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Doctoral Thesis

Ecology and Taxonomy of limno-terrestrial diatoms from East Antarctica.

Ekologie a taxonomie limno-terestrických rozsivek z Východní Antarktidy.

Supervisors

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Prof. Dr. Bart Van de Vijver (Meise Botanic Garden / University of Antwerp)

Prague, June 2020

I hereby declare that this dissertation has not been submitted in order to obtain the same or any other academic degree earlier or at another institution. My involvement in the research presented in this dissertation is expressed in the authorship order of the included publications and manuscripts. All publications and other sources used in writing this dissertation have been properly cited.

In Prague, June 2020

Jordan Bishop

JUSTIFICATION OF THE CONTRIBUTION TO THE DIFFERENT PUBLISHED PAPERS

I declare that the contribution of the PhD-candidate, Jordan Bishop, to the published and/or submitted papers can be considered more than sufficient to justify the inclusion of these papers in this PhD thesis.

Jordan Bishop is the first author for Chapters 2, 3 and 4 that were included as original papers. Chapter 2 was published as "*Sabbea* gen. nov., a new diatom genus (Bacillariophyta) from continental Antarctica". Chapters 3 and 4 have been submitted and are entitled, "*A re–investigation of lake sediment diatoms from the Vestfold Hills, Antarctica, using an updated, fine–grained taxonomy*" and "*Do water and nutrient availability influence the diatom communities found in mosses and lichens in the Windmill Islands, East Antarctica?*", respectively.

For all chapters, Jordan Bishop analysed the prepared diatom samples, photographed the diatoms, enumerated diatom valves and assembled the plates for the publications. For chapter 4, Jordan prepared the initial moss and lichen samples to be utilized for diatom analysis. Statistical analyses were performed by Jordan under the guidance of the co-authors with help in determining the appropriate analyses and data interpretation. He wrote the initial drafts of the publications, with later assistance of the co-authors to more fully developed presented ideas. The contribution of the co-authors has been limited to guidance, assistance to the formal descriptions of new species, help with finding the appropriate literature and stimulating discussions during the writing of the manuscripts and dissertation.

For the co-authors

Mgr. Kateřina Kopalová, Ph.D.
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For my mother, Cindy, and my family, Bianca, Maurizio, Angelo, Jayla & Santino.

For Maurizio, Pietro & Lucia.

Jordan

ABSTRACT

Diatoms are single-celled photosynthetic eukaryotes that substantially contribute to global primary productivity. They are also among the most diverse groups of organisms in Antarctica. Biogeographically, Antarctica is divided into three distinct regions including the Sub-Antarctic, Maritime Antarctic, and Continental Antarctic. Recent taxonomic revisions of diatoms within the Sub-Antarctic and Maritime Antarctic Regions have uncovered a number of endemic taxa initially misidentified as cosmopolitan due to species "force-fitting". Within Continental Antarctica, this taxonomic uncertainty has led to confusion about the environmental drivers of limno-terrestrial diatom communities, although this knowledge is important given the use of diatoms as regional bioindicators for environmental change. The purpose of this dissertation is to reevaluate the diatom flora of Continental Antarctica and determine variables that structure their communities within two historically and biologically important localities within East Antarctica; the Vestfold Hills and Windmill Islands. The erection of the genus *Sabbea* was performed to accommodate a long-misidentified species, *Sabbea adminensis,* that occurs within the Vestfold Hills and McMurdo Sound Region where it had been the source of taxonomic confusion since the early 20th century (Chapter 2). The re-evaluation of the Vestfold Hills saline lakes benthic diatom flora revealed 183 taxa, from the 67 previously described, with shared endemic taxa from other East Antarctic localities. Here, benthic lake diatom communities are structured primarily by salinity and secondarily by alkalinity (Chapter 3). In a nutrient and water addition experiment on terrestrial vegetations within the Windmill Islands, moss and lichens hosted significantly different diatom communities. However, neither nutrients nor water additions altered diatom communities (Chapter 4). These updated records and new ecological data can be widely applied across Antarctica, as well as in global microbial biodiversity and biogeography studies, and provide a baseline for investigating climate change impacts.

ABSTRAKT

Rozsivky jsou jednobuněčné fotosyntetické eukaryotní organismy významně přispívající ke globální primární produkci. Zároveň v Antarktidě patří mezi druhově nejrozmanitější skupinu organismů. Z pohledu biogeografie, Antarktidu tradičně dělíme na tři oblasti a to subantarktickou, přímořskou a kontinentální Antarktidu. Nové taxonomické revize rozsivek v subarktické a přímořské oblasti v nedávné době odhalily řadu endemických druhů, které byly v minulosti špatně určeny a zařazeny mezi kosmopolitní druhy. Nejen v rámci kontinentální Antarktidy vedla tato taxonomická nepřesnost například ke zkresleným závěrům v rámci environmentálních faktorů ovlivňujících společenstva limno-terestrický rozsivek. Tato znalost je důležitá vzhledem k použití rozsivek jako regionálních bioindikátorů pro změnu životního prostředí. Cílem této disertační práce byla revize rozsivkové flóry kontinentální Antarktidy a stanovení faktorů, které tyto společenstva strukturují ve dvou historicky a biologicky významných lokalitách východní Antarktidy, Vestfold Hills a Windmill Islands. Popis nového rodu *Sabbea* bylo provedeno u dlouho špatně zařazeného druhu, *Sabbea adminensis*, který se vyskytuje v oblasti Vestfold Hills a McMurdo Sound Region, kde byl zdrojem taxonomického zmatku již od počátku 20. století (kapitola 2). V rámci revize a studování bentické flóry jezer z oblasti Vestfold Hills bylo nově identifikováno 183 taxonů rozsivek, včetně mnoha endemických, oproti 67 dříve popsaným druhům. Společenstva těchto bentických rozsivek jsou primárně strukturovány salinitou a sekundárně alkalinitou (kapitola 3). V rámci experimentu s přidáváním živin a vody na suchozemskou vegetaci v oblasti Windmill Islands bylo zjištěno, že společenstva rozsivek z mechů a lišejníků se významně liší, avšak živiny ani přidaná voda tyto společenstva rozsivek neovlivnily (kapitola 4). Výsledky této disertační práce lze široce využít nejen v oblasti Antarktidy, ale i v dalších studiích zabývajících se mikrobiální rozmanitostí, biogeografií či při zkoumání vlivu klimatických změn.

