10												
ADLABRYA		18								2												2			2							
ADLACFBR																	2															
ADLASPC1	11						109																									
ADLASPC2											4							2	18													
ADLASPC5																											2	2				
ADLATENU	1																															
ANGUCHIL	2	1			4	40				4								14		2			29	12			94					
ANGUCOSM				2																	337				45		10					2
ANGUCRAW			2				5				10	2			62																	
ARCADESM				10							195								32													64
BRACNEOE		4																		6										2		
CALOMARN															2																	
CAVIHERO										2																						
CHAMAUST																			16													
CHAMSOEH		2																														

Table E1: continued

CHAMSPC2		1																														
CHAMSPC3							22																									
COCCPLAC			20	23				3	22	68												183		2	2			23		122		
DELIDELI																		2														
DIATBALF			2	6		2				2	8				8			18	95	2				4	105		10	2		4	6	168
DIPLSUBO		11		8							4				24			4		2										2		
ENCYNEOG		6																														
ENCYSPC1	4	2																														
ENCYSP14																				2												
ENCYSP15																				2												
ENCYSPC2			6							2												4										
ENCSSPC1		2	2																													
ENCSSPC3		2						2						2																		
ENCSSPC6																														2		
EPITADNA		11																						2	6							
EUNOBIDE	11																						2			1						
EUNOPAPI	1																															
EUNOSPC1	21	4					94					80	200					2		18						2			2			
EUNOSPC2	60																			40												
EUNOSP12																				10			6									
FEROHOUK				2	25								2	33			340						153								16	
FRAGCAPU			57	14				2	185			4								12								4	6	56		
FRANDALE			9	2														2							100							
FRUSCRAS	2							6	x			2																				
FRUSSAXO	42		4						2									2						2						4		

Table E1: continued

FRUSSPC1																			2													
FRUSSPC4		11																														
FRUSSPC6																				10			2									
FRUSSPC7									2																						2	
GEISSPC1					4																											
GOMPSP13																				2												
GOMPSP3		2	4			2																2										
GOMPSP6			6	12																6									2	16		
GOMPSP8								34																					2	26		
GOMPSTON			2	8					30										8	20		2						2				
HANZSPC1																											10					
HANZSPC2																									52							
HANZAMPH																											4	4				
HUMIARCU												20						20	4					26		64						158
HUMIBICEP		4											6	4									8	68			6				4	6
HUMICOST	97		1		4	112	10					10					4	4		2				38		78	28	2			220	
HUMICROZ											16				2																	
HUMIINGE																											34					
HUMINIEN	11	6		2	21	10				6	10	83			2		4	2		8											10	2
HUMISPC6					292	158	8																									
HUMISPCA											18			4	6				2								28					
HUMISPCB							4					12											175									
INCESPC1														2																		
INCESPC2							2												2													
KOBASUBA	28																															

Table E1: continued

LECOGENI	29	14	4																													
LUTICROZ					12		6					4								2				150			2				10	
LUTIMUTI																											2					
LUTISPC4	3						4							13																		
LUTISPC5														12													4					
LUTISPC6																					4											
NAVIBICE					2																											
NAVIGREG				2						8												4										
NAVISPC1		1	2																	2												
NAVISP10													2																			
NAVISP11							2																									
NAVISPC2			6																													
NAVISPC4																									2							
NAVDELOR													4														4					
NITZACID		14																							14							
NITZARCH				2																												
NITZCOMM																									4							
NITZGRAC													2																			
NITZPALU					2																											
NITZSPCA				6																												
NITZTUBI		6																														
NUPECHIL		9		2	4	16	2											10														
NUPESPC1	1		2			8												26						4			140		2		8	
PINNACID	4		2																											12		
PINNAMAE													2																			

Table E1: continued

PINNAUST					2									231																		
PINNCART	5	3		2			48	2				6				2	2														2	
PINNBORE	1				2		8										48							12						2	32	
PINNLIND													60							2			2									
PINNMICR			4			6																										
PINNSILV							10						60							6			4								2	
PINNMIRO													46																			
PINNPERA	3																															
PINNSPC1	1					2							2							4												
PINNSP4																										2						
PINNSP7		3													4																	
PINNSPC8							6																									
PINNSPCA									8		2	1	2		2					4												
PINNSUEL					4																						2					
PINNVIRI																				8			15									
PINVELEG							16						2	4							59											
PINVGENU							36							93									2				20		2			
PLANAUER		38	2	8						6		2						16		18										4		
PLANCYCL								20		2						4			87									4		2		
PLANRENE		10	65	201		12		151	48	244	123				256	210		2				169		4				194	248	8		
PLANSUBA			46	66		6		36	32	20	6				18	4						28						29		8		
PLTSOBLO			5	4			2		59			59												2				4				
PSAMABUN		4						2										16														
PSAMANTA		6				2										2		6	2	8				27							2	
PSAMCOFF		75	37	4		12		24		24	4							195	2				2			8		88		4		

Table E1: continued

PSAMCONF	5	9						36				22				68		2		134						22		18	64	58		
PSAMINCO	23									2		13						22		38		2		6		81				24	10	
PSAMCNEG	29																															
PSAMGERM	2																															
PSAMMANG	2				2							2						8	46	2				23		34					6	
PSAMMANN					20							14							14							108					70	
PSAMSUBA												34						19		8												
RHOPGIBB																									32			4				
RHOPRUPE		91	108																						36			18				
ROSSSPC1				10				80	6	4						108				8		2							72	44		
SELLBACI															10			4														
SELLSAUG		5																														
SELLSPC1		3																														
SELLSPC5							6																									
SELLSPCC													4		2																	
SELLSUBA																			68													
SELLTUMI															2																	
STAUEXIG																		2														
STNEFRAU			2																	2												
STNEKRIE		2		2				2					6			2																
STNEPSEU																			2													
SURISPC1		5										6																				
SURISPC2									6																			2				

APPENDIX F. FREQUENCIES AND RELATIVE ABUNDANCES OF GENERA FOR ALL ISLANDS

Table F1: Frequencies and relative abundances (%) of the genera for all islands.

	Campbell Island		South Shetland		Kerguelen		Crozet		Heard Island		Prince Edward		South Georgia	
	FR (%)	RA (%)	FR (%)	RA (%)	FR (%)	RA (%)	FR (%)	RA (%)	FR (%)	RA (%)	FR (%)	RA (%)	FR (%)	RA (%)
Achnanthes	15,6	0,22	11,4	0,31	16,9	0,11	5,0	0,03	19,4	0,13	1,4	0,00	19,4	1,56
Achnanthidium	6,3	0,12	2,5	0,10	93,0	11,37	74,3	3,16	43,2	1,40	61,6	6,96	22,2	0,91
Actinella	9,4	0,27	0,0	0,00	0,0	0,00	0,0	0,00	0,0	0,00	0,0	0,00	0,0	0,00
Adlafia	37,5	1,37	19,0	0,13	86,6	5,01	90,1	5,63	91,4	12,56	52,5	1,31	2,8	0,05
Amphora	0,0	0,00	35,4	0,78	10,5	0,05	3,0	0,02	7,2	0,11	0,5	0,00	0,0	0,00
Angusticopula	59,4	5,30	0,0	0,00	12,2	0,66	3,0	0,34	0,0	0,00	4,6	0,68	0,0	0,00
Arcanodiscus	12,5	2,35	0,0	0,00	5,2	0,10	3,0	0,05	0,0	0,00	2,3	0,06	0,0	0,00
Aulacoseira	0,0	0,00	0,0	0,00	52,3	1,48	49,5	2,91	0,7	0,01	46,1	2,97	13,9	0,14
Brachysira	9,4	0,09	53,2	1,69	9,9	0,19	0,0	0,00	0,0	0,00	0,0	0,00	0,0	0,00
Caloneis	3,1	0,02	24,1	0,20	23,3	0,10	21,8	0,16	52,5	0,76	5,0	0,02	5,6	0,03
Cavinula	3,1	0,02	0,0	0,00	33,1	0,78	11,9	0,03	36,0	0,19	13,7	0,07	0,0	0,00
Chamaepinnularia	9,4	0,32	79,7	5,49	75,6	4,59	45,5	1,25	92,1	10,33	81,7	7,14	27,8	0,48
Cocconeis	34,4	3,73	0,0	0,00	1,2	0,00	6,9	0,15	0,0	0,00	4,1	0,03	5,6	0,02
Craticula	0,0	0,00	0,0	0,00	3,5	0,01	4,0	0,02	0,7	0,00	18,3	0,23	0,0	0,00
Cyclotella	0,0	0,00	0,0	0,00	0,0	0,00	0,0	0,00	0,0	0,00	0,0	0,00	5,6	0,30
Cymbella	0,0	0,00	0,0	0,00	0,0	0,00	0,0	0,00	0,0	0,00	0,0	0,00	11,1	0,19
Cymbopleura	0,0	0,00	0,0	0,00	0,0	0,00	5,0	0,05	0,0	0,00	0,0	0,00	0,0	0,00
Delicata	3,1	0,02	0,0	0,00	0,0	0,00	0,0	0,00	0,0	0,00	0,0	0,00	0,0	0,00
Diatomella	50,0	3,45	0,0	0,00	65,1	1,20	44,6	0,52	33,8	0,91	11,0	0,35	0,0	0,00
Diploneis	21,9	0,43	0,0	0,00	44,2	0,35	41,6	0,51	10,8	0,26	25,6	0,20	22,2	0,23
Distrionella	0,0	0,00	0,0	0,00	72,1	6,00	68,3	4,54	33,8	0,69	36,5	1,77	75,0	5,07
Ehrenbergia	0,0	0,00	0,0	0,00	0,0	0,00	0,0	0,00	0,0	0,00	0,5	0,01	0,0	0,00
Encyonema	18,8	0,22	0,0	0,00	15,7	0,08	18,8	0,13	42,4	0,93	5,9	0,03	0,0	0,00
Encyonopsis	15,6	0,09	0,0	0,00	30,8	0,18	0,0	0,00	20,9	0,23	0,0	0,00	0,0	0,00
Eolimna	0,0	0,00	6,3	0,09	2,3	0,03	29,7	0,51	9,4	0,08	13,7	0,75	11,1	0,50
Epithemia	9,4	0,15	0,0	0,00	0,0	0,00	0,0	0,00	0,0	0,00	0,0	0,00	0,0	0,00
Eucocconeis	0,0	0,00	0,0	0,00	26,2	0,24	27,7	0,16	17,3	0,13	14,2	0,30	0,0	0,00
Eunotia	31,3	4,33	21,5	1,25	77,9	4,42	73,3	10,61	50,4	4,13	83,6	11,77	77,8	21,66
Fallacia	0,0	0,00	0,0	0,00	0,0	0,00	0,0	0,00	0,0	0,00	0,9	0,02	0,0	0,00
Ferocia	21,9	4,46	0,0	0,00	0,6	0,02	0,0	0,00	3,6	0,13	0,0	0,00	0,0	0,00
Fistulifera	0,0	0,00	8,9	0,10	0,0	0,00	0,0	0,00	0,0	0,00	0,0	0,00	0,0	0,00
Fragilaria	28,1	2,66	67,1	7,49	79,7	8,80	76,2	9,06	57,6	6,26	42,0	4,02	13,9	0,34
Fragilariopsis	0,0	0,00	0,0	0,00	4,7	0,00	5,0	0,02	19,4	0,08	14,6	0,08	27,8	0,30
Frankophila	12,5	0,88	0,0	0,00	55,8	2,35	58,4	4,02	3,6	0,03	11,0	0,45	0,0	0,00
Frustulia	40,6	0,76	0,0	0,00	37,2	0,40	42,6	0,56	33,8	0,32	30,6	0,45	0,0	0,00
Geissleria	3,1	0,03	0,0	0,00	13,4	0,09	5,9	0,03	15,1	0,48	5,0	0,02	2,8	0,02
Gomphonema	37,5	1,47	79,7	5,25	83,1	3,00	75,2	2,59	51,1	0,66	25,6	0,38	38,9	0,83
Hantzschia	9,4	0,55	58,2	4,09	5,8	0,01	7,9	0,06	18,0	0,09	10,5	0,03	58,3	3,99

Table F1: continued

Hippodonta	0,0	0,00	7,6	0,17	1,2	0,01	3,0	0,02	0,0	0,00	0,5	0,00	0,0	0,00
Humidophila	75,0	15,19	93,7	12,54	93,6	6,94	83,2	10,05	80,6	15,36	91,3	12,69	25,0	2,13
Incertae	9,4	0,05	0,0	0,00	0,0	0,00	0,0	0,00	0,0	0,00	0,0	0,00	0,0	0,00
Kobayasiella	3,1	0,22	0,0	0,00	12,2	0,65	17,8	0,33	0,0	0,00	40,2	2,11	0,0	0,00
Lecohuia	9,4	0,37	0,0	0,00	65,1	2,25	67,3	2,60	23,0	0,87	21,9	0,59	2,8	1,67
Luticola	31,3	1,78	54,4	2,18	11,6	0,20	12,9	0,14	28,8	0,69	12,8	0,16	38,9	1,64
Mayamaea	0,0	0,00	3,8	0,11	5,2	0,02	9,9	0,08	25,9	0,43	9,6	0,72	2,8	0,37
Melosira	0,0	0,00	0,0	0,00	0,0	0,00	0,0	0,00	15,8	2,12	27,4	1,32	2,8	0,02
Michelcostea	0,0	0,00	0,0	0,00	2,3	0,01	5,9	0,04	10,1	0,12	0,0	0,00	0,0	0,00
Microstatus	0,0	0,00	0,0	0,00	0,0	0,00	0,0	0,00	0,0	0,00	5,0	0,30	0,0	0,00
Muelleria	0,0	0,00	22,8	0,66	4,1	0,02	1,0	0,01	12,2	0,08	7,3	0,03	2,8	0,03
Navicula	31,3	0,26	72,2	4,83	16,9	0,11	32,7	1,57	56,8	1,12	40,2	1,57	5,6	0,05
Naviculadicta	6,3	0,06	0,0	0,00	28,5	0,39	44,6	0,62	53,2	1,45	56,2	3,24	5,6	0,02
Neidium	0,0	0,00	0,0	0,00	11,6	0,03	20,8	0,12	28,1	0,18	20,1	0,13	0,0	0,00
Nitzschia	15,6	0,39	97,5	24,39	45,3	1,13	77,2	4,64	66,9	3,11	61,2	4,03	50,0	7,20
Nupela	37,5	1,83	0,0	0,00	0,0	0,00	18,8	0,09	0,7	0,00	0,0	0,00	0,0	0,00
Opephora	0,0	0,00	0,0	0,00	0,0	0,00	0,0	0,00	0,0	0,00	0,5	0,02	0,0	0,00
Orthoseira	0,0	0,00	17,7	0,24	8,1	0,04	9,9	0,19	0,7	0,01	5,5	0,22	13,9	0,11
Pinnularia	71,9	5,52	92,4	8,68	86,0	2,49	93,1	4,58	98,6	15,07	95,9	11,93	97,2	18,94
Pinnunavis	21,9	1,83	0,0	0,00	0,6	0,00	2,0	0,00	5,0	0,09	16,4	0,36	0,0	0,00
Placoneis	0,0	0,00	32,9	0,34	0,0	0,00	0,0	0,00	0,0	0,00	0,0	0,00	0,0	0,00
Planothidium	59,4	19,20	65,8	3,93	90,1	8,52	92,1	11,25	81,3	4,23	39,3	2,22	47,2	6,17
Platessa	21,9	1,05	0,0	0,00	5,2	0,06	32,7	0,45	2,2	0,13	33,8	1,14	0,0	0,00
Psammothidium	68,8	12,95	86,1	13,27	98,3	8,76	93,1	9,26	80,6	6,18	87,7	13,27	83,3	21,78
Pseudostaurosira	0,0	0,00	0,0	0,00	13,4	0,18	3,0	0,62	0,7	0,02	1,4	0,00	0,0	0,00
Rhopalodia	12,5	2,26	0,0	0,00	20,3	0,33	33,7	1,29	12,2	0,43	2,3	0,06	0,0	0,00
Rossithidium	28,1	2,61	0,0	0,00	0,0	0,00	0,0	0,00	0,0	0,00	0,0	0,00	0,0	0,00
Sellaphora	18,8	0,81	30,4	0,87	31,4	1,27	30,7	0,81	18,7	0,85	15,1	0,85	0,0	0,00
Stauroforma	3,1	0,02	7,6	0,07	58,7	9,01	51,5	1,69	40,3	2,68	52,1	2,25	13,9	0,20
Stauroneis	25,0	0,16	0,0	0,00	9,3	0,04	9,9	0,04	36,0	0,44	7,3	0,05	16,7	0,30
Stauroptera	0,0	0,00	0,0	0,00	0,0	0,00	0,0	0,00	0,7	0,00	1,4	0,05	0,0	0,00
Staurosira	0,0	0,00	1,3	0,04	1,2	0,00	5,9	0,04	17,3	3,23	4,1	0,26	19,4	0,39
Staurosirella	0,0	0,00	25,3	0,69	65,1	5,87	56,4	2,32	10,1	0,04	12,3	0,32	41,7	0,64
Surirella	12,5	0,15	0,0	0,00	8,1	0,03	0,0	0,00	20,9	0,12	4,6	0,02	0,0	0,00
Tabularia	0,0	0,00	0,0	0,00	0,6	0,00	1,0	0,00	0,7	0,00	0,0	0,00	2,8	0,09
Thalassionema	0,0	0,00	0,0	0,00	5,2	0,02	1,0	0,00	7,9	0,04	0,9	0,00	22,2	0,97
Thalassiosira	0,0	0,00	0,0	0,00	0,6	0,00	0,0	0,00	7,9	0,03	4,6	0,01	22,2	0,65

APPENDIX G. SCIENTIFIC ACTIVITIES DURING COURSE OF THESIS

Scientific publications

- Goeyers C. & Van de Vijver B. (2020) Revision of the non-marine melosiroid diatom flora of the sub-AntarcticCampbell Island (southern Pacific Ocean) with the description of 5 new species. *European Journal of Taxonomy.* 694:1–30
- Goeyers C. & Van de Vijver B. (2020) Typification and emended description of *Achnanthes muelleri* Carlson, a widespread Antarctic freshwater species. *Notulae algarum.* 127:1-5
- Van de Vijver B., Ballings P. & Goeyers C. (2020) *Frankophila dalevittii,* a new freshwater diatom (Bacillariophyta) from Campbell Island. *Phytotaxa.* 429(1):57-64
- Van de Vijver B., Goeyers C. & de Haan M. (2019) Analysis of type material of *Navicula tenuis* Krasske (Bacillariophyta) and its transfer to the genus Adlafia. *Notulae algarum.* 115:1-3

Scientific presentations

- Poster & presentation: Goeyers C. & Van de Vijver B. (2019) Moss-inhabiting diatoms from Campbell Island Conference: 5th annual meeting on Plant Ecology & Evolution (AMPEE5). Meise, BE, 29 November 2019

Scientific conferences

- 5th Annual Meeting on Plant Ecology & Evolution (AMPEE5) (Meise, BE, 29 November 2019)
- Convocatie Nederlands-Vlaamse Kring van Diatomisten (NVKD) (Meise, BE, 3 October 2019)
- 13th European Diatom Meeting (Cardiff, UK, POSTPONED TO 2021)

Awards

- Award for Best Poster: Goeyers C. & Van de Vijver B. (2019) Moss-inhabiting diatoms from Campbell Island Conference: 5th annual meeting on Plant Ecology & Evolution (AMPEE5). Meise, BE, 29 November 2019

APPENDIX H. PUBLISHED WORK

European Journal of Taxonomy 694: 1–30
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2020 · Goeyers C. & Van de Vijver B.

Research article

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

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Abstract. During a survey of the moss-inhabiting diatom flora of the sub-Antarctic Campbell Island, located in the southern Pacific Ocean, several unknown centric diatoms were observed that could not be identified using the currently available literature. Detailed light and scanning electron microscopical observations and comparisons with the characters of several species of *Melosira*, *Angusticopula*, *Ferocia* and *Arcanodiscus* worldwide indicated that five of them should be described as new to science: *Angusticopula cosmica* Goeyers & Van de Vijver sp. nov., *Arcanodiscus crawfordianus* Goeyers & Van de Vijver sp. nov., *A. indistinctus* Goeyers & Van de Vijver sp. nov., *A. saundersianus* Goeyers & Van de Vijver sp. nov. and *Ferocia houkiana* Goeyers & Van de Vijver sp. nov. A sixth species, *Angusticopula chilensis*, was illustrated for the first time using SEM and as a result is considered to differ sufficiently from *A. dickiei* to warrant epitypification as *A. chilensis*. The new species were first described in genera that formerly were included within the genus *Melosira*. All six species are morphologically characterized and compared with similar species within their respective genera. Their presence and distribution on Campbell Island are discussed based on the observations made in the available samples.