AIMS OF THE DISSERTATION

This dissertation contains five chapters. There is a general introduction followed by three chapters as papers and concludes with a general discussion chapter summarizing the main findings. Two appendices are included. Appendix 1 is a table showing the taxon identity alongside brief notes for each taxon and refers to image plates (1–13) containing taxa that were not shown within the submitted papers. Appendix 2 shows my complete *Curriculum Vitae*. The aim of this dissertation was to add to our knowledge of the taxonomy and ecology of non-marine diatoms from Continental Antarctica through LM, SEM, field experiments, and comparisons of current and historic literature from throughout the Antarctic Realm.

This was accomplished by:

1) Revising a taxon from East Antarctica that demonstrated a history of improper, or ambiguous, placement within the literature through the description of a new genus within two scientifically important Antarctic localities: the McMurdo Sound region and the Vestfold Hills (Chapter 2)
2) A re-evaluation of the taxonomy and ecological interpretation of diatom communities inhabiting saline lakes from the Vestfold Hills (Chapter 3)
3) Characterizing epiphytic diatom communities inhabiting bryophyte and lichen vegetation types growing under experimental nutrient and water additions within the Windmill Islands (Chapter 4).

DISSERTATION OUTLINE

Chapter 1 provides background information for diatoms, with a discussion of their taxonomic practices, general ecology and the factors that structure their communities at large. This is followed by an introduction to the Antarctic Realm, and its three biogeographic sub-regions. Finally, open questions regarding the ecology and taxonomy of Continental Antarctic non-marine diatoms, with respect to East Antarctica in particular, are discussed to provide context for the research in this dissertation.

Chapter 2 details the process by which the genus of *Sabbea* Van de Vijver, Bishop & Kopalová was erected. A finely silicified taxon described as *Navicula adminii* D.Roberts & McMinn from the Vestfold Hills was also found in the McMurdo Sound Region. Here, it was the subject of taxonomic confusion with variety of similarly structured Naviculoid taxa, reported first by West and West (1911) as *N. perlepida* Grunow. By comparing monographs of type materials and specimens from the Vestfold Hills and McMurdo Sound Region, *N. adminii* was transferred into the new genus of *Sabbea,* as *Sabbea adminensis* (D.Roberts & McMinn) Van de Vijver, Bishop & Kopalová*,* as the overall morphostructure does not align with the genus *Navicula* Bory *sensu stricto.*

Chapter3 focuses upon updating the diatom flora from within the saline lakes of the Vestfold Hills and then assessing if the refined taxonomy changes the ecological interpretation of the lakes. Samples used within the original study, first collected as part of Roberts and McMinn (1999) were re-examined and the diatom flora revised. Diversity increased overall for the study, with a shift from cosmopolitan species to endemic Antarctica taxa. This was due in part to taxonomic revisions since the original study was performed, as well as taxa that were not reported from the first study. From this revised flora, the original lake chemistry and environmental data was used to determine if increased taxonomic resolution altered the interpretation of diatom community structuring. The present study confirms the original findings of Roberts and McMinn (1999) that salinity and alkalinity structured the diatom community within the Vestfold Hills. In this regard, improved taxonomic resolution did not alter the interpretation of lake chemistry variables structuring diatom communities. However, taxonomic resolution did aid in better describing the salinity tolerances of taxa, as a number of taxa that were previously “lumped together” were revised since the original study and now show narrower salinity tolerances.

Chapter 4 focuses upon the terrestrial epiphytic moss diatom flora from the Windmill Islands. This chapter examines the diatom flora present upon two bryophyte and two lichen vegetation types. Water and nutrient treatments were added to all four vegetation types that aligned with estimates of projected availability due to climate change for the Windmill Islands with the goal of determining how these diatom communities will change in the future. Interestingly, diatom communities were primarily structured by the underlying vegetation type and did not appear to respond to nutrient or water availability. Thus, this chapter presents experimental evidence that changes in the abundance of moss and lichen vegetations in the face of climate change may impact resident diatoms.

Chapter 5 concludes the dissertation with a summarization of the main findings. These findings have wide applicability as datapoints in biogeographic studies, as well as serving as a record of a still pristine Antarctic Continent, before anticipated climate change and anthropogenic impacts cause irreparable damages to East Antarctica.

Appendix 1 contains a long form table showing the taxon identity, distribution within the study areas and brief notes for each taxon encountered across the studies. The table refers to image plates (1–13) containing taxa that were not shown in the submitted papers.

Appendix 2 shows my *Curriculum Vitae,* including a complete listing of publications, presentations and teaching experience.

Chapter 1

Introduction

Introduction

Diatoms form the base of the food chain for many of the world's ecosystems and are responsible for significant portions of terrestrial and oceanic productivity on an annual basis (Field et al. 1998). The contribution of diatoms to global oceanic primary productivity ranges from 20–75%, depending on the ocean zones investigated (Nelson et al. 1995, Tréguer et al. 2018). Although terrestrial primary productivity is driven largely by vascular plants, diatoms are often the main drivers of primary productivity within lake and stream ecosytems (Reynolds 1984, Geider et al. 2001, Yeung et al. 2012).

Diatoms are photosynthetic eukaryotes belonging to the stramenopiles, or heterokonts, group based on the presence and morphology of two unequal flagella. Although diatom vegetative cells lack flagella, this structure is observed within sperm cells of sexually reproducing centric diatom lineages (Poulíčková and Mann 2019). Despite the confusing nature of the placement of the diatoms within the group based upon morphological structures, molecular evidence still firmly roots the diatoms within the stramenopiles (Burki et al. 2020). The diatom photosynthetic plastid, or chloroplast, originated from a red alga secondary endosymbiotic event, resulting in a chloroplast bound by four membranes (Medlin et al. 2000). Molecular evidence places the emergence of diatoms at approximately 250 ma (Sorhannus 2007) although fossil records date diatoms only to the Jurassic, approximately 190 ma (Sims et al. 2006, Medlin 2015, 2016)

Diatom cells are protected by a frustule, entirely composed of silicon dioxide (Armbrust et al. 2004). This frustule consists of two overlapping valves (Figure 1), a slightly larger epivalve resting upon the smaller, inferior hypovalve, banded together by the cingulum, an often complex system of girdle bands called copulae (sing. copula). Copulae that lay in direct contact with the valve are referred to as the valvocopulae (Round et al. 1990). The outward facing portion of the valve is known as the valve face, whereas the mantle is the portion

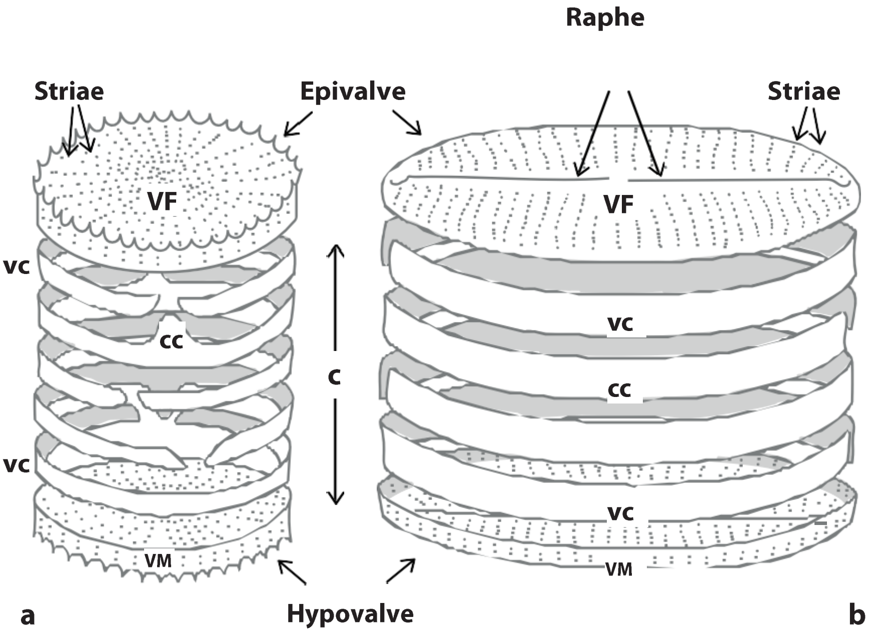

Figure 1. A conceptualized diagram showing overall diatom frustule morphology, with a comparison of a centric diatom (a) alongside a pennate (b) diatom. A slightly larger epivalve sits atop a slightly smaller hypovalve. Collectively, the cingulum (c), also called girdle bands, or copulae, are composed of individual cingula (cc), also known as a copula or girdle element. Those copula in direct contact with a valve are referred to as valvocopula (vc) (pl: valvocopulae). Morphological characters on the valve itself include, the striae, composed of a series of single areolae. The raphe may be present on the valve face (VF), or partially upon the valve mantle (VM).

that when viewed from the side is often in contact with the girdle bands (Ross et al. 1979). The principal discriminating characters of the valve include the structure of the raphe, as well as the striae and their composing areolae. The diatom raphe is a slit through the valve, often present upon the valve face, or partially upon the mantle, and allows the diatom to move through the water column (Ruck and Theriot 2011). Not all diatoms possess this structure, but for those that do, the detailed morphology of the collective raphe structures can be used as a discriminating characteristic separating different taxa (Kulikovskiy et al. 2016a). Areolae or pores are another structure that, like the raphe, allows the diatom to interact with the extracellular environment (Cox 1999). However, areolae do not aid in movement, but instead allow the exchange of nutrients into the cell and removal of wastes (Hale and Mitchell 2001). Areolae are generally present on the valve and mantle organized in rows called striae. The size, shape, and fine structure of areolae, including inner and outer occlusions, are useful in determining species but can often only be seen with the help of SEM (Cox 2012).