Keywords. Sub-Antarctica, Campbell Island, centric diatoms, new species, morphology.

Goeyers C. & Van de Vijver B. 2020. 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

Introduction

The non-marine diatom flora of the sub-Antarctic Islands in the southern Pacific Ocean has received far less attention than the flora in the (sub-)Antarctic parts of the Indian and Atlantic Oceans (see for instance Van de Vijver *et al.* 2002; Zidarova *et al.* 2016 and references therein). The Pacific sector of the sub-Antarctic region comprises only a few small islands: Macquarie Island (128 km^2), Snares Island (3.3 km^2), Auckland Island (626 km^2), Campbell Island (113 km^2), Antipodes Island (21 km^2) and Bounty Island (1.35 km^2) (Chown *et al.* 1998). Only a few studies have been published on the diatom flora of these islands (Van de Vijver & Beyens 1999). Most published information comes from

Macquarie Island, a small Australian island situated between Tasmania and the Antarctic Continent. The oldest records of Macquarie Island date back to 1954 when Bunt made a first account of 64 terrestrial diatoms of the island. Most of the reported diatoms on his list were either cosmopolitan or marine taxa. Evans (1970, reporting 84 taxa), Keenan (1995), and especially the work of Dr T.P. McBride (McBride & Selkirk 1999; McBride *et al.* 1999; McBride 2009) and Dr K. Saunders (Saunders *et al.* 2009) dealt with some aspects of the Macquarie Island diatom flora, although none of them made a thorough taxonomic analysis of the non-marine diatom flora of this island. Three new diatom species have recently been described from Macquarrie Island and, to date, only from there: *Gomphonema isabellae* Van de Vijver & T.P.McBride (2006), *Navicula bergstromiana* Van de Vijver & Verleyen (in Sabbe *et al.* 2019) and *Psammothidium hodgsonianum* Van de Vijver (2019). The analysis of the latter species was made when revising all taxa showing some similarity with *Psammothidium manguinii* (Hust.) Van de Vijver. During this revision, a first new species for Campbell Island, *Psammothidium mannensianum* Van de Vijver, was described (Van de Vijver 2019). A second new species was recently described in the genus *Frankophila*, living on wet mosses collected on Campbell Island (Van de Vijver *et al.* 2020).

The diatom flora of Campbell Island was studied by Hickmann & Vitt (1973) who found 59 taxa living epiphytically on mosses. A second study in 2015 by Saunders *et al.* analyzed the relationship between aquatic diatom communities and water chemistry in 54 lakes and ponds on the island. They observed a high floristic similarity between Campbell Island and the sub-Antarctic Islands in the southern Indian Ocean (Van de Vijver *et al.* 2002) and with the flora in the Tasmanian and New Zealand mountain lakes (Vyverman *et al.* 1995; Hodgson *et al.* 1997; Kilroy 2007; John 2018).

During a visit to the moss herbarium at the British Antarctic Survey (Cambridge, UK), the original moss samples that were collected by Dale Vitt and used in their diatom survey (Hickmann & Vitt 1973) were retrieved and subsampled in the BAS herbarium. After preparation for diatom analysis, it was clear that the diatom flora in these moss samples was very well preserved. Analysis of the slides revealed the presence of several centric taxa that could not be identified using the currently available literature.

The genus *Melosira* was originally published in 1827 by Agardh but it was Kützing (1844) who included a large number of taxa in the genus. Later authors revised parts of the genus and split off several, often newly described, genera such as *Aulacoseira* Thwaites (1848), *Orthoseira* Thwaites (1848), *Paralia* Heib. (Heiberg 1863) and *Ellerbeckia* R.M.Crawford (1988). Nevertheless, a large number of taxa remained in the genus *Melosira*. In 2017, the genus *Melosira* was revised, which resulted in the description of several new genera: *Ferocia* Van de Vijver & Houk (in Van de Vijver *et al.* 2017), *Angusticopula* Houk *et al.* (2017) and *Arcanodiscus* Maidana & E.Morales (in Maidana *et al.* 2017). The description of the new genera resulted in a revision of all diatom taxa belonging or formerly belonging to the genus *Melosira* in the sub-Antarctic region. Four new taxa were described: *Ferocia ninae* Van de Vijver (in Van de Vijver *et al.* 2017), *F. subantarctica* Van de Vijver & Houk (2019), *Arcanodiscus desmetianus* Van de Vijver (in Van de Vijver & Houk 2019) and *Melosira jeanbertrandiana* Van de Vijver & Crawford (2019) whereas the correct taxonomic identity of two other taxa was established: *Angusticopula dickiei* (Thwaites) Houk *et al.* and *A. chilensis* (Grunow) Houk *et al.* (Houk *et al.* 2017). These revisions, however, only concerned those taxa that were observed on the islands in the southern Indian Ocean. The recent survey of the Campbell Island moss samples partly fills this gap in our knowledge of the sub-Antarctic melosiroid diatom flora.

Five unknown taxa were found and after a thorough analysis of light and scanning electron microscopy observations and comparison with previously described taxa worldwide, they are described as new to science: *Angusticopula cosmica* sp. nov., *Ferocia houkiana* sp. nov., *Arcanodiscus crawfordianus* sp. nov., *A. indistinctus* sp. nov. and *A. saundersianus* sp. nov. Several populations of a sixth species, *Angusticopula chilensis*, were analyzed in more detail and compared with published images of the

Grunow type slide (in Houk *et al.* 2017: pl. 63, figs 1–6). As unmounted material of this taxon is no longer available (A. Igersheim, Vienna, pers. comm.), one of the Campbell Island populations will be designated as epitype for this species. In the present paper, the morphology of the new species is discussed and the species are compared with similar species worldwide and more specifically with taxa described from the sub-Antarctic region.

Material and methods

Campbell Island (52°32′24″ S, 169°8′42″ E) is the main island of a small volcanic archipelago situated in the southern Pacific Ocean, at approx. 600 km south of New Zealand and 3800 km north of the Antarctic Continent. The island has a total surface area of 113 km^2, reaching an altitude of 569 m. Saunders *et al.* (2015) provide details on the climate, geomorphology and vegetation of the island.

During a National Science Foundation expedition between December 1969 and February 1970, a large number of moss samples were collected by Prof. Dale Vitt (Southern Illinois University Carbondale, USA) (Hickmann & Vitt 1973; Vitt 1974). Part of the samples were retrieved from the British Antarctic Survey herbarium (Cambridge, UK). Several of these samples contained fairly large populations of several melosiroid diatoms. Three samples in particular, containing large populations of the unknown centric diatoms, were chosen for further analysis:

- BAS284: Moubray Hill, 818 ft, *Holomitrium perichaetiale*, on rocks (coll. date 12/01/1970);
- BAS286: South side Mt. Fizeau, *Hypopterygium novae-seelandiae*, dark wet recess (coll. date 22/01/1970);
- BAS303: North side Perseverance Harbour, East of Moubray Hill, *Racopilum strumiferum*, wet rock (coll. date 12/01/1970).

Subsamples of the selected material were prepared for light microscopy (LM) observation following the method described in Van der Werff (1955). Small parts of the samples were cleaned by adding 37% H_2O_2 and heating to 80°C for about one hour. The reaction was completed with the addition of saturated kmnO_4. After digestion and centrifugation (3 × 10 minutes at 3700 g), the material was diluted with distilled water to avoid excessive concentrations of diatom valves. Cleaned diatom valves were mounted in Naphrax®. Samples and slides are stored at the BR-collection (Belgium). The slides were analyzed using an Olympus BX53 microscope, equipped with Differential Interference Contrast (Nomarski) and the UC30 camera connected to the Cell Sense Standard program. For scanning electron microscopy (SEM), part of the suspension was filtered through polycarbonate membrane filters with a pore diameter of 1 µm, pieces of which were fixed on aluminum stubs after air-drying. The stubs were sputter-coated with 10 nm of Pt and studied in a JEOL JSM-7100F at 2 kV (Meise Botanic Garden, Belgium). For each new taxon, the number of specimens measured at random on the type slide is indicated (n = X). Terminology follows Round *et al.* (1990), Maidana *et al.* (2017), Van de Vijver *et al.* (2017) and Houk *et al.* (2017). The morphology of the new species was compared with species described or discussed in Maidana *et al.* (2017), Van de Vijver *et al.* (2002, 2017) and Houk *et al.* (2017 and references therein) and Van de Vijver & Houk (2019).

For the typification of the new species, we chose to use the entire slide as the holotype following Art. 8.2 of the International Code for Botanical Nomenclature (Turland *et al.* 2018). Diatoms show a broad variability along their cell cycle making the choice for the entire population on the slide more obvious.

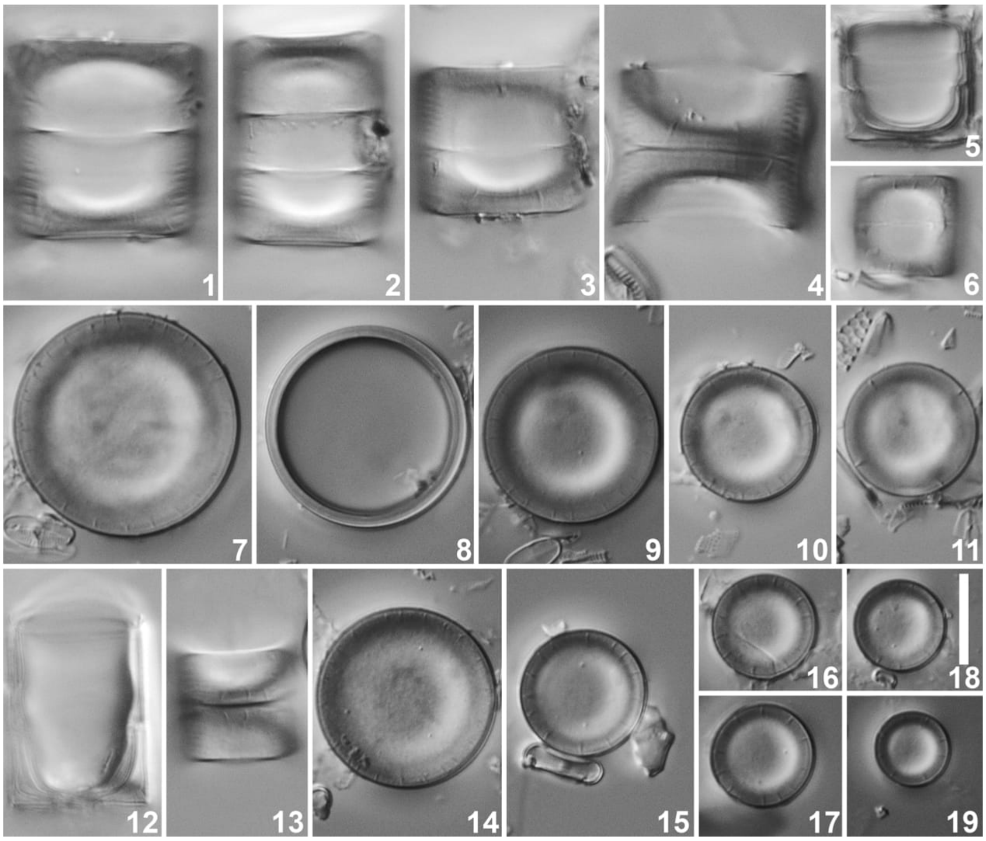
Results

Class Coscinodiscophyceae Round & R.M.Crawford in Round *et al.* (1990) emend.
Medlin & Kaczmarska
Subclass Coscinodiscophycidae Round & R.M.Crawford in Round *et al.* (1990)
Order Melosirales R.M.Crawford in Round *et al.* (1990)
Family Melosiraceae Kütz. (Kützing 1844) emend. R.M.Crawford in Round *et al.* (1990)
Genus *Angusticopula* Houk *et al.*

Angusticopula chilensis (Grunow) Houk *et al.*
http://phycobank.org/102314
Figs 1–27

Basionym

Melosira dickiei forma *chilensis* Grunow in Van Heurck (1882: pl. 90, figs 13–14).

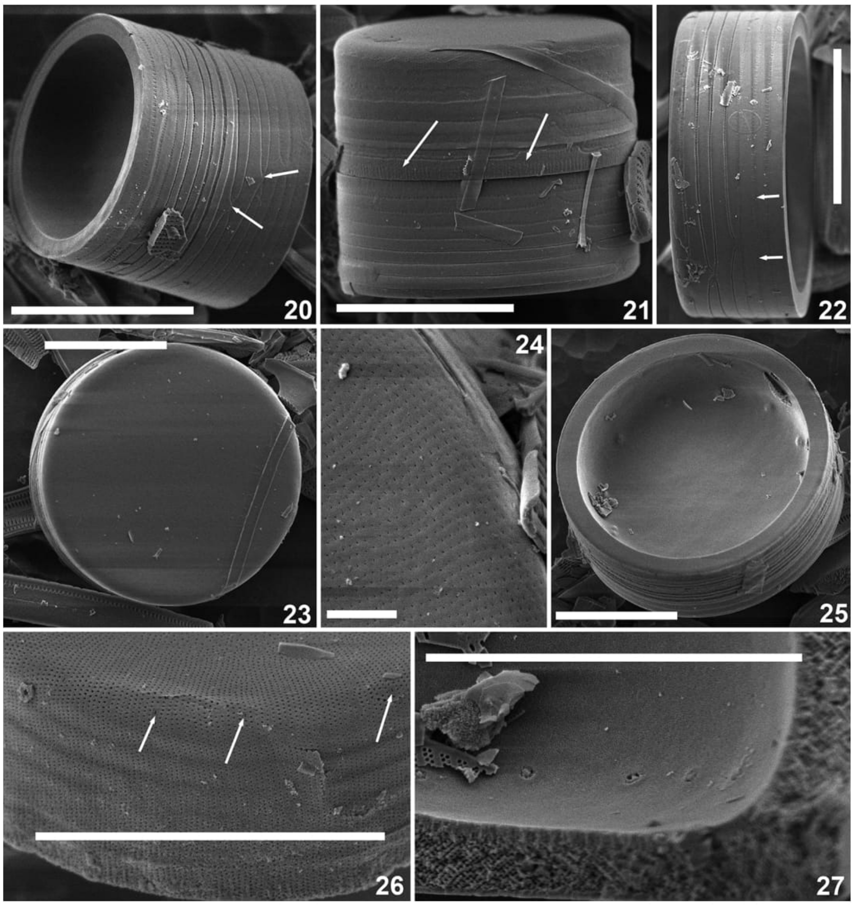


Figs 1–19. *Angusticopula chilensis* (Grunow) Houk *et al.* LM. Campbell Island epitype population, sample BAS286. **1–6**, **12–13**. Several frustules in girdle view. **5**, **12**. Internal valves. **7–11**, **14–19**. Several valves in valve face view clearly showing the marginal rimoportulae. Scale bar = 10 µm.

Material examined

Since only the original slide 1015 in the Grunow collection (V) is available as type material and unmounted material is no longer present (A. Igersheim, Grunow Collection, Vienna, pers. comm.), we designate sample BAS286 as epitype to illustrate in more detail the morphological structures of this species.

Epitype (here designated)
CAMPBELL ISLAND • sample BAS286; 12 Jan. 1970; D. Vitt leg.; BR-4576.



Figs 20–27. *Angusticopula chilensis* (Grunow) Houk *et al*. SEM. Campbell Island epitype population, sample BAS286. **20–22**. SEM view of several valves in girdle view showing the ligulate, open, narrow girdle bands. The arrows indicate the ligulae in Fig. 20, the rimmed mantle edge in Fig. 21 and the fimbriate pars interior of the copulae in Fig. 22. **23**. External view of a valve face. **24**. External detail of the very fine striae and the small, rounded areolae. **25**. Internal view of an entire valve showing the rimoportulae and the thick mantle. **26**. External view of the mantle/valve face junction with several openings of the rimoportulae (arrows). **27**. Internal detail of the valve mantle with some rimoportulae. Scale bars: 20–23, 25–26 = 10 µm; 24, 27 = 1 µm.

Description

Light microscopy (Figs 1–19)
Frustules cylindrical to short barrel-shaped. Cells most likely forming short chains, as often two sibling valves are found attached to each other. Valve diameter (n = 20): 8–25 µm, mantle height (n = 10): 4.5–11 µm. Valves showing thick wall (Fig. 8), having a relatively low mantle and rounded, flat valve face. Internal valves occasionally present (Figs 5, 12). Rimoportulae organized in marginal ring close to the valve face margin, visible as a series of tube-like channels. Striae and areolae not discernible in LM.

Scanning electron microscopy (Figs 20–27)
Girdle composed of a large number (up to 8) of narrow, open copulae (Figs 20–22) showing a fimbriate pars interior (Fig. 22, arrows). Small ligulae fill the gaps created by the open copulae (Fig. 20, arrows). Mantle rather high, densely punctated, clearly rimmed (Figs 21, arrows, 26). Valve faces clearly flat (Fig. 23), lacking granules and spines (Figs 23–24), finely perforated by very small areolae, arranged in irregular, uniseriate striae, ca 80 in 10 µm (Fig. 24). External rimoportula openings visible as slightly elongated slits (Fig. 26, arrows). Valves very thick (Fig. 27). Internally, sessile rimoportulae arranged in an irregular ring near the valve face/mantle junction, visible as slightly raised projections (Figs 25, 27).

Ecology and distribution

The largest populations of *A. chilensis* were found in mosses growing on cliffs next to a waterfall dominated by several species of *Humidophila*, *Diatomella balfouriana* Grev. and *Achnanthes muelleri* C.F.W.Carlson emend. Van de Vijver & Goeyers. The latter species are all known to thrive mostly in aerophilic, moist environments (Van de Vijver *et al.* 2002). *Angusticopula chilensis* was also found on several sub-Antarctic islands located in the southern Indian Ocean such as Iles Crozet (Van de Vijver *et al.* 2002), Iles Kerguelen (Van de Vijver *et al.* 2001) and the Prince Edward Islands (Van de Vijver *et al.* 2008). The species was almost always incorrectly identified as *Melosira* sp. or *Melosira varians* C.Agardh.

Angusticopula cosmica Goeyers & Van de Vijver sp. nov.

http://phycobank.org/102315
Figs 28–43

Etymology

The specific epithet refers to the general outlook of the valves in scanning electron microscopy giving the impression, due to the many granules, of a cosmos with numerous stars.

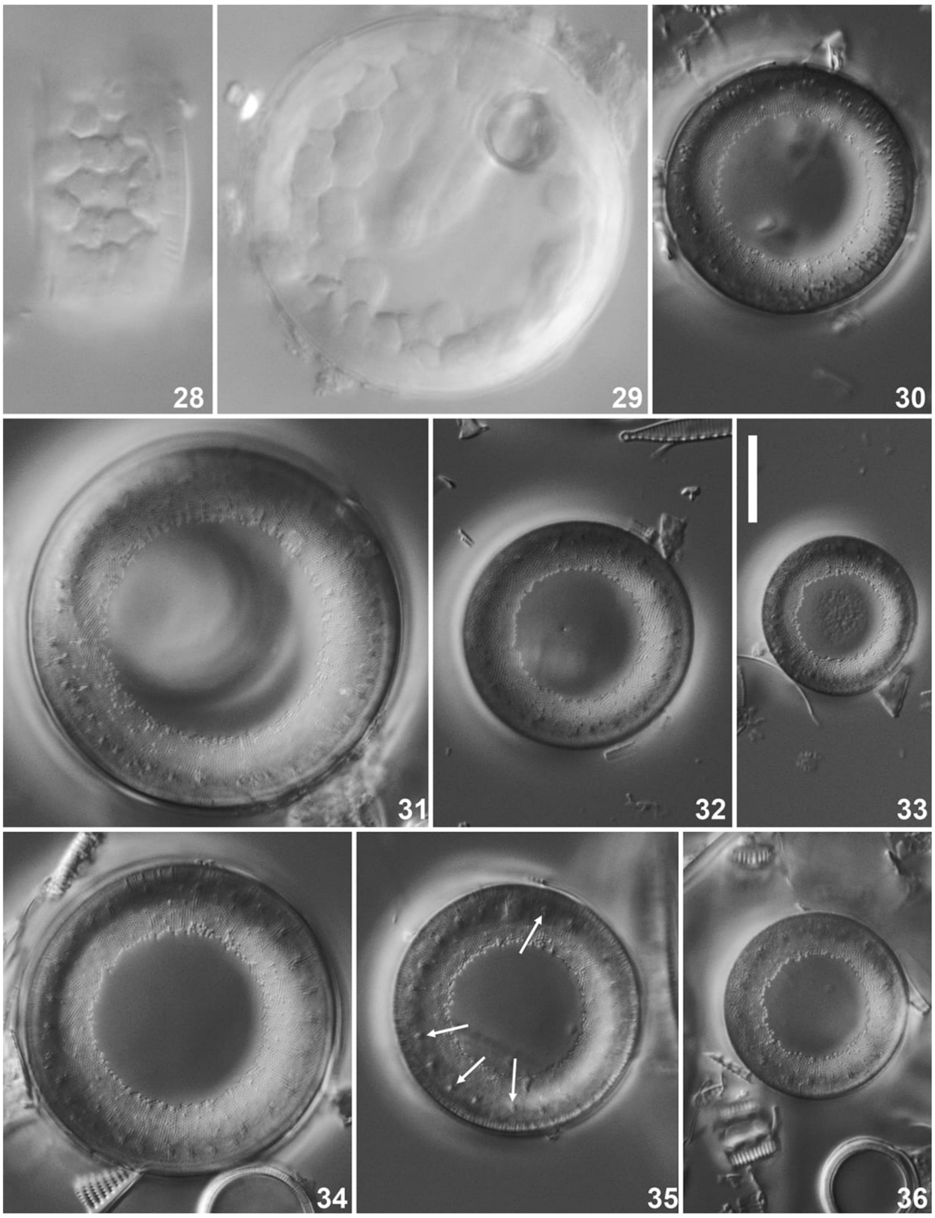
Material examined

Holotype
CAMPBELL ISLAND • sub-Antarctic region; sample BAS303; 12 Jan. 1970; D. Vitt leg.; BR-4577.

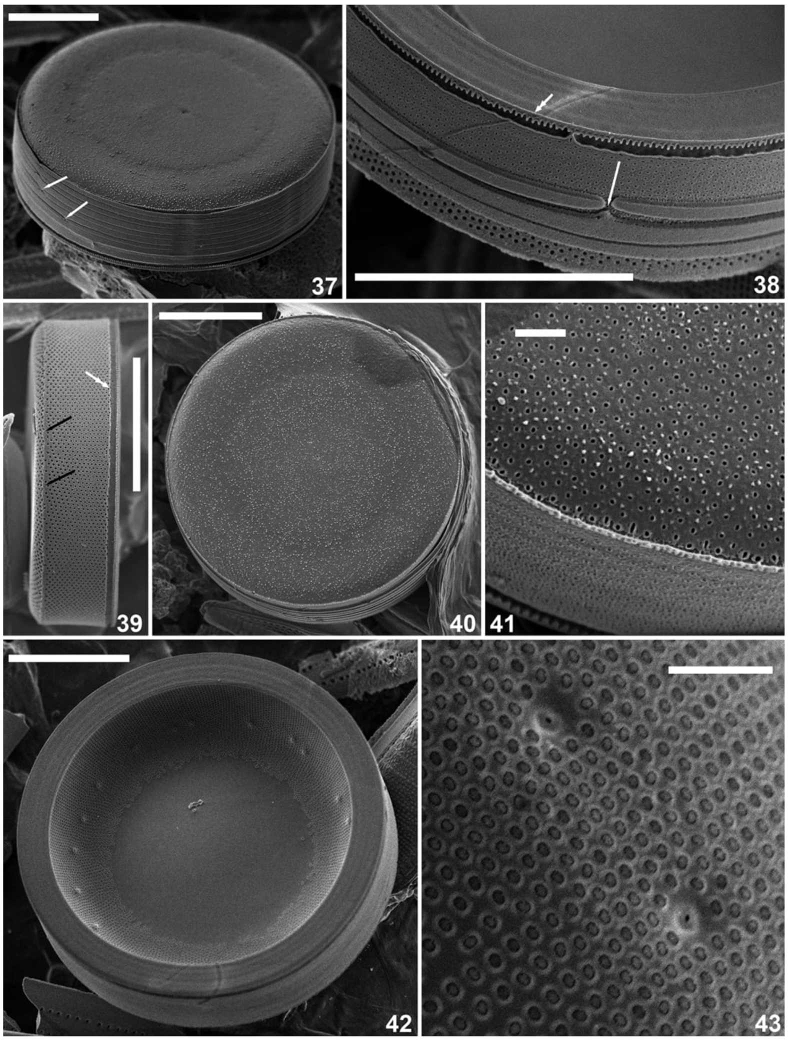
Isotype
CAMPBELL ISLAND • same collection data as for holotype; slide at University of Antwerp, Belgium; PLP-368.

Description

Light microscopy (Figs 28–36)
Frustules rectangular with valve diameter much larger than the mantle height. Cells always solitary; chains, even short ones, never observed. Numerous discoid plastids present. Valve diameter (n = 50): 18–45 µm, mantle height (n = 1): ca 8 µm. Valves with a low mantle and flat valve face. Internal valves never observed. Central area large, diameter 10–25 µm (50–60% of the total valve diameter, irregularly



Figs 28–36. *Angusticopula cosmica* Goeyers & Van de Vijver sp. nov. LM. Campbell Island holotype population, sample BAS303 (BR-4577). **28**. Frustule in girdle view showing the discoid chloroplasts. **29**. Frustule in valve face view showing the discoid chloroplasts. **30–36**. Several valves in valve face view showing clearly the submarginal ring of rimoportulae (arrows) and the striated valve face margin. Scale bar = 10 µm.



Figs 37–43. *Angusticopula cosmica* Goeyers & Van de Vijver sp. nov. SEM. Campbell Island holotype population, sample BAS303 (BR-4577). **37**. Frustule showing both the valve face and girdle formed by open, narrow copulae. The arrows indicate the ligulae. **38**. Detail of the mantle valve with the serrated mantle edge (double arrow) and the ligulate copulae (single arrow). **39**. Valve in girdle view showing the striated mantle, the narrow ridge bordering the mantle/valve face junction (black arrows) and the typical groove bordering the mantle edge (double white arrow). **40**. External view of a valve face showing the dense pattern of granules. **41**. External detail of the very fine striae, the small, rounded areolae and the narrow ridge bordering the valve margin. **42**. Internal view of an entire valve showing the rimoportulae and the thick mantle. **43**. Internal detail of the valve with some rimoportulae. Scale bars: 37–39, 42 = 10 µm; 40 = 5 µm; 41, 43 = 1 µm.

bordered by marginal striae. Marginal striae radial, clearly punctate, 31–35 in 10 µm, clearly visible in LM. Ring of rimoportulae visible close to the valve face/mantle junction (Fig. 35, arrows).

Scanning electron microscopy (Figs 37–43)
Girdle comprising a large number (up to 8) of narrow, open, non-perforated copulae (Fig. 37). Small ligulae filling the gaps created by the open copulae (Figs 37, arrows, 38). Mantle rather shallow, with dense uniseriate striation pattern, composed of very small, rounded areolae. Mantle edge with a constricted rim bordered by a serrate marginal edge (Figs 38, 39, double white arrows). Valve face/mantle junction gently sloping showing a shallow marginal ridge (Figs 39, black arrows, 40). Valves faces clearly flat (Fig. 40), entirely covered by irregularly scattered small granules (Figs 40–41). Central area weakly raised, clearly visible in oblique view (Fig. 37). Spines absent (Fig. 40). Valve face striation restricted to a broad marginal zone. Striae uniseriate, forming rather irregular series of small areolae bordered by a very shallow siliceous rim (Fig. 41). Internally, valves weakly dome-shaped (Fig. 42), perforated by a marginal pattern of small areolae, closed by individual hymenes. Areolae clearly arranged in striae, separated by very narrow interstriae. Irregular ring of rather large rimoportulae present near the mantle edge (Figs 42–43). Rimoportulae visible internally as short raised tubes (Fig. 43).

Ecology and distribution

Angusticopula cosmica sp. nov. was described from a *Racopilum* moss vegetation collected from a wet rock east of Moubray Hill. The sample was dominated by *Frankophila dalevittii*, a recently described endemic species for Campbell Island (Van de Vijver *et al.* 2020), *Diatomella balfouriana* and *Diatomella colonialis* Van de Vijver & Le Cohu.

Class Coscinodiscophyceae Round & R.M.Crawford in Round *et al.* (1990) emend. Medlin & Kaczmarska
Subclass Coscinodiscophycidae Round & R.M.Crawford in Round *et al.* (1990)
Order Melosirales R.M.Crawford in Round *et al.* (1990)
Family Melosiraceae Kütz. (Kützing 1844) emend. R.M.Crawford in Round *et al.* (1990)
Genus *Ferocia* Van de Vijver *et al.*

Ferocia houkiana Goeyers & Van de Vijver sp. nov.
http://phycobank.org/102316
Figs 44–73

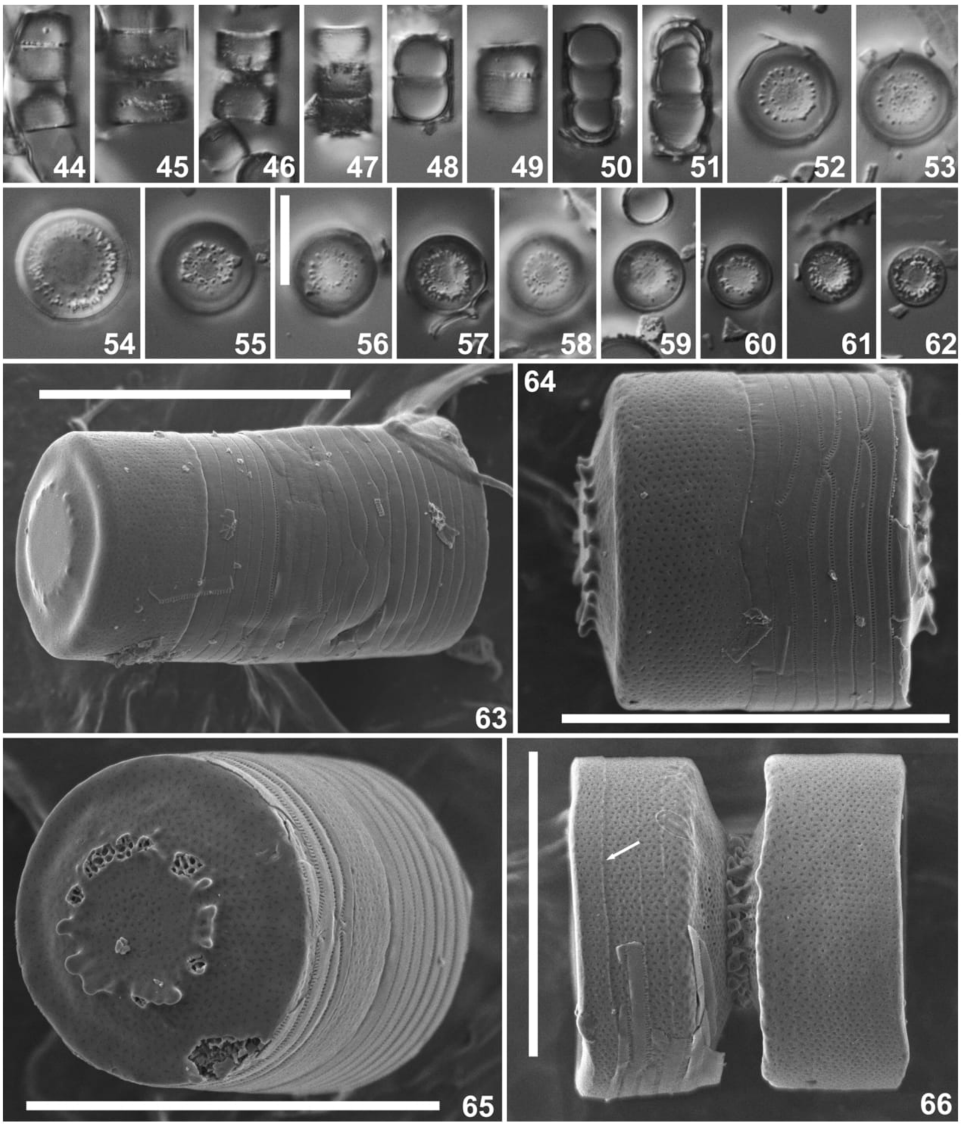
Etymology

The species is named in honour of our colleague and friend Dr Václav Houk (Institute of Botany, Czech Republic) to acknowledge him for his work on melosiroid diatoms.

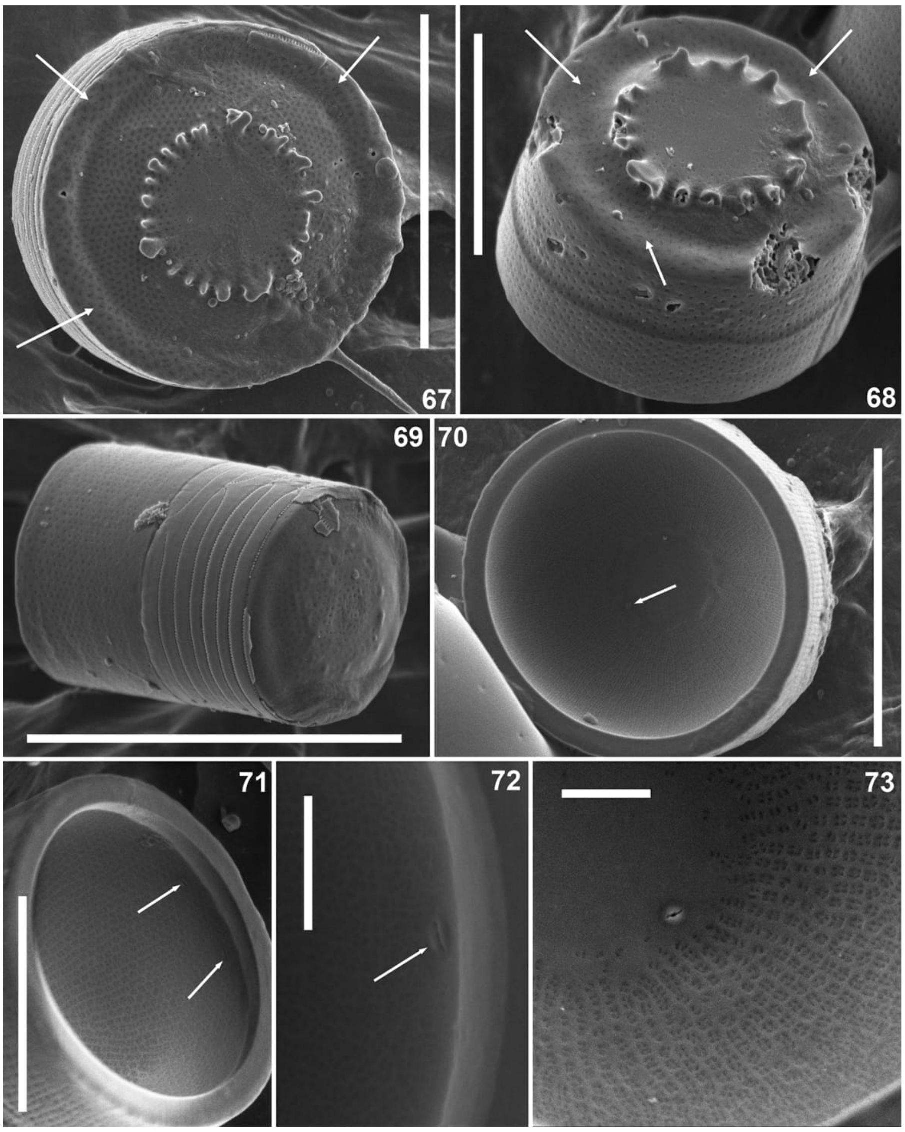
Material examined

Holotype
CAMPBELL ISLAND • sub-Antarctic region; sample BAS284; 12 Jan. 1970; D. Vitt leg.; BR-4578.

Isotype
CAMPBELL ISLAND • same collection data as for holotype; slide at University of Antwerp, Belgium; PLP-369.



Figs 44–66. *Ferocia houkiana* Goeyers & Van de Vijver sp. nov. LM and SEM. Campbell Island holotype population, sample BAS284 (BR-4578). LM. **44–49**. Several frustules in girdle view, often connected to each other. **50–51**. Internal valves. **52–62**. Several valves in valve face view clearly showing the central ring of spines. SEM. **63**. Frustule in girdle view with the narrow copulae. **64**. Frustule in girdle view with the narrow copulae on one side and one the side showing the broad mantle with one indicated rimoportula. **65**. External view of a valve face and the girdle. Note the central ring of partly hollow spines. **66**. External view of two valves connected via their linking spines. The arrow indicates the Müller step. Scale bars = 10 µm.



Figs 67–73. *Ferocia houkiana* Goeyers & Van de Vijver sp. nov. SEM. Campbell Island holotype population, sample BAS284 (BR-4578). **67–68**. Two external valve face views with the typical spines, the rounded to slit like areolae and the Müller step. **69**. External girdle view of a valve lacking the typical central ring of spines. Note the spines vestiges that are present in the central area. **70**. Internal view of an entire valve showing clearly the central rimoportulae (arrow) and the small central area. **71**. Internal view of an entire valve showing clearly the submarginal rimoportulae (arrows). **72**. Internal detail of the valve with one rimoportula indicated by the arrow. **73**. Internal detail of the valve central area with the central rimoportula. Scale bars: 67, 69–70 = 10 µm; 68, 71 = 5 µm; 72–73 = 1 µm.

Description

Light microscopy (Figs 44–62)
Frustules rectangular. Cells connected via a central ring of spines, forming short chains. Numerous discoid plastids present. Girdle composed of large number of very narrow copulae, covering two adjacent valves. Valve diameter (n = 20): 4–11 µm, mantle height (n = 5): 4.0–5.5 µm. Valves with a relatively low mantle and rounded, flat valve face. Internal valves occasionally observed (Figs 50–51). Central area dominated by a regular crown of spines. Scattered spines present on the entire valve face. Striae not discernible in LM.

Scanning electron microscopy (Figs 63–73)
Girdle composed of a large number (up to 20) of narrow, open, non-perforated copulae (Fig. 63). Girdle bands attached to one of the valves of a cell extending over one of the new daughter valves after each cell division, meeting and overlapping with the bands attached to the other parent valve, covering that way two new valves of the daughter cells (Fig. 63). Copulae fimbriate on pars inferior giving the misleading impression of perforated girdle bands in non-eroded girdles (Figs 63, 65). Valves connected via central crown of large, wedge-shaped spines (Fig. 64). Müller step on mantle occasionally observed (Fig. 66, arrow). Mantle striae straight, composed of small, rounded areolae (Figs 64, 66). Near mantle edge, areolae very much smaller than near and at valve face/mantle junction, areolae irregularly scattered (Fig. 64). Mantle edge not rimmed. Rimoportula openings on the mantle not distinguishable from mantle areolae. Valve face/mantle junction thickened, relatively abrupt (Figs 63, 66). Valve face dominated by a central regular ring of large, relatively low, wedge-shaped spines (Figs 67–68). Spines hollow but apparently chambered with small silica walls inside the spines (Fig. 68). Spines occasionally lacking or reduced to series of low silica outgrowths (Fig. 69). Central area clearly raised, bordered by a narrow flat valve face edge, covered by an irregular pattern of small, rounded to slit-like areolae (Figs 67, 68, arrows). Striation pattern not detectable in the areolae. Internally, a few sessile rimoportula visible close to the mantle edge (Figs 71, 72, arrows), irregularly scattered. One rimoportula present near the valve center on the valve face (Figs 70, 73, arrow). Internal valve surface covered by numerous small areolae (Fig. 73).

Ecology and distribution

Ferocia houkiana sp. nov. is a frequently observed species on Campbell Island. It was found in several moss samples on rocks and next to waterfalls, usually dominated by species belonging to the genera *Pinnularia*, *Pinnunavis* and *Eunotia*. The type sample is dominated by the new species of *Ferocia* and is accompanied by *Pinnularia borealis* s. lat. Ehrenb. which points to a drier character of the environment, often influenced by sea spray (Van de Vijver *et al.* 2002).

Class Coscinodiscophyceae Round & R.M.Crawford in Round *et al.* (1990) emend.
Medlin & Kaczmarska
Subclass Coscinodiscophycidae Round & R.M.Crawford in Round *et al.* (1990)
Order Arcanodiscales E.Morales & Maidana in Maidana *et al.* (2017)
Family Arcanodiscaceae E.Morales & Maidana in Maidana *et al.* (2017)
Genus *Arcanodiscus* E.Morales & Maidana in Maidana *et al.* (2017)

Arcanodiscus crawfordianus Goeyers & Van de Vijver sp. nov.
http://phycobank.org/102318
Figs 74–80, 116–124

Etymology

The species is named in honor of our colleague Dr Richard M. Crawford to acknowledge his work on melosiroid diatoms.

Material examined

Holotype

CAMPBELL ISLAND • sub-Antarctic region; sample BAS303; 12 Jan. 1970; D. Vitt leg.; BR-4579.

Isotype

CAMPBELL ISLAND • same collection data as for holotype; slide at University of Antwerp, Belgium; PLP-370.