Diatom growth occurs through successive additions of girdle bands, through an increase in girth, moving the valves further apart. The valves, themselves, remain unchanged in this process. When undergoing vegetative (asexual) cell division, the parental frustule splits, becoming one half of each of the two “new” daughter cells. The parental hypocingulum becomes the epicingulum of one daughter cell while the parental epicingulum remains the epicingulum for the second daughter cell (Figure 2).

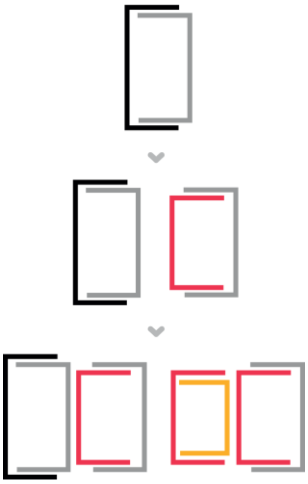

Figure 2. Cell size reduction following the MacDonald-Pfitzer rule. Through each successive cell division (indicated by down arrows here), there is a gradual reduction in the mean cell size within the diatom population.

This results in the gradual reduction in cell size within a population over successive reproductive cycles, known as the MacDonald-Pfitzer rule (Werner 1977). Upon reaching the end of the diminution series, auxosporulation “restores” valve size (Kaczmarska et al. 2013) and is often, but not always, linked to concomitant sexual reproduction (Poulíčková and Mann 2019).

Global biodiversity of the diatoms is still unknown, with estimates ranging from 30,000 to 100,000 species (Mann and Vanormelingen 2013). Individual diatom species have been historically determined by a morphological species concept based upon descriptions of the valve ultrastructure. These descriptors have characterized overall valve polarity (e.g. isopolar, heteropolar) as well as qualitative descriptions of valve outline (e.g. lanceolate, rhomboidal). Cox (1995, 2012) suggests shape descriptions following a standardized definition to limit wide interpretation, which highlights the difficulty in overreliance upon these terms. However, these descriptive data are accompanied by a range of quantitative descriptions. These data can include presence/absence of particular structures such as the raphe, as well as the placement and type of occlusions associated with areolae. Lastly, measurements of frustule structures and landmarks (e.g. valve length and width, striae density per 10µm) are recorded in addition to qualitative shape descriptions (Mann 1999, Pappas et al. 2014).

Using molecular tools, cell physiology, and ultrastructural features, other characteristics have helped to further refine and improve upon the framework discussed within Round et al. (1990) with slight differentiations in higher classifications. Medlin and Kaczmarska (2004) were the first in a series of papers, as discussed within Sims et al. (2006) and Medlin (2016), to offer an alternative classification scheme based upon molecular evidence for three classes: Coscinodiscophyceae, Mediophyceae, and Bacillariophyceae, that contains both the raphid and araphid pennate diatoms (Medlin 2016). Cox (2015) revises and adds another Class to those discussed within Round et al. (1990) that were primarily based from upon valve morphological and reproductive characteristics, noting revisions at the sub-Class, Order and Family level have been due to recent molecular work within the particular groups. The Classes within Cox (2015) are defined as follows: Coscinodiscophyceae, Mediophyceae, Fragilariophyceae, and Bacillariophyceae. Coscinodiscophyceae demonstrate circular valves with radial symmetry, whereas the Mediophyceae cells may be circular or demonstrate a number of different poles, colloquially termed the "bipolar or multipolar centrics". Lastly, Fragilariophyceae are elongate valves without raphes whereas Bacillariophyceae are elongate cells with raphes present on one or both valves.

At present, molecular methods have become tailored to investigate wide ranging questions concerning diatom species delimitation (Medlin 2018). The approach of combining high resolution images from both LM and SEM, alongside molecular markers has become widespread within taxonomic studies (Kulikovskiy et al. 2016b, Jahn et al. 2017, 2019, Barkia et al. 2019). This approach has yielded interesting results, revealing cryptic species complexes, where species are indiscernible morphologically, differing only within molecular sequence data (Pinseel et al. 2019, 2020). These same molecular tools have also been used to answer questions about diatom evolution, albeit within larger datasets. Using an even larger number of targeted genes (11 in total), compiling over 1000 strains, Nakov et al. (2019) investigated diatom rates of diversification within the freshwater and marine environments. Nakov et al. (2019) showed that both planktonic and benthic freshwater diatoms are more diverse than their marine counterparts due to larger turnover rates (defined therein as speciation + extinction). Their work suggests that the high turnover rates of freshwater diatoms reflect the high turnover of freshwater environment, due to climatic events such as glaciation or drought. Lastly, Kociolek et al. (2019) investigated homoplasy, the multiple gains or losses of a trait, and occurrences of adaptive radiation within pennate diatoms. It was shown that there is evidence for multiple, possibly five or six, independent evolutions of morphological characteristics such as valve symmetry and raphe number. In sum, combined molecular and traditional morphological methods still have much to explore in regard to diatom diversity and evolutionary processes.