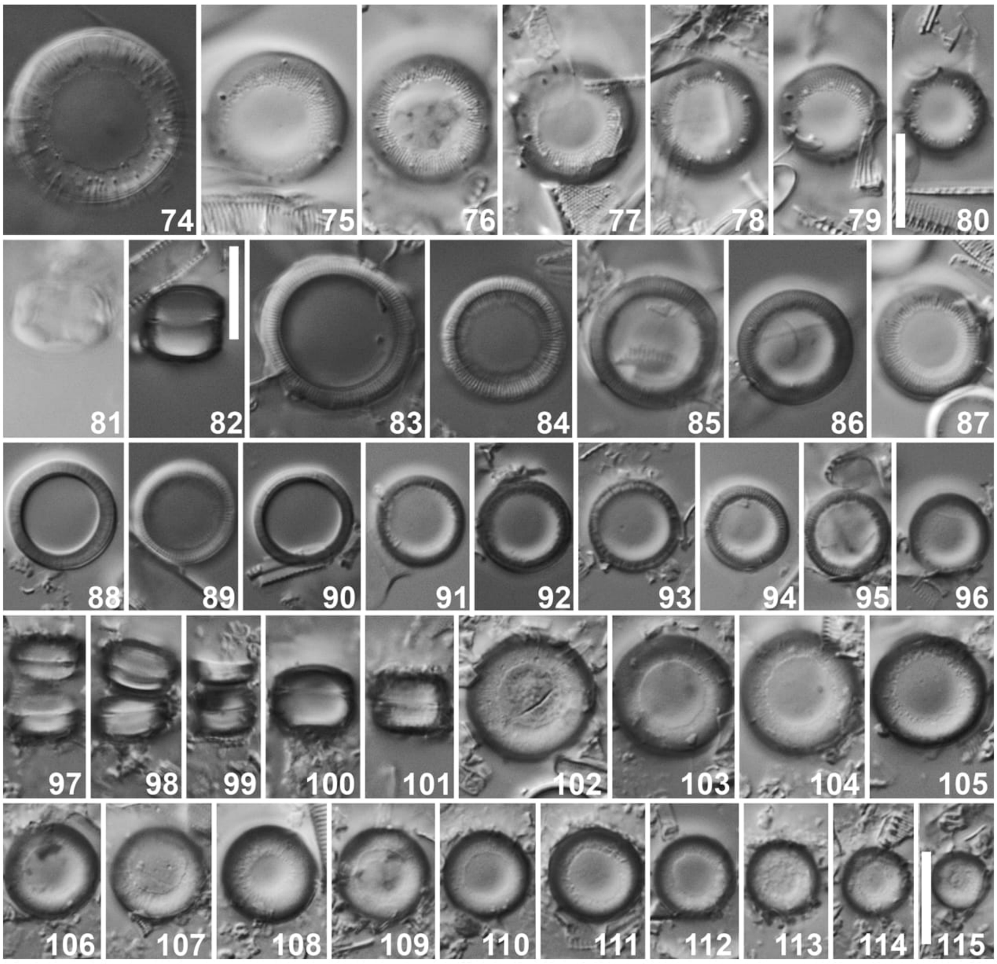
Description

Light microscopy (Figs 74–80)

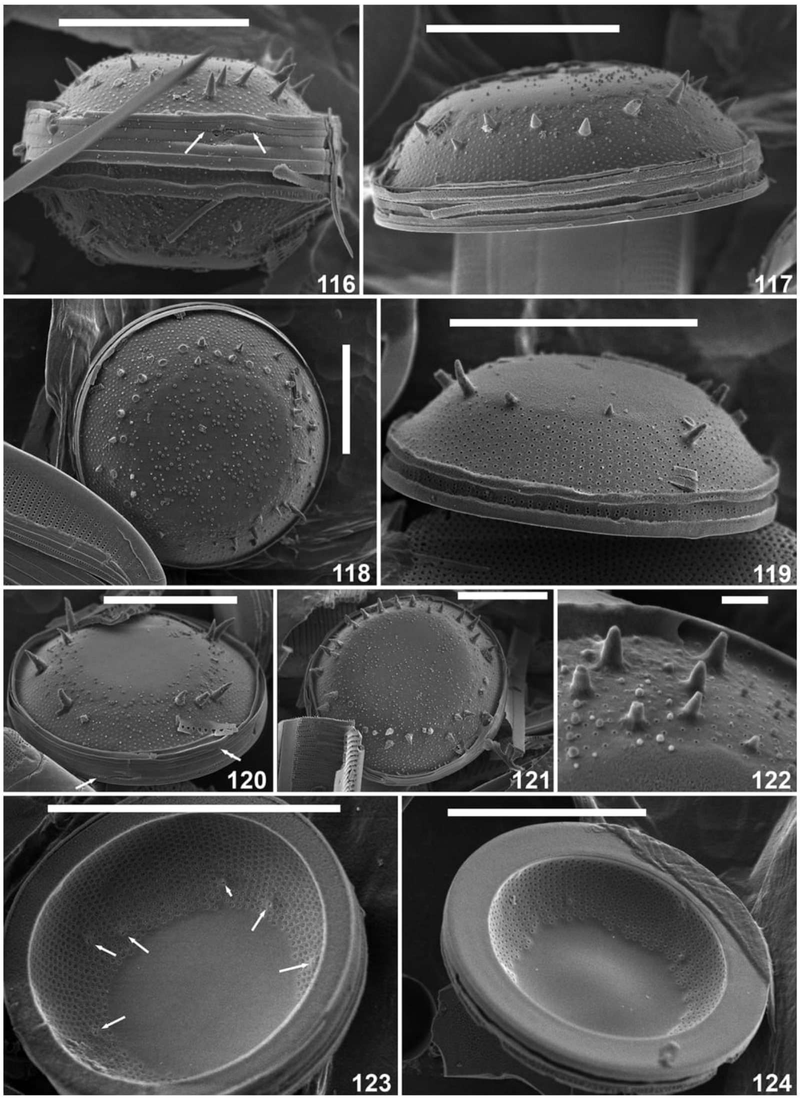
To date, frustules in girdle view not observed in LM. Valves strongly silicified, rounded with a thick mantle and clearly convex, weakly domed valve face. Valve dimensions (n = 10): valve diameter 9–18.5 µm. Central area formed by a large, smooth, hyaline zone, 6–11 µm, ca 60% of the total valve diameter, surrounded by a striated, irregularly bordered marginal zone. Thick spines, scattered in the marginal zone distinctly present. Marginal striae discernible in LM, 30–33 in 10 µm. Visible tube processes lacking.

Scanning electron microscopy (Figs 116–124)

Frustules discoid with very heavily silicified valves, visible as a thick mantle (Figs 116, 123–124). Frustule height approx. 11 µm. Cingulum comprising at least 4, rather narrow, very thin, non-perforated, open, ligulate copulae (Figs 116, 120, double arrow). Pars interior clearly fimbriate (Figs 116, 117, arrows) giving the impression of perforated copulae. Valve face with large, flat hyaline, almost rounded central area, free of areolae, but with a dense covering of small silica granules (Figs 119–121). Marginal zone distinctly sloping towards the mantle with a very narrow flat zone immediately next to the valve face/mantle junction. Regular striation pattern present on sloping marginal zone. Irregular marginal ring of large, acute, solid spines present (Figs 120–122) close to the hyaline central area, placed between the areolae. Irregular pattern of small granules (Fig. 122) extending between the spines, though never reaching the mantle. Striae composed of small, strictly rounded areolae. Areolae externally covered by perforated occlusions (Figs 118, 120). Openings of portulae not distinguishable from areolae even in SEM. Striae continuing over the valve face/mantle junction, interrupted by a thick marginal ridge running entirely around the mantle (Fig. 119), usually covered by girdle bands. Mantle edge rather narrow. Between marginal ridge and mantle edge, relatively deep groove present, bearing several rows of strictly rounded areolae.



Figs 74–115. Three new *Arcanodiscus* species from Campbell Island. **74–80**. *Arcanodiscus crawfordianus* Goeyers & Van de Vijver sp. nov. LM. Campbell Island holotype population, sample BAS303 (BR-4579). Several valves in valve face view showing clearly the large central area, the irregularly scattered spines and the marginal striae. **81–96**. *Arcanodiscus indistinctus* Goeyers & Van de Vijver sp. nov. LM. Campbell Island holotype population, sample BAS303 (BR-4580). **81**. Frustule in girdle view showing the discoid chloroplasts. **82**. Frustule in girdle view. **83–96**. Several valves in valve face view. Note the thick mantle in some of the valves and the large central area. **97–115**. *Arcanodiscus saundersianus* Goeyers & Van de Vijver sp. nov. LM. Campbell Island holotype population, sample BAS272 (BR-4581). **97–101**. Several frustules in girdle view, often connected to each other. **102–115**. Several valves in valve face view. Note the thick mantle in some of the valves and the relatively small central area. The marginal striae are hardly visible in LM. Scale bars = 10 µm.



Figs 116–124. *Arcanodiscus crawfordianus* Goeyers & Van de Vijver sp. nov. SEM. Campbell Island holotype population, sample BAS303 (BR-4579). **116**. Frustule in girdle view. The arrows indicate the fimbriate pars interior of the copulae. **117**. External view of a valve in girdle view showing the domed valve face, the marginal spines and some of the narrow, unperforated copulae. **118**. External valve face view of an entire valve. Note the spines, the granules in the central area and the striae on the sloping margin. **119**. External view of a valve in girdle view showing the domed valve face, the marginal spines, the distinct marginal ridge and the mantle edge bordered by the relatively large groove. **120–121**. Several valve face views to show the irregular rings of spines. **122**. External detail of the spines and the granules. **123–124**. Internal views of an entire valve showing the rimoportulae (arrows). Scale bars: 116, 118–121, 123–124 = 10 µm; 117 = 5 µm; 122 = 1 µm.

Internally, areolae large, clearly rounded, each showing a distinct rota, organized in a regular striation pattern (Fig. 123). Mantle edge very broad, heavily silicified (Figs 123–124). Central area formed by a large hyaline, irregularly bordered, central zone (Fig. 123). Several perforated, thickened protuberances which we presume to be the inner openings of portulae are irregularly scattered between the areolae, never organized in a regular marginal ring (Fig. 123, arrows). Inner openings of these processes rounded, smaller than the areolae, weakly raised above the surface (Fig. 124).

Ecology and distribution

Arcanodiscus crawfordianus sp. nov. was described from a *Racopilum* moss vegetation collected from a wet rock east of Moubray Hill. The sample, in which also the newly described *Arcanodiscus indistinctus* sp. nov. and *Angusticopula cosmica* sp. nov. were observed, was dominated by *Frankophila dalevittii* (Van de Vijver *et al.* 2020), *Diatomella balfouriana* and *Diatomella colonialis*. The presence in other samples needs to be confirmed with SEM observations.

Arcanodiscus indistinctus Goeyers & Van de Vijver sp. nov.

http://phycobank.org/102319
Figs 81–96, 125–131

Etymology

The specific epithet ‘*indistinctus*’ refers to the lack of any specific peculiarity of this species as a distinguishing feature.

Material examined

Holotype

CAMPBELL ISLAND • sub-Antarctic region; sample BAS303; 12 Jan. 1970; D. Vitt leg.; BR-4580.

Isotype

CAMPBELL ISLAND • same collection data as for holotype; slide at University of Antwerp, Belgium; PLP-371.

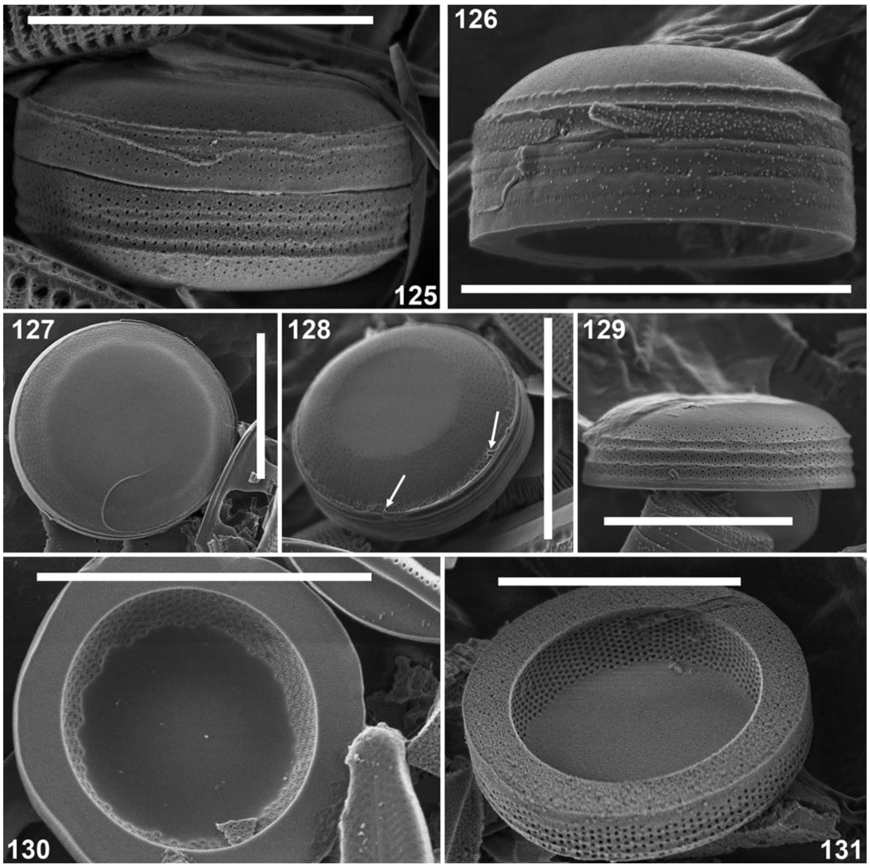
Description

Light microscopy (Figs 81–96)
Frustules discoid, almost square to rectangular with broadly rounded edges and convex valve faces. Frustules never seen attached to each other, always solitary. Multiple discoid chloroplasts present. Girdle bands not discernible in LM. Valves rather strongly silicified, rounded with a thick mantle and convex, weakly domed valve face. Valve dimensions (n = 25): valve diameter 9–17 µm, frustule height (n = 2): 7–9 µm. Central area comprising a large, smooth, hyaline zone, almost 75% of the total valve diameter, surrounded by a clearly striated marginal zone, 27–35 striae in 10 µm. Visible processes lacking.

Scanning electron microscopy (Figs 125–131)
Frustules discoid with very heavily silicified valves, visible as a thick mantle (Figs 125, 130).

Girdle composed of several, narrow, non-perforated copulae (Fig. 126). Pars interior of the copulae clearly fimbriate giving the impression of perforate bands (Fig. 126). Valve face with large, flat hyaline, almost rounded central area, lacking areolae or any other ornamentation (Figs 127–128). Marginal zone gently sloping towards the mantle, entirely covered with short slit-like to almost rounded areolae (the latter when clearly eroded), ca 45 in 10 µm, roughly organized in irregular striae. Areolae externally covered by small, weakly raised, individual occlusions (Fig. 127). No obvious tube process openings apparent. Striae continuing over the valve face/mantle junction, interrupted by a series of up to 3 thin, parallel ridges running entirely around the mantle (Fig. 129). Irregular silica thickenings, often connected to the first marginal ridge, present at the valve face/mantle junction (Fig. 128, arrows). Mantle areolae small, clearly rounded. Mantle edge very narrow, irregularly bordered (Fig. 129).

Internally, areolae large, each showing a clear rota, covered by very thin hymenes, organized in irregularly running striae (Fig. 130–131). Central area consisting of a large hyaline, irregularly bordered, central zone (Fig. 130). No thickened protuberances (called 'portulae') observed (Fig. 130). Mantle edge very broad, strongly silicified (Figs 130–131).



Figs 125–131. *Arcanodiscus indistinctus* Goeyers & Van de Vijver sp. nov. SEM. Campbell Island holotype population, sample BAS303 (BR-4580). **125**. Frustule in girdle view with eroded girdle showing the mantle with the parallel ridges. **126**. External view of a valve in girdle view showing the domed valve face, several marginal ridges and some of the narrow, unperforated copulae. **127–128**. External valve face view of an entire valve. Note the large central area and the striae on the sloping margin. On Fig. 128, note the siliceous outgrowth on the valve face margin. **129**. External view of a valve in girdle view showing the domed valve face, the distinct marginal ridges and the narrow mantle edge. **130–131**. Internal views of an entire valve showing the lack of rimoportulae. Scale bars = 10 µm.

Ecology and distribution

Arcanodiscus indistinctus sp. nov. was described from a *Racopilum* moss vegetation collected from a wet rock east of Moubray Hill. The sample was dominated by by *Frankophila dalevittii* (Van de Vijver *et al.* 2020), *Diatomella balfouriana* and *Diatomella colonialis*. In the same sample, *Arcanodiscus crawfordianus* sp. nov. and *Angusticopula cosmica* sp. nov. were also observed. The presence in other samples needs to be confirmed with SEM observations.

Arcanodiscus saundersianus Goeyers & Van de Vijver sp. nov.

http://phycobank.org/102320

Figs 97–115, 132–138

Etymology

The species is named in honour of our colleague Dr Krystyna Saunders (Australian Nuclear Science and Technology Organisation, Kirrawee, Australia) to acknowledge her for her ecological and paleo-ecological diatom research on the sub-Antarctic islands in the Pacific Ocean.

Material examined

Holotype

CAMPBELL ISLAND • sub-Antarctic region; sample BAS272; 26 Dec. 1969; D. Vitt leg.; BR-4581.

Isotype

CAMPBELL ISLAND • same collection data as for holotype; slide at University of Antwerp, Belgium; PLP-372.

Description

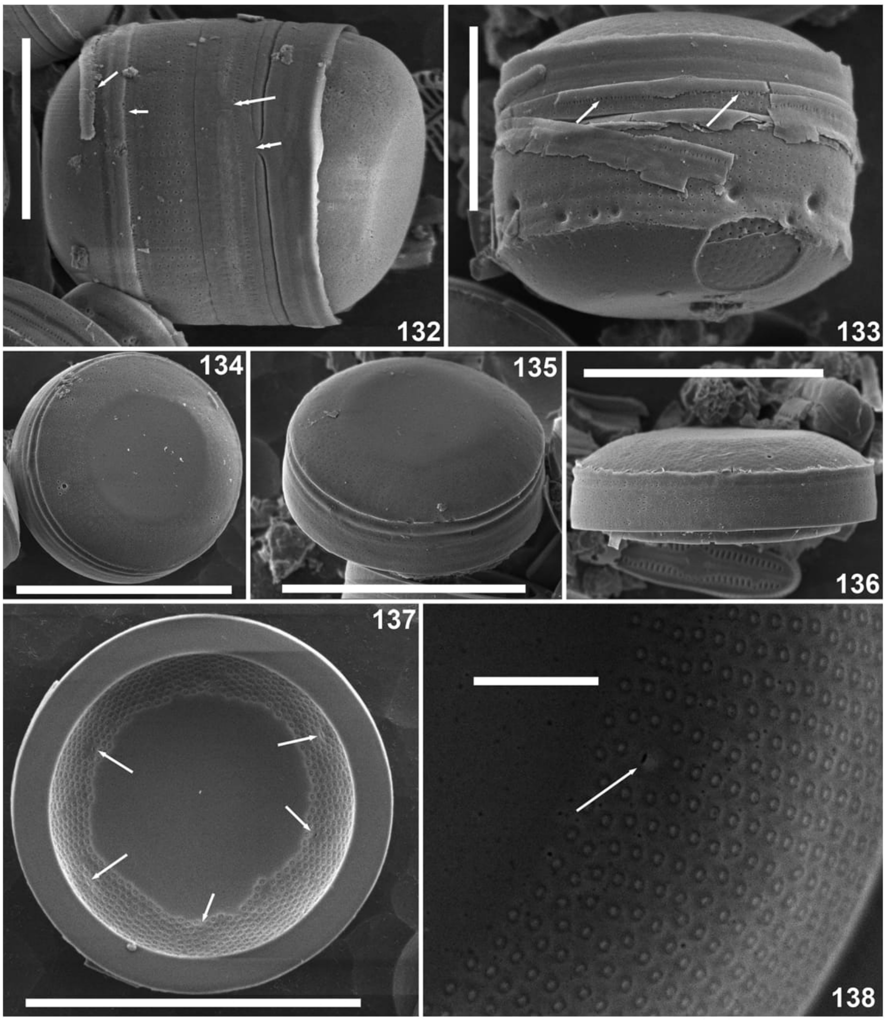
Light microscopy (Figs 97–115)

Frustules broadly discoid, almost square to rectangular with broadly rounded edges and convex valve faces. Frustules often found attached to each other. Chains composed of more than 2 cells however never observed. Multiple discoid chloroplasts present. Girdle bands not discernible in LM. Valves rather strongly silicified, rounded with a thick mantle and convex, weakly domed valve face. Valve dimensions (n = 25): valve diameter 6–17.5 µm, frustule height (n = 10): 4.5–7.0 µm. Central area is a large, smooth, hyaline zone, 3.0–7.5 µm, 50–55% of the total valve diameter, surrounded by a more rugose, irregularly shaped, marginal zone where striae are difficult to distinguish. Visible processes lacking.