Ecology

Diatoms have evolved to thrive in a diversity of habitats forming one component of the loosely defined, polyphyletic grouping colloquially known as the algae (Gibbs 1992, Andersen 1992, Burki 2014). "Algae' is a non-taxonomic, functional term that indicates non-vascular aquatic photoautotrophs. Diatoms, like many other algal organisms (such as chlorophytes), may be solitary or colonial, filling niches in aquatic ecosystems within both planktonic and benthic habitats (Dodd 1987). Colonial diatom forms are usually planktonic such as the stellate colonies of *Asterionella* Hassall or can be in tubes (e.g. *Frustulia* Rabenhorst and *Berkeleya* Greville). Terrestrial diatoms on the other hand not only appear in the soil matrix itself but may be associated with bryophytes (Poulíčková et al. 2004), biological soil crusts (Borchhardt et al. 2017), thin water films (van Kerckvoorde et al. 2000) and other vegetation types as a component of the epiphytic algal community (Veselá and Johansen 2009, Neustupa et al. 2013).

Different abiotic factors control diatom growth and distribution, and may be critical for their persistence. For example, the macronutrient Nitrogen is utilized for protein synthesis, whereas Phosphorus is an important component in genetic material (Sterner and Elser 2002, Litchman and Nguyen 2008). Both of these nutrients can be limiting in aquatic environments. Bioavailable silica and pH can furthermore influence a range of diatom cellular processes (Stevenson et al. 1996, Winder et al. 2009, Carey and Fulweiler 2012). As it is the main component in their cell walls, diatoms play a major role in the global silica cycle within both freshwater and marine habitats (Brzezinski et al. 2003). pH is especially important, as it can affect silica deposition upon newly created valves (Hervé et al. 2012), as well as determine the form of dissolved inorganic carbon (DIC) within the water column. Conductivity and salinity are also important parameters influencing diatom growth and community structure (Potapova and Charles 2003). While sometimes used interchangeably, conductivity is the measure of electrical conductance of ions such as Cl^-, Na^+, Ca^{2+}, Mg^{2+} within the water column, whereas salinity is the measure of the total dissolved salts within the water column (Wetzel 2001).

Individual species often have narrow environmental tolerances and are noted for their rapid response to environmental change and stress (Lowe 1974, Brazner et al. 2007). pH and conductivity tend to be among the principal variables within diatom communities across both terrestrial and aquatic ecosystems. For example, pH, soil type, and land use have been shown to structure terrestrial diatom communities (Antonelli et al. 2017, Blanco et al. 2017), along with both temperature and moisture content can significantly influence terrestrial diatom communities and their survivability (van Kerckvoorde et al. 2000, Souffreau et al. 2010, 2013a). Conductivity has been shown to be the most influential environmental factor determining diatom community structure within Finnish boreal streams (Soininen et al. 2004) as well as temperate, shallow water European lakes (Blanco et al. 2014). Finally, in a number of studies of lakes and streams within the Northern Hemisphere, pH and conductivity were shown as primary drivers determining the structure of diatom communities (Soininen 2007). Given these relationships, diatoms can be used as bioindicators, as taxa can be distributed across a wide span of environmental gradients (Kelly et al. 1998, Wood et al. 2019). Furthermore, as the siliceous remains of diatoms are readily preserved within the fossil record, diatoms are often used as proxy data for paleoreconstructions of freshwater and marine environments (Verleyen et al. 2004, Abrantes et al. 2007).

Biogeography and Dispersal

Biogeography is the study of the geographic distribution of organisms, often divided into two interacting, complimentary processes of historical and ecological biogeography (Futuyma 2002). Historical, or phylogenetic biogeography, is concerned with determining the evolutionary, phylogenetic relationships of organisms within a particular area, whereas ecological biogeography based upon physiological needs and community associations (Wiens and Donoghue 2004). As these disciplines have historically focused on macroscopic organisms, long-appreciated patterns in species distributions and turnover have been observed along latitudinal and elevational gradients in plants, mammals and invertebrates (Pianka 1966, Futuyuma 2002, Economo et al. 2018) and elevational gradients, with one of the most famous patterns being the increasing diversity observed with decreasing latitude (Mittelbach et al. 2007).

Vellend (2010) proposed four ecological processes responsible for the geographic distribution of organisms, which were refined and expanded upon by Hanson et al. (2012) for microbial biogeography. These four processes include speciation, selection, dispersal, and ecological drift. Speciation is the process by which new species are formed, adding to the community and increasing diversity. Selection dictates the ability of a species to survive and reproduce within a community given biotic and abiotic pressures. Dispersal is the movement of species from one area to another. A successful dispersion means that a species colonizes a new area and can persist there beyond the initial dispersal event. Lastly, ecological drift refers to the stochastic (neutral) effects, i.e. the random fluctuation of a species' abundance in a particular area.

The study of microbial biogeography has sought to investigate whether microbes demonstrate similar predictable and largescale trends comparable to those seen within macroscopic organisms. In studies examining these patterns in bacteria, for example, there have been mixed results, with some cases supporting similar largescale trends reporting increased richness within high marine latitudes (Raes et al. 2018). Other studies show that local variables, instead of latitude, were responsible in soil bacteria community structuring (Fierer and Jackson 2006). However, there are difficulties in studying the individual processes for microbes, especially with regard to dispersal, since these events are difficult to directly observe.

Historically, microbial dispersal was assumed to be frequent and widespread, and Baas-Becking (1934) famously stated that "Everything is everywhere, the environment selects". This came to be known as the Baas-Becking, or Ubiquity hypothesis, and Finlay (2002) argued that given this, microbes should not demonstrate restricted biogeographical distributions similar to macroscopic organisms, such as mammals, higher plants or arthropods due to the small "body" sizes and correspondingly large microbial populations, which should make dispersal events quite common. However, successful colonization and establishment should be limited by the conditions of the new environment, and thus despite frequent dispersal events, it is possible that a new area cannot be physiologically tolerated, and establishment never takes place.

Recent work has suggested that diatom community structure may exhibit influences of both dispersal limitation and selection. For example, in a survey of Swedish lakes, diatom community composition was explained by both large spatial scale and local environmental characteristics, suggesting that dispersal limitation takes place at large spatial scales, and species-specific responses to environmental factors at smaller scales (Keck et al. 2018). Telford et al. (2006) also demonstrated the importance of dispersal limitation within European and North American datasets, and in the tropics, a network of water reservoirs demonstrated the effects of environmental variables and connectivity in structuring diatom communities (Zorzal-Almeida et al. 2017). Verleyen et al. (2009) investigated dispersal and local abiotic factors within a global dataset and found scale-dependent results. Local abiotic factors explained the variation in lake diatoms within close proximity, yielding little to no signal of dispersal until larger geographic distances (>2000km) were observed. At the regional scale, within the tropical Andes mountain ranges and nearby Amazon lowlands of South America, biogeographic patterns were demonstrated by a low proportion of shared species between sites and weak signal of a negative latitudinal species richness gradient (Benito et al. 2018), though the authors posit that this may be the relic of climatic variables that change with latitude.

It is likely that a number of factors contribute towards diatom biogeography, including confounding anthropogenic influences. Benthic stream diatoms within the contiguous United States showed distinct biogeographic provinces when both spatial and environmental factors were investigated (Potapova and Charles 2002). These factors were not shown to impact all species homogenously. Instead, subsets of species whose distributions were better explained by either spatial or environmental characteristics at the regional scale. At the national scale, a third of the variation in diatom species composition was due to spatial factors with the remaining influence of environmental factors was driven largely by pH. However, Potapova and Charles (2002) discuss that pH can vary greatly between regions due to land use and degradation, namely through agriculture or urban influences, compared to forested land cover. In addition to anthropogenic influences, influences that increase trophic complexity, such as grazing (Vilmi et al. 2017), could potentially make uncovering diatom biogeographical trends more difficult.

The Antarctic Realm

The Antarctic Realm is comprised of three distinct biogeographic regions (Figure 3) that can be defined both geographically and climactically: The Sub-Antarctic Region, the Maritime Antarctic Region, and the Continental Antarctic Region (Convey 2010). The Sub-Antarctic Region comprises a series of islands and archipelagos across the Southern Ocean between roughly 45–55 degrees south latitude (Chong et al. 2015). This area is encompassed within the 20–30km wide Antarctic Convergence Zone as the northern-most boundary (Gordon 1971, Pickard and Seppelt 1984), and is the mildest in terms of climactic conditions, with a substantial portion of the year above 0°C. No permafrost is observed (Convey 2007), and because there is