Scanning electron microscopy (Figs 132–138)

Frustules discoid with very heavily silicified valves, visible as a thick mantle (Figs 132, 137). Cingulum comprises several, narrow, very thin, non-perforated, open copulae (Fig. 132). Pars interior of the copulae clearly fimbriate giving the impression of perforations on the copulae when girdle not eroded (Figs 132, 133, arrows). Copulae clearly open, ligulate (Fig. 132, double arrows).

Valve face with large, flat hyaline, clearly rounded central area, lacking areolae and any other ornamentation (Figs 134–136). Marginal zone gently sloping towards the mantle, entirely covered with rounded to slit-like areolae, ca 45 in 10 µm, organized in irregular striae, the latter ca 40 in 10 µm. Areola occlusions externally not observed (Figs 134–135). External openings of portulae not distinguishable from areola openings. No silica thickenings, close to valve face/mantle junction (Fig. 135). Striae continuing over the valve face/mantle junction, usually interrupted by a series of up to 3 parallel ridges running entirely around the mantle (Figs 134–135). Parallel ridges, usually covered by girdle bands (Fig. 133), occasionally lacking and resulting in a broad, flat mantle (Fig. 136). Areolae on the mantle strictly rounded. Mantle edge indistinct.



Figs 132–138. *Arcanodiscus saundersianus* Goeyers & Van de Vijver sp. nov. SEM. Campbell Island holotype population, sample BAS272 (BR-4581). **132**. Frustule in girdle view with the narrow copulae. The arrows indicate the ligulae. **133**. Frustule in girdle view with the narrow copulae. The arrows indicate the fimbriate pars interior of the copulae. Note also the domed valve face. Parts of the upper layer are eroded showing small areolae. **134–135**. External valve face views showing the relatively small central area and the well-developed marginal ridges. **136**. External view of a valve in girdle view showing the low, almost flat valve face, the absence of marginal ridges and the broad mantle edge. **137**. Internal views of an entire valve showing several rimoportulae (arrows). **138**. Internal detail of the valve with an indicated rimoportula. Note also the rota on the areolae. Scale bars: 132–137 = 10 µm; 138 = 1 µm.

Internally, areolae rather large, each showing a clear rota, covered by very thin hymenes, organized in irregularly running striae (Fig. 138). Central area a large hyaline, irregularly bordered, central zone (Fig. 137). Large number of perforated, thickened protuberances visible, irregularly scattered between the areolae, never organized in a regular marginal ring (Fig. 137, arrows). Inner openings of these protuberances rounded, smaller than the areolae, lacking rota (Fig. 138).

Ecology and distribution

Arcanodiscus saundersianus sp. nov. was found in a sample collected from a dripping bluff limestone. The sample is entirely dominated by the new species of *Arcanodiscus*. Sub-dominant species include *Achnanthes muelleri*, *Diatomella balfouriana* and several species of *Humidophila*.

Discussion

The centric diatom flora of Campbell Island is represented by at least three different genera: *Angusticopula*, *Ferocia*, both belonging to the Melosirales, and *Arcanodiscus* that was placed in the order of the Arcanodiscales (Maidana *et al.* 2017). All species are characterized by the presence of numerous narrow, often unperforated girdle bands which is typical of these genera but entirely different from *Melosira* s. str. which has broad, perforated copulae (Houk *et al.* 2017). Additionally, the position and number of rimoportulae separate the three genera further from *Melosira* s. str. Table 1 gives an overview of the four genera and highlights the distinguishing features. Based on this table, it is possible to place each of the new species in one of the new genera. Characterizing features guiding these decisions include the presence/absence and position of rimoportulae, presence/absence of internal cells, the shape of the valve (domed, flat, sloping mantle or not), the presence/absence of marginal rings and the presence/absence of large, linking spines.

Both *Ferocia* and *Angusticopula* contain a large proportion of species that prefer aerial habitats (Van de Vijver *et al.* 2017; Houk *et al.* 2017). As these habitats are likely to dry out occasionally, cells should protect their content from drying out. The presence of internal valves might be an important way to protect the cells against desiccation. The two genera possess these internal valves in many of their species. *Melosira*, considered to be a more aquatic genus (Round *et al.* 1990) is not known to present internal valves (Houk *et al.* 2017). Species of *Arcanodiscus* also seem not to present internal valves but still can be found in aerial habitats. It is, however, unclear why internal valves are lacking.

The description of the three new taxa of *Arcanodiscus* requires slight, but important changes to the original genus description (Maidana *et al.* 2017). Careful reanalysis of the original description of the type species and the accompanying illustrations shows that the girdle bands are open and not closed as stated in the genus description. Each new species of *Arcanodiscus* presents narrow, thin open girdle bands with clear ligulae (see Figs 116, 132, arrows). Moreover, the girdle bands are not perforated, but in fact possess a fimbriate pars interior that could give the impression of being perforated. This is actually clearly visible on fig. 17 in Maidana *et al.* (2017). In the description of *A. desmetianus* (Van de Vijver & Houk 2019), a similar fimbriate pars interior was also observed although in the description, the copulae were considered being perforated. Other features that seem to be different from the original genus description is the apparent lack of portulae in *A. indistinctus* sp. nov., the presence of external, though open areolar coverings, the presence of spines in *A. crawfordianus* sp. nov. and the position of the portulae, being more irregular than organized in a submarginal ring as in *A. crawfordianus* sp. nov. and *A. saundersianus* sp. nov. Therefore, the original genus description by Maidana *et al.* (2017) needs to be emended.

Table 1. Morphological characters of *Melosira* s. str. and several genera recently split off from *Melosira* s. lat.

	Melosira	***Angusticopula***	***Ferocia***	***Arcanodiscus***
	Houk *et al.* (2017)	Houk *et al*. (2017)	Van de Vijver *et al*. (2017)	Maidana *et al.* (2017)
girdle	several very broad, perforated copulae	large number of narrow, unperforated copulae	large number of narrow, unperforated copulae	numerous, narrow, closed perforated copulae
spines	present or absent	present or absent	very large, well-developed	absent
internal valves	absent	present	present	absent
granules	present or absent	present or absent	present	absent
rimoportulae	valve face + marginal ring	marginal ring	marginal ring	absent
mantle	broad	broad	broad	narrow, showing typical raised parallel ridges
colonies	present	present	present	absent

Arcanodiscus **Maidana & E.Morales in Maidana *et al.* (2017) emended Van de Vijver**

Frustules discoid, solitary or in short chains. Valves with flat and solid hyaline central area and a thicker mantle, the latter with faint radial lines corresponding to the mantle tubular areolae. Striae continuous from valve face margin to mantle. Areolae disposed in a quincunx arrangement, internally covered by rotae. Gradual or abrupt transition between valve face and mantle. Mantle usually bearing several parallel undulations upon which the girdle elements rest. Rimoportulae and fultoportulae absent, but a reduced type of portula with an internal opening situated on a prominence and a simple external opening is often present, usually scattered between the areolae but occasionally forming a submarginal ring at the abvalvar portion of the mantle. Cingulum comprising numerous, thin, open, ligulate, non-perforated elements. Pars interior of the copulae clearly fimbriate, suggesting the copulae being perforated.

The genus *Arcanodiscus* shows some resemblance to two marine genera: *Podosira* Ehrenb. and *Hyalodiscus* Ehrenb. (Round *et al.* 1990). *Podosira* possesses rimoportulae scattered over the entire valve face whereas *Hyalodiscus* shows a ring of marginal rimoportulae. Maidana *et al.* (2017) already discussed the differences between *Hyalodiscus*, *Podosira* and *Arcanodiscus*, and based most of the discrimination on the presence/absence of these rimoportulae and the girdle structure. *Hyalodiscus* shows bullulate areolae, a feature however never observed in any of the species of *Arcanodiscus* known at present, and the girdle bands in the latter are clearly closed, and not open as in *Arcanodiscus*, confirming the discrimination between *Hyalodiscus* and *Arcanodiscus*. *Podosira* on the other hand has open girdle bands, similar to *Arcanodiscus*, non-bullulate areolae (as in *Arcanodiscus*) and often a flat valve face (Round *et al.* 1990). A better structural analysis of the portulae and rimoportulae in these three genera should also shed more light on the possible relationship between them, although this is outside the scope of the present paper. Therefore, an emendation of the order and family description of *Arcanodiscus* is inappropriate at the moment, as this may obscure the relationships between the three genera.

The description of three new species of *Arcanodiscus* brings the total number in this genus now to five, all of them occurring in the southern hemisphere and (for four of them) more specifically in the sub-Antarctic region. Only the generitype species, *A. plattii* Maidana & E.Morales, was described from southern Patagonia (Maidana *et al.* 2017). The three new species can be distinguished from the two previously described species of *Arcanodiscus*. Table 2 highlights the main morphological features of

Table 2. Comparison of all species belonging to the genus *Arcanodiscus* E.Morales & Maidana.

	A. plattii Maidana *et al.* (2017)	*A. desmetianus* Van de Vijver & Houk (2019)	*A. crawfordianus* sp. nov. this study	*A. indistinctus* sp. nov. this study	*A. saundersianus* sp. nov. this study
valve diameter (µm)	12.5–16	10–16	9–18.5	9–17	6–17.5
frustule height (µm)	8.5–11	7–9	ca 11	7–9	4.5–7
diameter central area (% of total diameter)	up to 80%	< 50%	up to 60%	up to 75%	50–55%
number of striae (in 10 µm)	30–50	ca 35	30–33	27–35	ca 40
number of areolae (in 10 µm)	30–50	???	ca 40	ca 45	ca 45
valve mantle	narrow mantle edge	very broad mantle edge	narrow mantle edge bordered by deep groove	narrow mantle edge	mantle edge indistinct
silica mantle rings	series (up to 5) of parallel undulations	series (up to 4) of parallel undulations	only one mantle undulation present	series (up to 4) of parallel narrow undulations	series of up to 3 parallel, narrow undulations, occasionally lacking forming flat, broad mantle
areolae	in regular rows, but concentrically forming a quincunx arrangement	mantle areolae gradually changing from small, rounded to slit-like near valve face/mantle junction	in regular rows, rounded throughout entire valve	mantle areolae small and rounded, valve face areolae slit-like to almost rounded (when eroded)	rounded to slit-like on valve face, strictly rounded on mantle
spines	absent	absent	large, solid, acute, arranged in irregular ring near central area	absent	absent
granules	absent	absent	dense pattern present in central area	absent	absent
portulae	several, irregularly organised in submarginal ring	irregularly scattered on mantle, never organised in submarginal ring	irregularly scattered on mantle, never organised in submarginal ring	absent	irregularly scattered on mantle, never organised in submarginal ring

each species. Based on valve diameter or frustule height, it is impossible to separate the five species as they all show overlapping dimensions (roughly between 6 and 20 µm in diameter). The combination of morphological features is however unique for each of the five species. *Arcanodiscus crawfordianus* sp. nov. differs from all other 4 taxa in possessing distinct spines, organized in an irregular ring bordering the central area. Moreover, the entire central area, extending between the spines, is covered by a dense pattern of small granules. Additionally, only one marginal ring (undulation as stated in the genus description) is present and a clear groove borders the thickened mantle edge. None of the other four species show any of these two features, justifying the separation of *A. crawfordianus* sp. nov. as a distinct species. *Arcanodiscus indistinctus* sp. nov. does not possess the typical portulae that can be seen in the other four species. Although a large number of valves have been investigated, portulae were never observed. The new species also present a very large hyaline central area, up to 75% of the total valve diameter. Only *A. plattii* shows an even larger central area (up to 80%) whereas the other two taxa have a hyaline central area that never exceeds 60% of the total valve diameter. The areolae in *A. indistinctus* sp. nov. are not arranged in a regular striation pattern, contrary to *A. plattii*. Additionally, even the largest specimens of each of the new species only have 3, rarely 4, marginal rings whereas *A. plattii* has up to 5 rings. Finally, *A. saundersianus* sp. nov. has an indistinct mantle edge, occasionally lacking marginal rings, scattered portulae, never arranged in a submarginal ring as in *A. plattii*, and a less gently sloping valve face margin, compared to *A. desmetianus* (Maidana *et al.* 2017; Van de Vijver & Houk 2019). *Arcanodiscus saundersianus* sp. nov. also shows the highest stria (up to 40) and areola (up to 45) density, higher than any of the other four species.

The recently described genus *Angusticopula* contains seven species, slightly more than in either *Ferocia* or *Angusticopula.* Table 3 shows the features of all species of *Angusticopula* known so far. One of them, *A. chilensis*, was only known from the original drawing by Grunow and several LM illustrations in Houk *et al.* (2017: pl. 63, figs 1–5). A search for original, unmounted material remained without result (A. Igersheim, Grunow collection, Vienna). The population found on Campbell Island (and also similar populations on the Prince Edward Islands and Iles Kerguelen; Van de Vijver, unpubl. res.) shows a very high resemblance to the type specimens as depicted in Houk *et al.* (2017). The presence of the rimoportula on the margin, clearly visible in LM, is very obvious and not observed in any other species of *Angusticopula*. The most similar species might be *A. dickiei*, but the latter possesses rimoportulae that are located close to the mantle edge and not on the valve face/mantle junction as is the case in *A. chilensis*. *Angusticopula chilensis* was described from Chile although neither the slide (Houk *et al.* 2017: pl. 63, fig. 7) nor the drawing in Van Heurck (1885: pl. 90, fig. 13) provide a more detailed indication of the correct locality. The presence of a diatom described from Chile on Campbell Island is, however, not surprising given the presence of more species originally described from southern South America on the island such as *Adlafia tenuis* Van de Vijver & Goeyers (Van de Vijver *et al.* 2019a) and *Planothidium aueri* (Krasske) Lange-Bert. (Goeyers & Van de Vijver, unpubl. res.). The only difference between the type population of *A. chilensis* and the Campbell Island population can be noticed in the valve dimensions. For the type material, a valve diameter and a mantle height of 10 µm was indicated by Houk *et al.* (2017). The Campbell Island population shows larger valves (diameter 8–25 µm, mantle height 4.5–11 µm). However, the populations investigated on Campbell Island were much larger than the illustrated type population.

The second species of *Angusticopula*, the newly described *A. cosmica* sp. nov., possesses several very distinct features that were not observed so far in the other species of *Angusticopula* such as the dense pattern of very small granules covering the entire valve face and the ring of submarginal rimoportulae. *Angusticopula tanakae* Houk, Klee & H.Tanaka, *A. robusta* Houk, Klee & H.Tanaka and *A. rowlingiana* Van de Vijver, Wilfert, D.M.John & Houk all show the presence of a marginal zone of granules but these are always larger and more robust and confined to the marginal zones of the valve face, never occurring in the central area (Houk *et al.* 2017; Van de Vijver *et al.* 2019b). Only *A. robusta* and *A. ruttneri* show

Table 3. Comparison of all species belonging to the genus *Angusticopula* Houk *et al.*

	A. dickiei Houk *et al.* (2017)	*A. scheffleri* Houk *et al.* (2017)	*A. tanakae* Houk *et al.* (2017)	*A. chilensis* Houk *et al.* (2017), this study	*A. robusta* Houk *et al.* (2017)	*A. ruttneri* Houk *et al.* (2017)	*A. rowlingeana* Van de Vijver *et al.* (2019b)	*A. cosmica* sp. nov. this study
valve diameter (µm)	10–20	10–15	10–15	10 // 8–25	12–45	10–60	11–15	18–45
mantle height (µm)	7–10	ca 5	5–10	10 // 4.5–11	7–9	15–20	5.5–6.5	ca 8
valve face	flat	flat	clearly domed	flat	clearly domed	flat	flat to weakly domed	flat with weakly raised central area
central area	hyaline, not differentiated from rest of valve face	very small, bordered by dense pattern of areolae	small, bordered by dense pattern of granules	hyaline, not differentiated from rest of valve face	small, hyaline central area	raised, dominated by crown of irregular ridges	relatively large, hyaline, bordered by marginal striae	large, weakly raised
areolae	very small, rounded	large, rounded	very small, rounded	very small, rounded	moderately large, rounded	very small, rounded	very small, rounded	very small, rounded
rimoportulae	irregular ring near mantle edge	???	irregular ring on mantle	irregular ring on valve face/mantle junction	irregular ring near mantle edge	numerous, irregular ring on valve face/mantle junction + scattered on valve face	irregular ring on valve face/mantle junction	ring of submarginal rimoportulae
spines	absent	absent	absent	absent	small, conical spines scattered over entire valve face	absent	absent	absent
granules	absent	absent	dense pattern of thick, large granules on valve margin, never on the central area	absent	irregularly formed granules	dense pattern on valve mantle	dense pattern of small granules on valve margin, never on the central area	dense pattern of small granules on entire valve face

Table 4. Comparison of all species belonging to the genus *Ferocia* Van de Vijver & Houk.

	F. setosa Van de Vijver *et al.* (2017)	*F. ninae* Van de Vijver *et al.* (2017)	*F. subantarctica* Van de Vijver & Houk (2019)	*F. houkiana* sp. nov. this study
valve diameter (µm)	5.5–22	4.5–19	5–14	4–11
valve height (µm)	4.0–8.5	4–6	3–5	4.0–5.5
valve shape	clearly dome-shaped	dome-shaped	dome-shaped	almost flat
central area	small, rounded, hyaline	small, irregular, with scattered rounded areolae	small, rounded, hyaline	large, dominated by central crown of spines
Müller step	often very large	often very large	often very large	only occasionally present
spines	linking spines very large, irregularly shaped, often plate-like with sharp, acute endings, scattered smaller spines and granules present in between	several concentric rings of large, acute, almost never plate-like, linking spines	arranged at valve face/mantle margin + irregularly scattered spines on valve face, spines acute	central crown of blunt, wedge-shaped spines, spines often reduced
areolae	slit-like, never rounded	slit-like throughout but rounded in the central area	small, rounded	relatively rounded, almost always rounded
rimoportulae	ring of slit-like rimoportulae present near the mantle edge, never equidistant, never on valve face	ring of slit-like rimoportulae present near the mantle edge, never equidistant, never on valve face	ring of slit-like, equidistantly placed rimoportulae present near the valve face/mantle junction, never on valve face	irregularly scattered areolae on mantle + 1 areola present near valve center on valve face

similar high valve diameters (up to 60 µm) whereas all other taxa have a maximal valve diameter never exceeding 20–25 µm. The largest valves in *A. cosmica* sp. nov. reach up to 45 µm. Finally, the weakly, but visibly raised central area in *A. cosmica* sp. nov. was not observed in any of the other seven species. The combination of these distinct features justify the separation of *A. cosmica* sp. nov. as a separate species.

The final species, *Ferocia houkiana* sp. nov., shows features of both the genera *Angusticopula* and *Ferocia* such as the narrow copulae and the scattered rimoportulae (Houk *et al.* 2017; Van de Vijver *et al.* 2017). The presence of the large central spines and the structure of the areolae, especially visible on the valve interior show more resemblance with *Ferocia* than with *Angusticopula* and therefore the species is placed within the former genus. The species is, however, unique within the genus *Ferocia* in having a distinct central ring of linking spines (Table 4). The other three *Ferocia* species lack spines in the central area but have instead often very large, acute or plate-like spines in the marginal zones of the valve face. The central rimoportula, at the edge of the central area, was not observed in the other three species of *Ferocia* (Van de Vijver *et al.* 2017; Van de Vijver & Houk 2019).

The description of the five new species almost doubles the number of melosiroid taxa in the sub-Antarctic region. Apart from these melosiroid species, the centric non-marine diatom flora in the entire Antarctic realm is rather limited. Recently, a new species of *Melosira*, *M. jeanbertrandiana* Van de Vijver & Crawford (2019) was published, found on the Îles Crozet in the southern Indian Ocean. The genus *Aulacoseira* is represented by two species (*A. principissa* Van de Vijver (2012) and *A. glubokoyensis* Oaquim *et al.* (2017)), *Orthoseira* is also present with two species (*O.* cf. *roeseana* (Rabenh.) Pfitser (Houk *et al.* 2017) and *O. biportulata* Van de Vijver & Beyens in Van de Vijver *et al.* (2002)) while a third species of *Orthoseira* was recently transferred to the genus *Guarreraea* (*O. limnopolarensis* (Van de Vijver & Crawford) Kociolek & Van de Vijver in Guerrero *et al.* (2018)). *Cavernosa kapitiana* Stidolph is present on the Iles Crozet and on Campbell Island (Goeyers & Van de Vijver, unpubl. res.) (Van de Vijver *et al.* 2002; Cremer *et al.* 2011). Only one species of *Cyclotella*, *C. deceusteriana* Van de Vijver & Dessein (2018) was observed whereas the genera *Stephanodiscus*, *Lindavia*, *Pantocsiella* and *Cyclostephanos* are entirely absent. Possible records of species belonging to these genera (or formerly placed in *Cyclotella*) should be considered as erroneous identifications or the result of contamination or force-fitting (Kellogg & Kellogg 2002). The almost complete absence of members of the latter five genera is most likely the result of the quasi-total absence of freshwater diatom plankton in Antarctica, a phenomenon that has up to now not been fully explained (Jones 1996; Van de Vijver & Beyens 1999). On the other hand, the melosiroid diatom flora seems to be overrepresented with 12 species, although only species belongs to *Melosira* s. str. The genera *Ferocia*, *Angusticopula* and *Arcanodiscus* are most likely composed of species typical of more aerophilic conditions influenced by seaspray and animals such as living on mosses, in soils exposed in cliffs, near waterfalls or near bird colonies (Cremer *et al.* 2011; Van de Vijver *et al.* 2017; Van de Vijver & Houk 2019). The observation of the five new species also highlights the diversity within the sub-Antarctic non-marine diatoms and, despite the taxonomic efforts of the past 15 years, the gap in our knowledge and the need of a continuous effort in documenting the biodiversity of these unique flora.