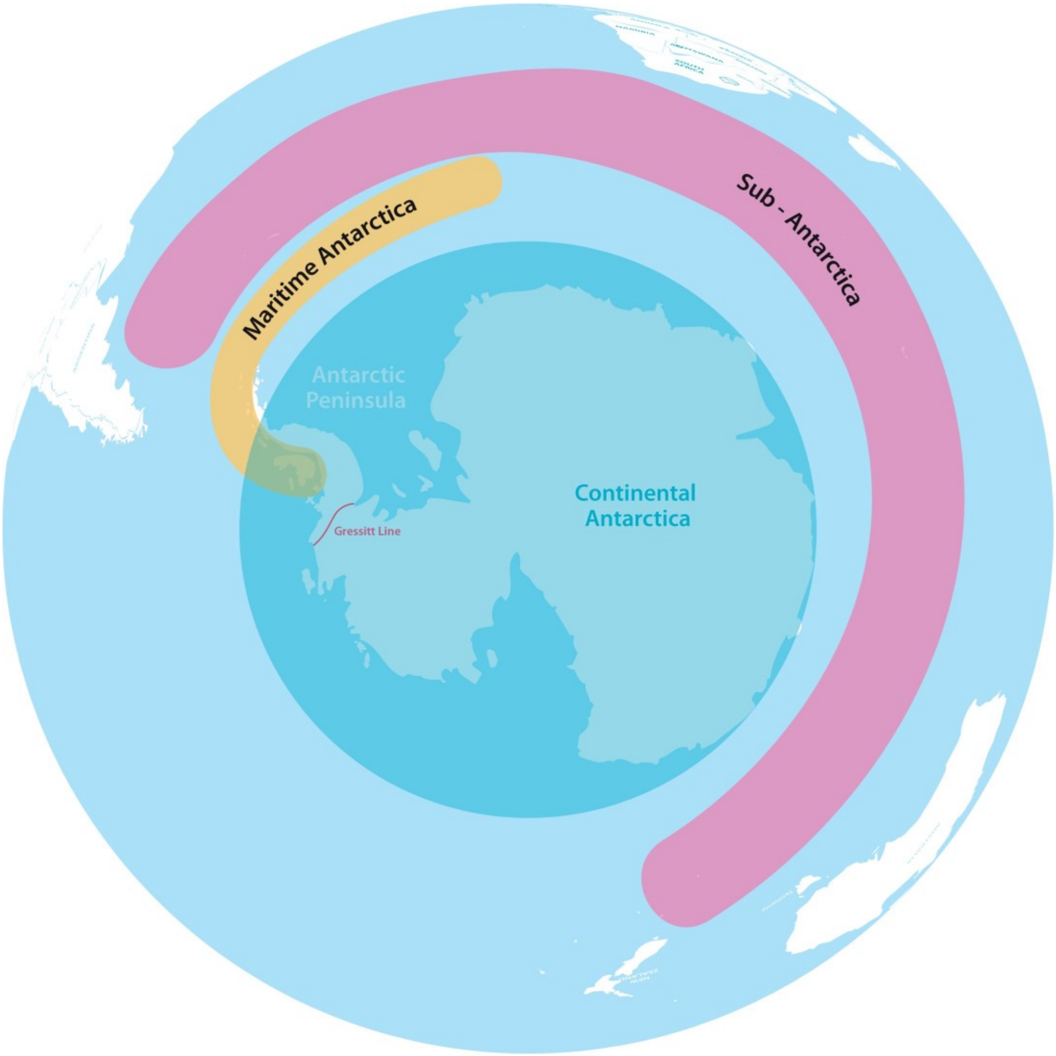

Figure 3. A map of the Antarctic Realm along with its three distinct biogeographic regions. These regions include the Sub-Antarctic, Maritime Antarctic, and Continental Antarctic. The Antarctic continent is further divided by the Gressitt Line, which serves as the boundary between the Antarctic Continent and Antarctic Peninsula.

ample precipitation (around 100cm) that collects in standing pools or lakes, water is not a limiting factor (Van de Vijver et al. 2002a, Van de Vijver and Beyens 2006). However, it is important to note that there may be conflicting definitions of what constitutes the Sub-Antarctic based upon the possible inclusion of Patagonia, as well as different definitions put forth by meteorologists and oceanographers (Selkirk 2007).

The Maritime Antarctic Region is comprised of the western portion of the Antarctic Peninsula extending south to Margherite Bay, including the South Shetland, S. Orkney, and S.

Sandwich and Bouvet Islands (Convey 2010). Holdgate (1970) proposed a definition that extends between 55–70 degrees south latitude, based largely upon the extensive presence of spermatophytes and bryophytes upon the aforementioned islands. In this region, the climate becomes much harsher, permafrost appears, and precipitation falls within a range from 25 to over 100cm (water equivalents) (Holdgate 1977). The Gressitt Line separates the milder, less extreme environment of the Antarctic Peninsula (as a component of the Maritime Antarctic) from the remainder of the Antarctic Continent, akin to the Wallace Line found within Southeast Asia (Chown and Convey 2007).

The Continental Antarctic Region comprises the remainder of the eastern portion of the Antarctic Peninsula, joined as part of the wider West Antarctica, alongside East Antarctica, separated by the Transantarctic Mountains. Upon Continental Antarctica the precipitation falls as snow, is quite limited, and water availability represents one of the largest stressors (Convey et al. 2014). For example, within Droning Maud Land, East Antarctica, snowfall occurs in episodes that may account for large percentages (up to 50%) of its annual amount (Schlosser et al. 2010). Collectively, the McMurdo Dry Valleys within Victoria Land form the largest ice-free areas on Antarctica. The region is one of the most extreme deserts on Earth, with an average precipitation of less than 10cm (water equivalents) annually, persistent strong winds, and temperatures averaging around -20°C in Taylor Valley (Fountain et al. 1999).

The Antarctic Continent as we know it today stems from the separation of the Antarctic Peninsula from the southern tip of South America by the opening of the Drake Passage as well as the concomitant formation of the Antarctic Circumpolar Current (ACC) (Livermore et al. 2007). This led to the first large scale glaciation of the continent during the Cenozoic, approximately 34ma, marking the start of a dynamic history of shrinking and expanding ice cover (Davies et al. 2012). Sparse habitable, ice-free coastal areas make the study of organism dispersal, colonization and community structuring within Antarctica quite unique. There is evidence that some areas within East Antarctica, such as the Bunger Hills and Syowa region, may have remained ice free even during the Last Glacial Maximum (LGM) (Convey et al. 2008), which lasted between approximately 22–17ka (Convey et al. 2009).

Some taxa have remained since the Gondwana separation upon the continent within ice-free "refuge" areas (Convey and Stevens 2007). Molecular evidence supports the notion that there were distinct, long persisting green algal lineages established since Pre-Gondwana within Continental Antarctica, as well as multiple, independent colonization events (Vyverman et al. 2010). Distinct Antarctic lineages have been confirmed within two diatom species complexes, *Pinnularia borealis* Ehrenberg and *Hantzschia amphioxys* (Ehrenberg) Grunow (Souffreau et al. 2013b). Furthermore, Pinseel et al. (2019, 2020), investigated worldwide lineages of *P. borealis* and determined that strains from Continental Antarctic and the Maritime Antarctic, formed separate and distinct clades distinct from one another, but also the remainder of the dataset. Fossil evidence exists for Pre-Gondwana diatom lineages, suggesting long-term residence upon the continent (Vyverman et al. 2010). Interestingly, a large number of genera present within the Miocene diatom flora are not found in the modern Continental Antarctic flora, suggesting that the extant flora became established after Miocene cooling (approximately 14ma) and concomitant intensification of glaciation (Lewis et al. 2008, Pinseel et al. 2016, 2020). Despite the size of the continent, ice-free areas form a relatively small portion (< 1%) of Antarctica (Hughes et al. 2015, Convey and Peck 2019). It is within these coastal ice-free areas that terrestrial Antarctica hosts a depauperate flora and fauna of microbes, insects, and lower plants (Convey et al., 2014).