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Typification and emended description of *Achnanthes muelleri* G.W.F.Carlson (*Achnanthaceae, Bacillariophyta*), a widespread Antarctic freshwater species

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Achnanthes muelleri G.W.F.Carlson (Carlson 1913: 23) was originally described from material collected by the Swedish Südpolar-Expedition 1901-1903 on South Georgia and the Falkland Islands/Islas Malvinas. Carlson (1913) lists four samples (three from South Georgia and one from the Falklands/ Islas Malvinas) in which he found the species. The taxon, however, was most likely previously described four years earlier when Otto Müller described *Achnanthes inflata* var. *sigmata* O.Müller (Müller 1909: 9, pl. 1: fig. 9) based on one rapheless valve showing some irregular deformation of the valve. Müller (1909) himself doubted whether this deformation was the result of an anomaly or was a true variety. Although both taxa seem conspecific, priority should be given to *Achnanthes muelleri* based on ICN Art. 11.2 (Turland *et al*. 2018) specifying that a name has "… no priority outside the rank at which it is published."

Achnanthes muelleri proved, however, not to be restricted to South Georgia and the Falklands/ Malvinas, but records showed it had a circum-Antarctic distribution. Its presence was confirmed (based solely on light microscopy observations) on South Georgia (Van de Vijver & Beyens 1997), Iles Crozet (Van de Vijver *et al*. 2002 and references therein), Iles Kerguelen (Le Cohu & Maillard 1983 as *A. inflata*, Van de Vijver *et al*. 2001, Le Cohu 2005), Heard Island (Van de Vijver *et al.* 2004), the Prince Edward Islands (Van de Vijver *et al*. 2008) and also in the Maritime Antarctic Region (Zidarova *et al.* 2016 and references therein). More recently, the species was also found on Campbell Island in the southern Pacific Ocean (Goeyers & Van de Vijver, unpubl. obs.). The species seems absent on continental Antarctica as no confirmed records could be found (Kellogg & Kellogg 2002).

Comparison with the original material used by Carlson (1913) unfortunately proved impossible. There is no indication where the material Carlson used might be preserved. Searches in the herbaria in Stockholm (where most of the bryophytes and lichens collected by Carl Skottsberg [1883-1963] are preserved), Göteborg (where Skottsberg worked) and Uppsala (where Carlson was given facilities according to his own account) were fruitless. Other major diatom collections worldwide do not seem to contain any material that Carlson used in his paper (Van de Vijver, pers. comm.). It is assumed therefore that the original material is lost. However, as the description of *Achnanthes muelleri* in Carlson (1913) is accompanied by three drawings showing both rapheless and raphe valve and a mantle view, one of these drawings is here designated as lectotype. Art. 40.5 of the ICN specified that for microalgae an "illustration" may be chosen as type. We interpret this as a group of figures (Carlson 1913: pl. 3: figs 5-7) as it is essential in diatoms that both raphe and rapheless valve are taken into account for correct species identification.

The present contribution illustrates and discusses the morphology of *Achnanthes muelleri* using recently collected material in the sub-Antarctic region. We detail all morphological features of the species with light and scanning electron-microscopy observations, based on a large population collected on South Georgia (sample SG-M317, leg. Louis Beyens, coll. date 2.xii.1992). The material was sampled from wet mosses during a short expedition in the vicinity of Stromness Bay. Several other relatively small populations (max. relative abundance < 5%) from the islands in the

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southern Indian Ocean (Iles Crozet, Iles Kerguelen, Heard Island) and the southern Pacific Ocean (Campbell Island) were likewise investigated. Comparisons were made with the observations from the Maritime Antarctic region, illustrated in Zidarova *et al*. (2016: plates 15 & 16, figs 5–8). All samples were collected during austral expeditions from 1997 to date) except for the Campbell Island material that was collected in 1970 by Dale Vitt (Hickmann & Vitt 1973).

We here designate slide BR-4575 from SG-M317 as epitype for the species (Art. 9.8; Turland *et al.* 2018). The original material was collected by Skottsberg in Cumberland Bay in 1902, on the northern coast of South Georgia. The new material was sampled from a locality near Stromness Bay, separated from Cumberland Bay only by a narrow peninsula (Larsen Point) justifying the choice for this epitype. Based on the new observations the original species description is emended but not to the exclusion of the type.

Achnanthes muelleri G.W.F.Carlson (Figs 1–16)

Original publication: *Achnanthes muelleri* G.W.F.Carlson *Wissenschaftliche Ergebnisse der Schwedischen Südpolar-Expedition 1901-1903 unter leitung von Dr. Otto Nordenskjöld*, Band IV, Lieferung 14: 23, pl. 3, figs 5-7, 1913.
Synonym: *Achnanthes inflata* var. *sigmata* O.Müller, *Beiblatt zu den Botanischen Jahrbüchern* 100: 9, pl. 1: fig. 9, 1909.

Lectotype (here designated): Plate 3, Figs 5-7, *Wissenschaftliche Ergebnisse der Schwedischen Südpolar-Expedition 1901-1903 unter leitung von Dr. Otto Nordenskjöld*, Band IV, Lieferung 14, 1913.

Epitype (here designated for the above lectotype of *Achnanthes muelleri* G.W.F.Carlson): dried material BR-4575 (BR, Meise Botanic Garden); sample SG-M317 (Stromness Bay, South Georgia, coll. date 2.xii.1992, leg. Louis Beyens); the epitype is here represented by Fig. 3 R-valve and Fig. 7 RL-valve

Emended description: Frustules clearly bent in girdle view with the rapheless valve dorsally and the raphe-bearing valve ventrally. Valves rhombic-lanceolate to broadly lanceolate with a clearly inflated central part and gradually tapering, occasionally protracted, then rostrate, apices. Small pseudosepta present on the raphe valves, absent on the rapheless valves. Transition from valve face to mantle abrupt. Valve dimensions (n=50): length 27.0-99.0 µm, width 9.5-17.0 µm. *Raphe valve*: axial area narrowly lanceolate, almost linear, only weakly widening towards the central area. Central area forming a narrow, usually asymmetrical, almost rectangular, narrow fascia with rarely short, isolated striae at the margins. Raphe branches almost straight to slightly undulating, externally with teardrop-like central raphe endings and clearly elongated, bent terminal raphe fissures, shortly continuing onto the mantle. Striae, 10-12 in 10 µm, radiate becoming more strongly radiate near the apices, uniseriate, composed of large, rounded areolae. Striae continuing without interruption on the mantle. Areolae clearly cribrate, usually covered by very thin, non-perforated external individual hymenes. Internally, central nodule thickened, forming a broader stauros reaching the valve margins. Internal central raphe endings unilaterally hooked. Terminal raphe endings terminating onto small helictoglossae. Virgae clearly raised between the sunken areolae. Vimines thickened. *Rapheless valve*: Thickened ridge, often broken into smaller parts, running at the valve face/mantle junction of the rapheless valve, only visible in SEM, interrupted at the apices. Ridge often lacking in certain populations. Valve face entirely surrounded by relatively broad hyaline zone. Pseudoraphe usually absent. Striae parallel in the middle becoming distinctly radiate towards the apices, 10-12 in 10 µm, continuing onto the mantle. Striae uniseriate composed of large, cribrate, rounded areolae, individually rimmed and usually covered by external thin hymenes. Terminal orbiculus present on the valve face at each apex, irregularly shaped. Internally, virgae raised, continuing from margin to margin separating the sunken areolae. Orbiculi clearly visible at

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the apices, closed by a perforated plate. Girdle composed of several broad, open copulae, bearing a continuous row of perforations, even visible in the LM.

The various populations on the sub-Antarctic islands all differ in minor details. The valve outline varies from clearly rhombic to more broadly lanceolate, although it is not possible to separate the populations based on their valve outline as different outlines can be present within the same population. Several populations, such as on the South Shetland Islands (Maritime Antarctic Region) seem to lack the usual marginal crest on the rapheless valve (Zidarova *et al.* 2016), but are similar in all other morphological features. Some populations, such as the ones observed on Campbell Island in the southern Pacific Ocean, lack the rims around the areolae on the rapheless valve. On the islands in the southern Indian Ocean, the marginal crest is subdivided into several smaller parts. Nevertheless, all other features correspond entirely with the original population on South Georgia indicating that there is some phenotypic plasticity within the *A. muelleri* populations in the Antarctic Region, but that all these populations should be considered conspecific. Molecular research will be necessary to elucidate whether the different populations should be considered being cryptic species or not.

Achnanthes muelleri is mostly found living on mosses in the sub-Antarctic islands. The largest populations were found on wet terrestrial mosses in seepage areas and small pools with a slightly more alkaline pH (>8.0) and moderate to higher conductivities (Van de Vijver & Beyens 1997, Van de Vijver *et al*. 2002, 2004, 2008). Müller found one valve in southern Patagonia but did not specify the exact locality except the indication 'Kark – Tümpel'. Most of the samples that were discussed in Müller (1909) originate from the border of Argentina and Chile near the Torres del Paine national park. On the islands in the Maritime Antarctic Region, *A. muelleri* was rather rarely found abundantly in terrestrial habitats in coastal areas with elevated salinity levels and higher nutrient input (Zidarova *et al.* 2016). Chattová *et al.* (2014) observed the species on Ile Amsterdam, a very isolated, small island in the southern Indian Ocean, just north of the sub-Antarctic Region. Although found on the Falklands/Malvinas, Campbell Island, Ile Amsterdam and southern Patagonia, no records exist to date from Tasmania or New Zealand, most likely indicating that the species is not present there (Hodgson *et al.* 1997, John 2018 and references therein).

The authors wish to thank Prof. Dr Louis Beyens who collected the sample on South Georgia. Dr Wolf-Henning Kusber is acknowledged for his advice on typification of *Achnanthes muelleri*. Mrs Petra Ballings helped with the SEM, providing all of our SEM pictures.

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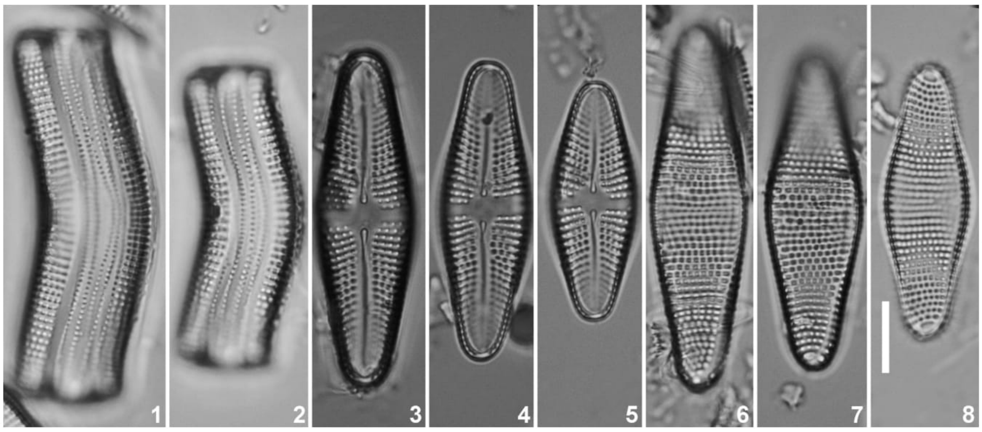
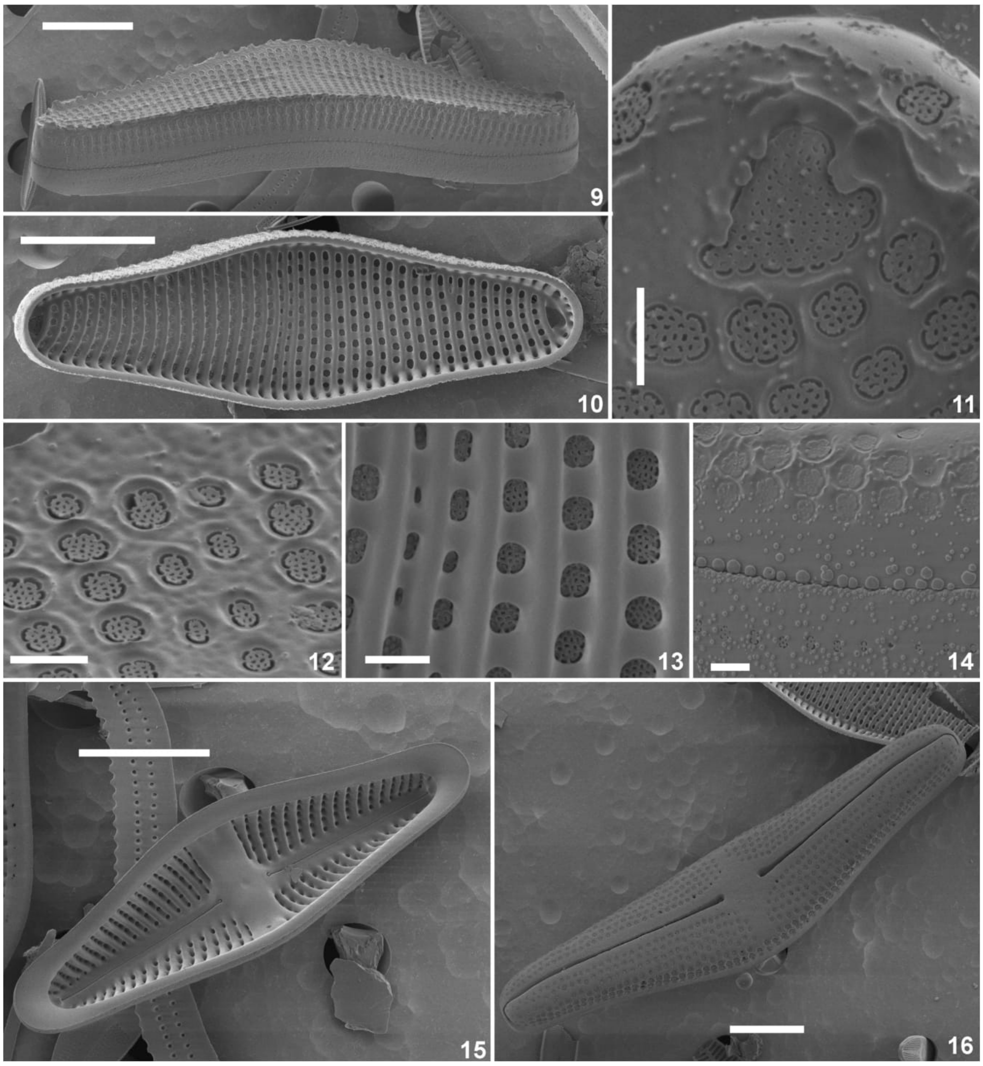


Figs 1–8. *Achnanthes muelleri* G.W.F.Carlson. LM images from the epitype collection, sample SG-M317 (Stromness Bay, South Georgia). Figs 1–2. Two frustules in girdle view. Figs. 3–5. Raphe valves. Figs 6–8. Rapheless valves. Scale bar represents 10 µm.



Figs 9–16. *Achnanthes muelleri* G.W.F.Carlson. SEM images from the epitype collection, sample SG-M317 (Stromness Bay, South Georgia). Fig. 9. Rapheless valve in girdle view with one of the copulae attached. Fig. 10. Internal view of a rapheless valve showing the two orbiculi (arrows). Fig. 11. External detail of the orbiculus. Fig. 12. External detail of the cribrate areolae. The external hymenes are eroded. Fig. 13. Internal detail of areolae between the raised virgae. Fig. 14. External detail of the mantle plaques and the granulate structure of the mantle and the copulae. Note the single row of areolae on the copulae. Fig. 15. Internal view of an entire raphe valve. Note the hooked central raphe endings and the pseudosepta. Fig. 16. External view of an entire view. Scale bar represents 10 µm except for figs 11–14 where scale bar represents1 µm.

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Frankophila dalevittii, a new freshwater diatom (Bacillariophyta) from Campbell Island

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Abstract

During a survey of the freshwater diatom flora of the sub-Antarctic Campbell Island, located in the southern Pacific Ocean, an unknown freshwater diatom was observed forming long colonies using linking spines. Detailed morphological analysis based on light and scanning electron microscopical observations and comparison with all known *Frankophila* taxa worldwide justified the description of this unknown taxon as a new species within the genus *Frankophila*: *Frankophila dalevittii* Van de Vijver & Goeyers sp. nov. The new taxon is characterized by the presence of well-developed linking spines, the absence of external raphe slits and the presence of internal raphe slits, biseriate striae composed of relatively large areolae and a large axial area. Despite the absence of the external raphe slits, the species is best placed within the genus *Frankophila*. The new species is described and illustrated and compared with all other *Frankophila* taxa.

Keywords: sub-Antarctica, Campbell Island, *Frankophila*, new species, raphe slits

Introduction

The freshwater diatom genus *Frankophila* Lange-Bertalot (1997: 66) was described in 1997 to accommodate small, chain-forming taxa having uni-, bi- or triseriate striae, well-developed linking spines positioned between the striae and vestigial raphe slits at the apices, visible on both the internal and external valves. All so far described species lack rimoportulae and apical porefields. Up to know, only seven species are known, most of them only reported from the southern hemisphere. Only *Frankophila loetschertii* (Lange-Bertalot in Lange-Bertalot & le Cohu 1985: 214) Lange-Bertalot (1997: 71) was described from Yellowstone National Park (Wyoming, USA). Several species seem to be restricted to South America: *F. similioides* Lange-Bertalot & U.Rumrich in Lange-Bertalot (1997: 66), the generitype of the genus, *F. horstii* U.Rumrich & Rumrich in Rumrich *et al.* (2000: 128), *F. sudamericana* Rivera & Cruces (2015: 374) and *F. wayqechae* Furey *et al.* (2012: 167) were all described from the Andes (Rumrich *et al.* 2000, Furey *et al.* 2012, Rivera & Cruces 2015). *Frankophila biggsii* Lowe *et al.* (2006: 42) is known only from New Zealand. The last species, *F. maillardii* (Le Cohu in Lange-Bertalot & Le Cohu 1985: 213) Lange-Bertalot (1997: 71), is somewhat unusual as it is the only species in this genus possessing uniseriate striae. The species is widespread on the sub-Antarctic islands in the southern Indian Ocean (Lange-Bertalot & Le Cohu 1985, Van de Vijver *et al.* 2001, 2002, 2004, 2008).

During a survey of the moss-inhabiting flora of the sub-Antarctic Campbell Island, located in the southern Pacific Ocean, an unknown freshwater diatom was found in several samples that could not be identified using the currently available literature. Detailed Scanning Electron Microscopy (SEM) observations indicated that the species most likely belongs to the genus *Frankophila*. Since it possesses a unique combination of morphological features, the species is described as *Frankophila dalevittii* Van de Vijver & Goeyers sp. nov. The current paper illustrates and discusses the morphology of the new species and compares it with all known *Frankophila* species worldwide. Special attention was given to the morphology of the spines, the absence of external vestigial raphe slits and several valve dimensional data such as the size and shape of the axial area, valve length and stria density. Short notes on its occurrence and accompanying flora on Campbell Island are added.

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Material and methods

Campbell Island (52°32'24"S, 169°8'42"E), the main island of a small volcanic archipelago located between New Zealand and the Antarctic Continent, has a total surface area of 113 km^2 culminating at 569 m. More details on its geomorphology, climate and vegetation can be found in Saunders *et al.* (2015). A large number of moss samples were collected by Prof. Dale Vitt (Southern Illinois University Carbondale, USA) (Hickmann & Vitt 1973; Vitt 1974) during the National Science Foundation expedition (December 1969–February 1970). Part of the samples were retrieved from the British Antarctic Survey herbarium (Cambridge, UK). Three samples contained a sufficiently large population of the unknown diatom and are included in the analysis:

BAS286 (*Hypopterygium novae-seelandiae* Müll. Hall. vegetation in dark wet recess. Large bluff on south side of Mt. Fizeau, leg. D. Vitt, coll. date 22/01/1970).

BAS288 (*Isopterygium limatum* (Hook.f. & Wilson) Broth. vegetation on cliff face. Large bluff on south side of Mt. Fizeau, leg. D. Vitt, coll. date 22/01/1970).

BAS303 (*Racopilum strumiferum* (Müll. Hal.) Mitt. vegetation on wet rock under large overhang in cave next to sea. Along shore on north side of Perseverance Harbour east of Moubray Hill, leg. D. Vitt, coll. date 12/01/1970).

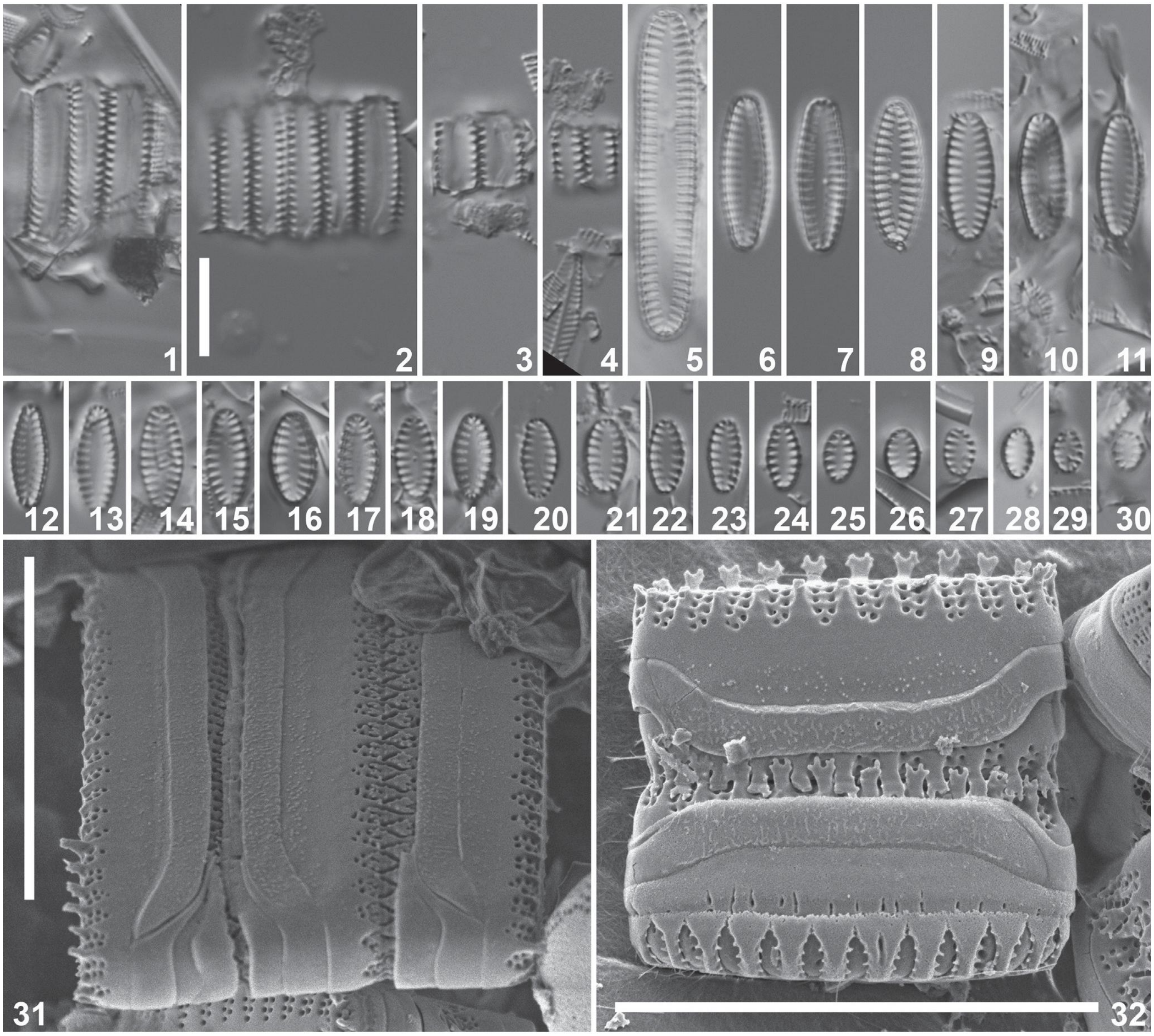
Parts of the three selected samples were prepared for light microscopy (LM) observation following the method described in van der Werff (1955). Small subsamples were cleaned by adding 37% H_2O_2 and heating to 80 °C for about one hour. The reaction was completed with the addition of saturated $KMnO_4$. After digestion and centrifugation (3 × 10 minutes at 3700g), the material was diluted with distilled water to avoid excessive concentrations of diatom valves. Cleaned diatom valves were mounted in Naphrax. Samples and slides are stored at the BR-collection (Belgium). The slides were analyzed at 1000x magnification using an Olympus BX53 microscope, equipped with Differential Interference Contrast (Nomarski) and the UC30 camera connected to the Cell Sense Standard program. For scanning electron microscopy (SEM), part of the diluted suspension was filtered through polycarbonate membrane filters with a pore diameter of 1 µm, pieces of which were fixed on aluminum stubs after air-drying. The stubs were sputter-coated with 10 nm of Pt and studied in a JEOL JSM-7100F at 2 kV (Meise Botanic Garden, Belgium). For the new taxon, the number of specimens measured at random on the type slide is indicated (n=X). For the typification of the new species, we chose to use the entire slide as the holotype. Diatoms show a broad variability along their cell cycle making the choice for the entire population on the slide more obvious.

Terminology follows Ross *et al.* (1979) and Lange-Bertalot (1997). The morphology of the new species was compared with species described or discussed in Lange-Bertalot & Le Cohu (1985), Lange-Bertalot (1997), Rumrich *et al.* (2000), Van de Vijver *et al.* (2002), Lowe *et al.* (2006), Furey *et al.* (2012) and Rivera & Cruces (2015).

Results

Frankophila dalevittii **Van de Vijver & Goeyers sp. nov.** (Figs 1–39)

LM (Figs 1–30): Frustules rectangular in girdle view, forming long chains of several tens of frustules, connected by relatively large, interdigitating linking spines (Figs 1–4). Valves linear-elliptical to elliptical and even elliptic-lanceolate. Smallest specimens almost rounded. Apices never protracted, always broadly rounded. Elliptic-lanceolate specimens with less broadly rounded apices. Valve dimensions (n=50): length 4–15 µm, width 3–5 µm. One initial valve observed: length 33 µm, width 6 µm. Axial area moderately wide, almost 1/3 of total valve width, lanceolate to linear-lanceolate. Central area lacking. Striae parallel in the valve centre becoming distinctly radiate towards the apices, 11–12 in 12 µm. Areolae not discernible in LM. SEM (Figs 31–39): Girdle composed of at least two open, non-perforated copulae (Figs 31, 33). Copulae often covered by irregular pattern of small ridges and granules (Figs 31, 32). Mantle very broad with clearly undulating edge (Fig. 32). Lower part of the mantle hyaline, covered with fine silica granules (Fig. 32). Frustules connected to each other via well-developed, interdigitating linking spines (Figs 31, 32, 34). Spines solid with dichotomously branching ends (Fig. 34), located on the virgae between the striae (Figs 35, 36). External raphe vestiges absent (Figs. 35, 36) although shallow depressions occasionally observed where slits were expected (Figs 35, 36, arrows). Striae composed of two rows of rather large, rounded areolae, terminating near the axial area by one areola. Striae continuing shortly but uninterruptedly onto the valve mantle. Rimoportulae and apical porefields absent (Figs 36, 38). Internally, short raphe slits visible near the valve apices (Figs 37, 38, 39, arrows), < 0.5 µm long. Areolae located in deep grooves (Figs 37, 38).



FIGURES 1–32. *Frankophila dalevittii* Van de Vijver & Goeyers *sp. nov*. Light microscopy (1–30) and scanning electron microscopy (31–32) views. Holotype population from Campbell Island (sample BAS303). 1–4. Frustules connected via linking spines to form long, band like colonies. 5. Possible initial valve. 6–30. Valve views showing the broad range of valve dimensions. 31–32. Two colonies of three (fig. 31) and two (fig. 32) frustules connected by linking spines. Scale bars represent 10 µm.

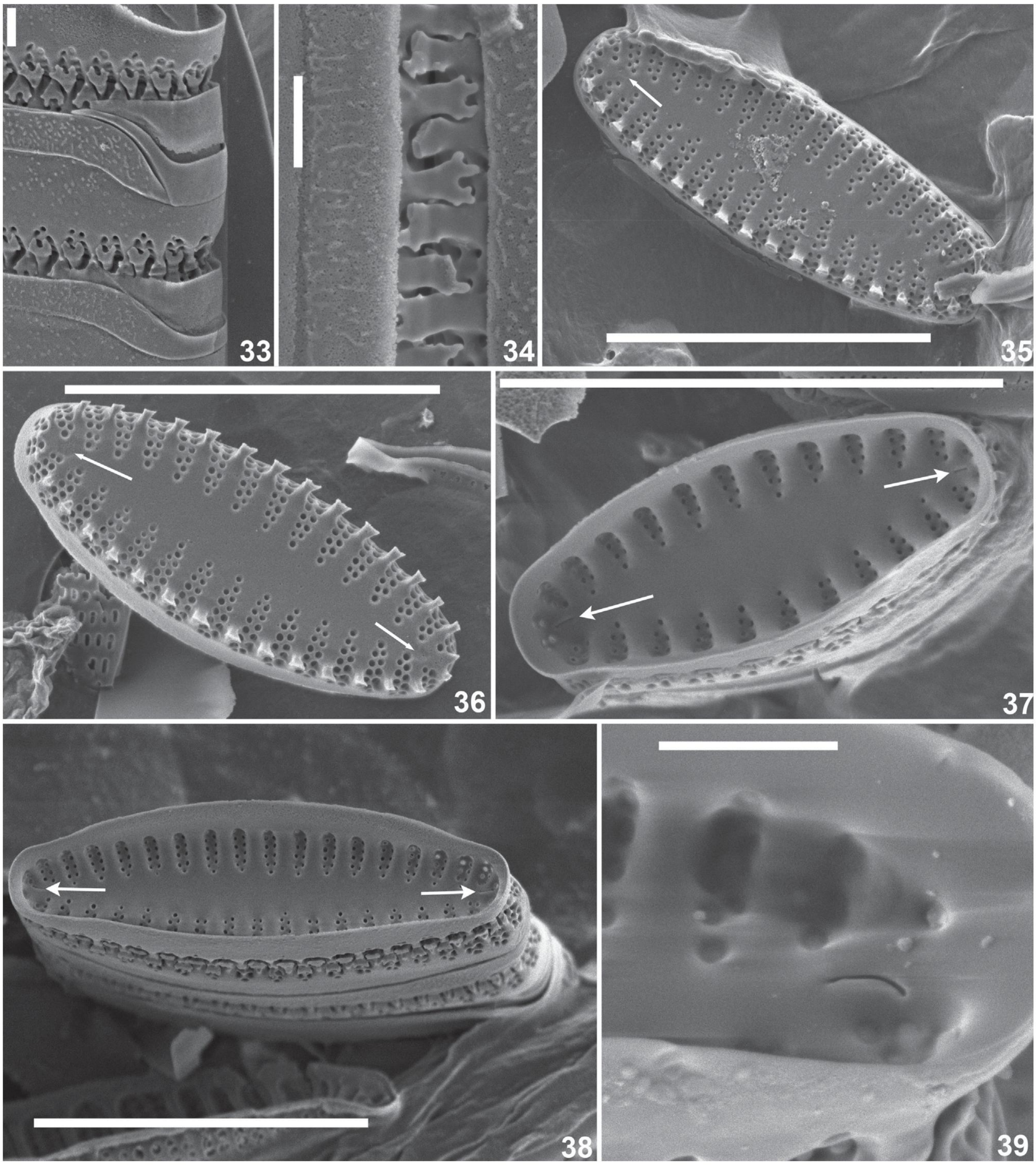
Type:—Perseverance Harbour east of Moubray Hill, Campbell Island, sub-Antarctic Region, sample BAS303 (leg. D. Vitt, coll. date: 12/01/1970) (holotype BR!, slide no. 4574, isotype PLP! slide no. 367, University of Antwerp, Belgium).

Etymology:—the species is named after Dr. Dale Vitt (Southern Illinois University Carbondale, USA), who collected in the austral summer of 1969–1970 the moss samples used in this study. His collection forms the base of an important contribution to the biogeography and biodiversity of the non-marine diatoms of the sub-Antarctic islands in the southern Pacific Ocean.

Ecology:—*Frankophila dalevittii* was observed in three moss samples on Campbell Island. The largest population (up to 10% of all diatom valves in the sample) was found in a *Racopilum strumiferum* vegetation on wet rock under a large overhang in a cave next to sea. The accompanying diatom flora is composed of several melosiroid taxa (that are currently being described as new taxa, Goeyers & Van de Vijver, unpubl. res.), *Rhopalodia* sp., *Diatomella balfouriana* Greville (1855: 259) and *Diatomella colonialis* Van de Vijver & Le Cohu (2017: 282).

TABLE 1. Comparison table showing the morphological features of all eight *Frankophila* species. The species are arranged according to the minimum length of their valves.

	Frankophila maillardii	*Frankophila wayqechae*	*Frankophila dalevittii*	*Frankophila similioides*	*Frankophila loetschertii*	*Frankophila biggsii*	*Frankophila sudamericana*	*Frankophila horstii*
	Lange-Bertalot & Le Cohu (1985)	Furey et al. (2012)	this study	Lange-Bertalot (1997)	Lange-Bertalot & Le Cohu (1985)	Lowe et al. (2006)	Rivera & Cruces (2015)	Rumrich et al. (2000)
length (µm)	3–10	4.5–8	4–15 (33)	6–10	6–14	8–15	8.5–12.5	16–22
width (µM)	3–6	3–4.5	3–5 (6)	4–5	4–6	4.5–5.0	4.5–6.0	9–12
valve outline	linear to elliptical with broadly rounded apices	strictly elliptical with broadly rounded apices	linear, linear-elliptical to broadly elliptical, occasionally elliptic-lanceolate with broadly to moderately narrowly rounded apices	broadly elliptical with broadly rounded apices	elliptical to linear elliptical, rarely slightly ovate with broadly rounded apices	elliptical to linear-elliptical with broadly rounded apices	strictly elliptical with broadly rounded apices	cruciform with broadly rounded apices
axial area	rather narrow, linear	very broad, elliptical, irregular depressions present	moderately broad, lanceolate	very broad, elliptical	rather narrow, linear	very broad	broad, elliptical	very broad, clearly narrowing towards the apices
raphe vestiges	internally and externally present	internally and externally present	externally absent, internally present	internally and externally present	internally and externally present	internally and externally present	internally and externally present	internally and externally present
stria density (in 10 µm)	11–16	11–12	11–12	12–14	6–12	11–12	9–10	10–11
stria structure	uniseriate, composed of one row of rather large, rounded areolae	rather short, composed of 2–3 rows of small, rounded areolae	moderately long, composed of 2 areolae, terminating in one areola	composed of 2 (rarely 3) rows of small, rounded areolae	long, composed of 2 rows of areolae	very short, composed of 2 rows of areolae, terminating in one areola	rather short, composed of 3 rows of areolae	long, composed of two rows of small, rounded areolae
spines	fine, often with spatulate ending, on virgae	solid, dichotomously branched, on virgae	solid, dichotomously branched, on virgae	rather fine, dichotomously branched, on virgae	fine dichotomously branched, on virgae	solid, dichotomously branched, on virgae	fine, short, truncated, on virgae	broadly spatulate, on virgae



FIGURES 33–39. *Frankophila dalevittii* Van de Vijver & Goeyers *sp. nov*. Scanning electron microscopy views. Holotype population from Campbell Island (sample BAS303). 33. SEM detail of several frustules connected by linking spines showing the girdle structure and the lack of an apical porefield. 34. SEM detail of the interdigitating linking spines. Also note the irregular siliceous ridges on the girdle band. 35–36. SEM external valve face views. Note the presence of the linking spines and the reduced external raphe slits (arrows). 37–38. SEM internal valve face views of two entire valves showing the reduced internal raphe slits (arrows). 38. SEM detail of the internal raphe slit. Scale bars represent 10 µm except for Figs 33, 34 & 39 where scale bars = 1 µm.

Discussion

The freshwater diatom genus *Frankophila* with at present eight known taxa, is a rather small genus compared to in LM similarly looking genera such as *Staurosira* Ehrenberg (1843: 424), *Staurosirella* D.M.Williams & Round (1988: 274) and *Pseudostaurosira* D.M.Williams & Round (1988: 276) that each count more than 50 taxa (Guiry & Guiry 2019).

Lange-Bertalot (1997) placed the genus within the Fragilariaceae based on its resemblance in LM and SEM to *Staurosira* (with the exception of the raphe slits). However, Lange-Bertalot (1997) also suggested that there might be a relationship with the Naviculaceae based on the presence of the raphe slits and the absence of apical porefields, the latter feature common in Fragilariaceae but absent in Naviculaceae. It was also suggested that *Frankophila* may be a 'missing link' between araphid diatoms and naviculoid raphids (Lange-Bertalot 1997, p. 74). A transfer of *Frankophila* from the araphid diatoms to a raphid order was also suggested by Lowe *et al.* (2006, p. 45) based on the presence of the raphe slits. Cox (2015) included *Frankophila* within the Fragilariales, a view commonly followed by platforms such as Algaebase (Guiry & Guiry 2019) and Diatombase (Kociolek *et al.* 2018). Mayama & Idei (2009) compared the structure of the raphid genus *Hygropetra* with *Frankophila*. Both show a reduced raphe system and a similar hexagonal areola arrangement, two features never observed in the Fragilariaceae but common in raphid orders. There are, however, differences such as the presence of linking spines in *Frankophila*, absent in *Hygropetra*. Additionally, Mayama & Idei (2009) commented on the difference between the raphe slits in *Hygropetra* and *Frankophila*, stating that in *Frankophila*, the raphe slits are *'more reduced or underdeveloped'* (Mayama & Idei 2009, p. 296). On the other hand, a few raphid diatom species, such as *Humidophila gallica* (W.Smith 1857: 11) R.L.Lowe *et al.* (2017: 281) possess linking spines joining frustules in long chains. Moreover, frustules placed within the colonies show reduced raphe systems entirely similar to what is observed in for instance *Frankophila maillardii* (Cox 2006).

At present, there are unfortunately no molecular data available that could help elucidate the taxonomic position of the *Frankophila*.

All previously described *Frankophila* taxa share several unique features such as the presence of external and internal raphe slits (Lange-Bertalot 1997) and the absence of both rimoportulae and apical porefields but differ in several other aspects. Most taxa (6 out of 7) have multiseriate (usually biseriate) striae with only *F. maillardii* having uniseriate striae. They all form long bandlike colonies with the frustules connected by solid, well developed linking spines. This is however not unique in small-celled araphid diatoms as it is also commonly observed in for instance *Staurosira* and *Staurosirella* (Williams & Round 1988, Round *et al.* 1990). The absence of rimoportulae is likewise observed in other small-celled araphid genera. *Staurosira*, *Pseudostaurosira*, *Staurosirella*, *Punctastriata* D.M.Williams & Round (1988: 278) and *Pseudostaurosiropsis* Morales (2001: 116) all lack rimoportulae but contrary to *Frankophila*, the latter five genera often possess apical porefields. The absence of both the apical porefield and rimoportulae most likely suggests that *Frankophila* does not belong with the Fragilariales but that a transfer to a raphid order may be more likely.

The newly described species shows a combination of features (absence of apical porefield and rimoportulae, colony-formation by linking spines, biseriate striae, internal raphe slits) that fits best with the genus *Frankophila*. *Staurosira*, *Staurosirella*, *Pseudostaurosira* and *Pseudostaurosiropsis* all possess uniseriate striae and lack raphe slits (Round *et al.* 1990, Morales 2001). Only *Punctastriata* has multiseriate striae but the latter also has apical porefields and lacks raphe slits (Williams & Round 1988).

Frankophila dalevittii is however unique within the genus *Frankophila* in lacking external raphe slits. In all observed populations, external raphe slits were never observed. Internal slits were present on both apices. All previously described *Frankophila* possess both external and internal raphe slits. Whether the lack of the external slits is a more primitive or a more evolved feature is unclear. Some valves (see for instance Fig. 35, arrow) show a very shallow depression on the spot where normally the external slits should be present. The presence of the well-developed internal slits and the absence of apical porefields justify, however, the taxonomic position of *F. dalevittii* within the genus *Frankophila*.

Table 1 shows all morphological features of all *Frankophila*. The table is an updated version of Furey *et al.* (2012) where several morphological features were only sparsely commented in the table. It is clear that, apart for *F. maillardii* having uniseriate striae (Lange-Bertalot & Le Cohu 1985, Van de Vijver *et al.* 2002), and *F. horstii* showing a cruciform valve outline (Rumrich *et al.* 2000), all *Frankophila* species have a very similar outlook and differ only in a combination of small morphological details. The most obvious morphological difference between *F. dalevittii* and the other taxa is of course the absence of external raphe slits. *Frankophila similioides* is the most similar species to *F. dalevittii* but can be separated based on a higher stria density, the finer linking spines, the almost strictly elliptical valve outline, the larger axial area and the lower valve length. *Frankophila biggsii* has very short striae, usually restricted to 2–3 series of areolae giving the species a very large axial area (Lowe *et al.* 2006). The valve outline in *F. sudamericana* is typically elliptical whereas in *F. dalevittii*, a considerable part of the population (>25 %) has a more elliptic-lanceolate valve outline. Moreover, *F. sudamericana*, has very small spines and it is even unclear whether the species forms colonies as they were never observed. The striae in *F. sudamericana* are composed of three rows of areolae contrary to the striae in *F. dalevittii* that are restricted to only two rows (Rivera & Cruces 2015). The valves in *F. wayqechae* are characterized in having distinct depressions in the very large axial area, a feature never observed in *F. dalevittii*. Since the striae in *F. wayqechae* are very short, the axial area is very large. Additionally, the valves in *F. wayqechae* are very small with a maximal length of 8 µm, contrary to *F. dalevittii* that has almost twice the valve length of *F. wayqechae* (Furey *et al.* 2012). Finally, *F. loetschertii* has very long striae reducing that way the axial area to a very narrow line. The stria density can also be lower in *F. loetschertii* (minimum 6 vs. minimum 11 in *F. dalevittii*).

Despite the description of this new species, the genus *Frankophila* remains species-poor. The presence of the raphe slits places the genus somewhat in between araphid and raphid diatoms and it is unclear at the moment what the correct position is. Molecular analysis of the species will be necessary to elucidate its correct taxonomic position and might probably also reveal hidden diversity in the populations of the different species worldwide.

Conclusions

Based on these differences, the description of *F. dalevittii* as a separate species is justified. The description of this new species, together with that of other unknown species from Campbell Island (Goeyers *et al.* in press), will facilitate the currently ongoing analysis of the moss diatom flora of this small island in the sub-Antarctic part of the Pacific region (Goeyers & Van de Vijver, unpubl. res.).

Acknowledgements

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Analysis of the type material of *Navicula tenuis* Krasske (*Bacillariophyta*) and its transfer to the genus *Adlafia*

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Navicula tenuis Krasske (1939, 385, pl. XI: fig. 51) was described based on a sample collected from sediment taken from a small pond ("*Grundschlamm des Teiches auf der Dachstein-Westplatte*") in southern Chile (Krasske 1939, Lange-Bertalot *et al.* 1996: 151). Krasske's species name was illegitimate as it was a later homonym of *Navicula tenuis* F.Meister (1937: 269). As a relationship with *Navicula tridentula* Krasske (1923: 198) was suggested, the taxon was later treated as a variety of this species, *Navicula tridentula* var. *tenuis* Lange-Bertalot & Willmann, in Lange-Bertalot *et al.* (1996: 151), essentially treating the variety as a new name with the same type.

Records of this entity in the literature are scarce. The species was recorded from Tasmania (Australia) by John (2018: 245, fig. 296 A), who incorrectly mentioned a possible record in Hodgson *et al.* (1997), although the latter actually discussed and illustrated the nominal variety, *N. tridentula* var. *tridentula* (Hodgson *et al*. 1997, pl. 15: fig. 8). Several valves of this taxon were recently observed in some peatbogs near Ushuaia, Tierra del Fuego, Argentina (Van de Vijver, unpubl. obs.).

During a survey of the diatom flora of an historic moss collection from the sub-Antarctic Campbell Island (southern Pacific Ocean), a very small population was discovered of *Navicula tridentula* var. *tenuis*. Comparison of the light microscopy observations with the illustrations in Lange-Bertalot *et al.* (1996, pl. 17: figs 4-6) did not show any morphological differences. Type material of *N. tenuis* Krasske (D III 163/4263 from the Krasske Collection, **KASSEL**), was retrieved but unfortunately, no unmounted type material was available. Therefore, material from Campbell Island was analysed with SEM to elucidate the ultrastructure of the Krasske taxon in order to establish its correct taxonomic identity.

Here we detail, using light and scanning electron microscopy observations, specimens from the type population and our Campbell Island population. The sample from Campbell Island (BAS255) was collected on 2 January 1970 by Dale Vitt from the moss *Breutelia elongata* (Hook.f. & Wilson) Broth. growing on soil at the base of a cliff on the northern slope of Mt. Dumas at an altitude of 1300–1500 ft (Dale Vitt, pers. comm.). We here designate BAS255 as epitype linked to the selected lectotype material.

Description: Valves linear with parallel, triundulate margins and clearly protracted, capitate apices. Valve dimension (n=15): length 13–21 µm, width 3.5–4.5 µm. Morphological structures, other that the raphe not discernible in LM. Raphe branches straight to weakly undulating, with simple, weakly deflected central endings and bent terminal raphe fissures (Fig. 11, arrow), although the latter not always visible in LM. Further morphological details only visible in SEM. Axial area relatively broad, linear and widening into an apically elliptical central area. Fascia never present due to shortened, marginal striae in the central area. Striae uniseriate, composed of large, rounded areolae covered externally by individual porous hymenes, ca. 45 in 10 µm. Central raphe endings simple, unilaterally deflected. Terminal raphe fissures unilaterally bent, terminating on the valve face in a relatively broad, shallow groove. Internal structure not observed. Girdle composed of several, open copulae, bearing one row of transapically elongated perforations.

Based on the observed morphological features, it is clear that the species does not belong to the genus *Navicula*, the latter being characterized by a different (never undulated) valve outline, striae composed of internally covered lineolae, terminal raphe fissures clearly hooked and continuing onto the valve mantle and a different girdle structure (Lange-Bertalot 2001). The only genus showing such a combination of features is *Adlafia*, described by Gerd Moser, Lange-Bertalot & Metzeltin (1998: 87) to accommodate species with a filiform raphe, simple central raphe endings, clearly bent terminal raphe fissures, uniseriate striae with areolae that are externally closed by individual porous hymenes and two open, perforated copulae (Moser *et al.* 1998: 87-88). As the Krasske taxon shows the same features as *Adlafia*, referral to this genus is proposed below.

Since *Navicula tenuis* Krasske 1939 is an illegitimate alter homonym, a new name can be introduced if the taxon is referred to a different genus (ICN Art. 6.11, Turland *et al.* 2018,). Lange-Bertalot *et al.* (1996) published "D III 163" as "holotype" of for this species although Krasske (1939) did not designate a holotype from the three collections he cited and, contrary to what Lange-Bertalot *et al.* (1996) stated, no marked specimen was found on Krasske's slide.

Adlafia tenuis Van de Vijver & Goeyers, *nom. nov.*
Replaced synonym: *Navicula tenuis* Krasske 1939, *Archiv für Hydrobiologie* 35: 385, fig. 11: 51, *nom. illeg., non Navicula tenuis* F.Meister.
Synonym: *Navicula tridentula* var. *tenuis* Lange-Bertalot & Willmann, *Iconographia Diatomologica* 3: 151, fig. 17: 4-6, 1996.
Lectotype (here designated): D III 163/4263 (Chile) in coll. Krasske, **KASSEL**.
Epitype (here designated): sample BAS255 (Campbell Island, coll. date 02/01/1970, leg. Dale Vitt, BR-4568, **BR**);

The authors wish to thank: Dr Dale Vitt who collected the sample of Campbell Island; Dr Peter Mansfeld (Krasske collection, **KASSEL**) is thanked for providing the type slide of *N. tenuis*; Dr Wolf-Henning Kusber for his nomenclatural advice; and Prof. Luc Ector for his help with a search for relevant literature.

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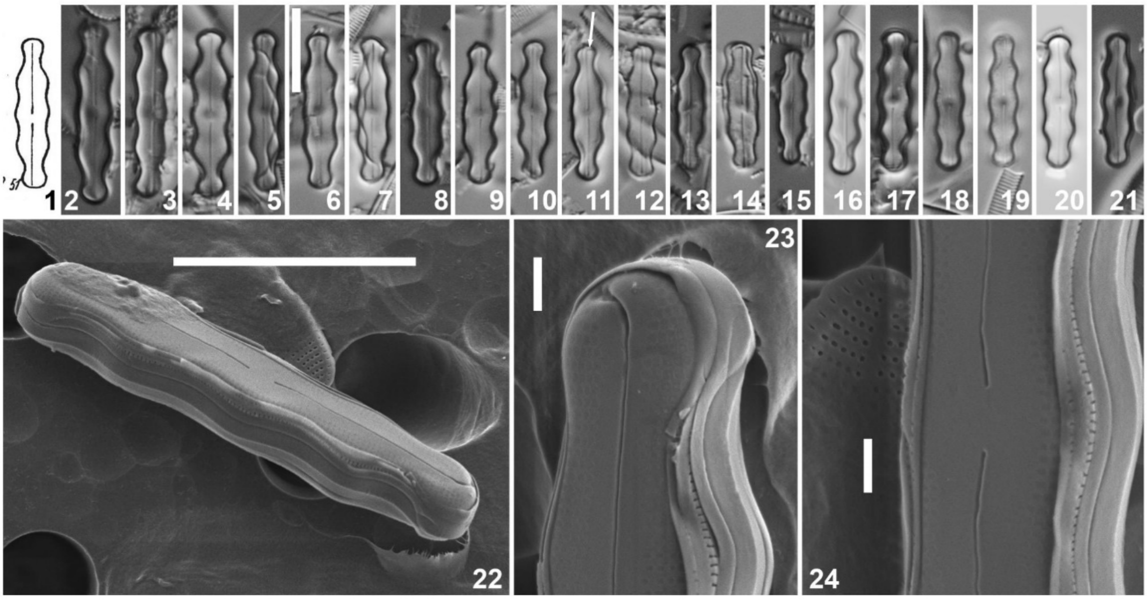

Figs 1–24. *Adlafia tenuis* Van de Vijver & Goeyers *nom. nov.* Fig. 1. Original drawing of *Navicula tenuis* Krasske (1939, pl 11, fig. 51). Figs 2–15. LM micrographs of the lectotype slide of *Navicula tenuis* Krasske (KASSEL D III 163/4263). Figs 16–21. LM micrographs of *Adlafia tenuis* (population of Campbell Island, sample BAS255). Figs 22–24. SEM micrographs (overview + details) of one specimen of *Adlafia tenuis* (population of Campbell Island, sample BAS255). Scale bar = 10 µm (Figs 2–22) and 1 µm (Figs 23–24).

MOSS-INHABITING DIATOMS FROM CAMPBELL ISLAND (SUB-ANTARCTIC)

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INTRODUCTION

Diatoms (Bacillariophyta) are one of the most abundant groups of algae in polar ecosystems, both in number of specimens as in number of species. Their characteristic silica or *glass* outer shell and their significant respons on changes in the physical and chemical environment make them excellent bio-indicators, used in both environmental, biogeographical and paleo-ecological studies. Especially in Polar regions, diatoms proved to be very useful indicators of environmental and climatic changes. It is generally accepted that current climate change will have the greatest impact in Polar regions. Despite this, our knowledge of diatoms in these areas is not profound. Due to outdated species taxonomy, force-fitting and incorrect identifications, a revision of the polar diatom flora is required. In the present study, the diatom flora found in a historic moss collection, sampled on the sub-Antarctic Campbell Island in 1969-1970 by Dale Vitt was analysed (Hickman & Vitt, 1973). This poster shows the preliminary results of the biodiversity study of the Campbell Island diatoms that started four months ago in the framework of a master thesis.

OBJECTIVES

1. Study the biodiversity of the Campbell Island diatoms
2. Increase our knowledge on the non-marine diatoms of the pacific part of the sub-Antarctic region
3. Update species taxonomy and refine identifications

RESULTS

A well-developed, species-rich diatom flora was observed in the samples, mainly belonging to the genera *Humidophila*, *Psammothidium*, *Planothidium* and *Pinnularia*

A large number of at present unknown diatoms were observed that could not be identified using the currently available literature.

Detailed analysis of light and scanning electron microscopy observations and comparisons with similar taxa worldwide led to the description of several new species and the transfer of *Navicula tenuis* to the genus *Adlafia* (Van de Vijver, de Haan & Goeyers, 2019)

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METHODS

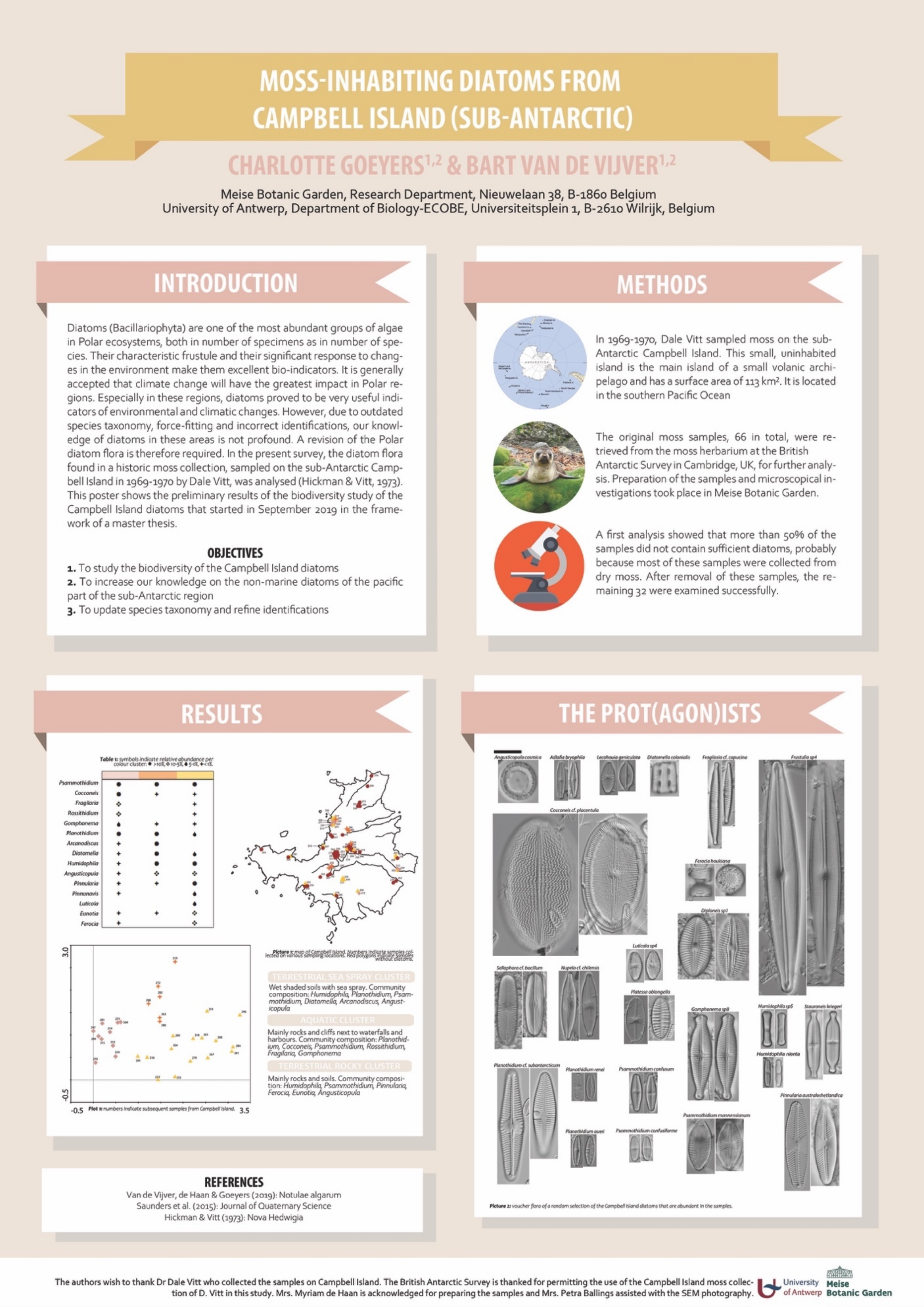
In 1969-1970, Dale Vitt sampled moss on the sub-Antarctic **Campbell Island**. This small, uninhabited island is the main island of a small volcanic archipelago and has a surface area of 113 km². It is located in the southern Pacific Ocean. In 2015, new diatom samples from the island were analysed (Saunders et al. 2015).

The original moss samples, 66 in total, were retrieved from the moss herbarium at the British Antarctic Survey in Cambridge, UK for further analysis.

A first analysis of the samples showed that more than 50% did not contain any or sufficient diatoms. Most of these samples were collected from dry moss vegetations. After removal of these samples from further analysis, the remaining 32 samples were examined.

THE PROT(AGON)ISTS

The authors wish to thank Dr. Dale Vitt who collected the samples on Campbell Island. The British Antarctic Survey (Cambridge, UK) is thanked for permitting the use of the Campbell Island moss collection of D. Vitt in this study. Mrs. Myriam de Haan is acknowledged for preparing the samples and Mrs. Petra Ballings assisted with the SEM photography.



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Diatoms (Bacillariophyta) are one of the most abundant groups of algae in Polar ecosystems, both in number of specimens as in number of species. Their characteristic frustule and their significant response to changes in the environment make them excellent bio-indicators. It is generally accepted that climate change will have the greatest impact in Polar regions. Especially in these regions, diatoms proved to be very useful indicators of environmental and climatic changes. However, due to outdated species taxonomy, force-fitting and incorrect identifications, our knowledge of diatoms in these areas is not profound. A revision of the Polar diatom flora is therefore required. In the present survey, the diatom flora found in a historic moss collection, sampled on the sub-Antarctic Campbell Island in 1969-1970 by Dale Vitt, was analysed (Hickman & Vitt, 1973). This poster shows the preliminary results of the biodiversity study of the Campbell Island diatoms that started in September 2019 in the framework of a master thesis.

OBJECTIVES

1. To study the biodiversity of the Campbell Island diatoms
2. To increase our knowledge on the non-marine diatoms of the pacific part of the sub-Antarctic region
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METHODS

In 1969-1970, Dale Vitt sampled moss on the sub-Antarctic Campbell Island. This small, uninhabited island is the main island of a small volanic archipelago and has a surface area of 113 km². It is located in the southern Pacific Ocean

The original moss samples, 66 in total, were retrieved from the moss herbarium at the British Antarctic Survey in Cambridge, UK, for further analysis. Preparation of the samples and microscopical investigations took place in Meise Botanic Garden.

A first analysis showed that more than 50% of the samples did not contain sufficient diatoms, probably because most of these samples were collected from dry moss. After removal of these samples, the remaining 32 were examined successfully.

RESULTS

Table 1: *symbols indicate relative abundance per colour cluster: ● >10%, ❖ 10-5%, ♦ 5-1%, ✦ <1%.*

	🟥	🟧	🟨
Psammothidium	●	●	●
Cocconeis	●	✦	✦
Fragilaria	❖		✦
Rossithidium	❖		✦
Gomphonema	♦	✦	✦
Planothidium	●	●	♦
Arcanodiscus	✦	●	
Diatomella	✦	●	♦
Humidophila	✦	●	●
Angusticopula	✦	❖	❖
Pinnularia	✦	✦	●
Pinnunavis	✦		♦
Luticola			♦
Eunotia	✦	✦	❖
Ferocia	✦		❖

Picture 1: *map of Campbell Island. Numbers indicate samples collected on various sampling locations. Red polygons indicate samples without diatoms.*

Plot 1: numbers indicate subsequent samples from Campbell Island.

TERRESTRIAL SEA SPRAY CLUSTER

Wet shaded soils with sea spray. Community composition: *Humidophila, Planothidium, Psammothidium, Diatomella, Arcanodiscus, Angusticopula*

AQUATIC CLUSTER

Mainly rocks and cliffs next to waterfalls and harbours. Community composition: *Planothidium, Cocconeis, Psammothidium, Rossithidium, Fragilaria, Gomphonema*

TERRESTRIAL ROCKY CLUSTER

Mainly rocks and soils. Community composition: *Humidophila, Psammothidium, Pinnularia, Ferocia, Eunotia, Angusticopula*

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Saunders et al. (2015): Journal of Quaternary Science
Hickman & Vitt (1973): Nova Hedwigia

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Picture 2: *voucher flora of a random selection of the Campbell Island diatoms that are abundant in the samples.*

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