In an effort to characterize biogeographic patterns across the Antarctic Realm, Terauds et al. (2012) compiled known biogeographical works across a number of phyla, cross referencing these areas to GIS data layers of ice-free areas. The result of Terauds et al. (2012) was the construction of 15 distinct Antarctic Conservation Biogeographic Regions (ACBRs), which was later expanded to 16 in Terauds and Lee (2016). These studies confirmed the separations between the three Antarctic sub-regions, but also demonstrated that the Continental Antarctica Region, despite being largely ice covered, possessed its own diversity of life lying with the variably sized, patchily distributed ice-free areas throughout East and West Antarctica. What remains unanswered, however, is whether or not the microbial flora of Antarctica, and diatoms specifically, follow these same trends of macroscopic organisms within the Antarctic Region.

The Antarctic Realm presents an opportunity to reduce the "noise" of ecological studies due to its low trophic complexity compared to temperate and tropical climates (Convey et al 2014). At the moment, impacts to the Antarctic Realm have remained relatively low due to its geographic isolation, allowing the opportunity to study a relatively "pristine" environment with limited influence of pollution, grazers, and invasive species. However, human influences, as well as impacts due to climate change are ongoing within the Antarctic Realm, and unsurprisingly, their results are not expected to be seen uniformly throughout the component regions (Convey and Peck 2019). Research has suggested that environmental best practices may be lacking and are not uniformly implemented across the 75 currently active bases across the Antarctica, where contamination may occur as pollution or inadvertent nutrient supplementation via gray water or other wastes generated by bases (Hughes 2010, Chown and Brooks 2019). In this regard, it is imperative that "baseline" biological studies are conducted while these relatively low disturbance levels persist.

Diatoms in the Antarctic Realm: Diversity and Taxonomy

Diatom communities demonstrate a high degree of endemism within Antarctica (Vyverman et al. 2007, 2010, Kociolek et al. 2017) though this may not be reflected within larger biodiversity studies. When forming the ACBRs, Terauds et al. (2012) and Terauds and Lee (2016) relied on compiled taxonomic lists for particular sections of Continental Antarctica. Not surprisingly, well-studied taxa such as mosses and birds were featured heavily within the studies, often with extensive historic records that have been checked for accuracy as new discoveries are made. The study of microbes has progressed at a rate where the accuracy of records do not reflect the latest advances. The wealth of historic diatom records, in particular, from Continental Antarctica is marred by varying quality. As a consequence, the aforementioned studies were forced to disregard records of diatoms specifically because of a lack of reliable records, resulting in the inability to draw conclusions for ACBRs. The omission of a number of records from East Antarctic diatoms from Terauds et al. (2012) highlights the lack of a comprehensive diatom flora Continental Antarctica as well as the need for a reexamination of the diatom records from this region.

A number of works have suggested that the flora of Antarctica is not composed primarily of cosmopolitan taxa, but rather appears so as a result of overly broad, poorly defined morphological species concepts. In this way, "species force-fitting" to European and American species concepts inflated the list of cosmopolitan taxa (Jones 1996, Tyler 1996). Seeing this, Kellogg and Kellogg (2002) compiled a list of records for non-marine diatoms from the three Antarctic Regions, spanning over 300 publications, in which the majority of taxa were listed as cosmopolitan. Kellogg and Kellogg (2002) "rated" the compiled references on a three-tiered system to evaluate their perceived validity, making extensive notes that their work was a compilation and served as a way to track records, as opposed to taxonomically revising them. Kellogg and Kellogg (2002) confirmed what other larger reviews had discussed (see Jones 1996). While some regions where long term research projects are based, such as the McMurdo Dry Valleys (MCM LTER) or one of the three bases managed by the Australian Antarctic Division, such as Casey Station, feature more updated records, others do not. Kellogg and Kellogg (2002) demonstrated the lack of consistency throughout Antarctic records. Some localities have incomplete, inconsistent data, or a lack of records. As an example, the floristic survey performed by Pankow et al. (1991) of the Schirmacher Oasis, should be treated with caution as micrographs do not feature scale bars (as discussed within Sabbe et al. 2003).

Through the gradual re-evaluation of ecological and taxonomic works on Continental Antarctica has taken place, some records are in particular need of revision. For example, Roberts and McMinn (1999) data were collected as a training, or calibration, set whereby diatom relative abundance data would be regressed with environmental variables to form a transfer function for salinity. This transfer function could then be used to infer salinity within other localities simply by determining diatom relative abundances. In order for the training set to be developed properly, proper identification of taxa is crucial. However, the training set (specifically, the diatom taxonomy to identify species) used for the analyses within the Vestfold and Windmill Islands is in need of taxonomic update. Recently, Van de Vijver et al. (2012) revised a number taxa from the McMurdo Sound Region, and these changes have not been implemented within further taxonomic or ecological analyses from within the Vestfold Hills. Though just one example, the need for revision is based upon a number of factors such as recent taxonomic updates (discussed below), as well as the reliance upon European floras, and other questionable Antarctic sources (when referenced to Kellogg and Kellogg 2002) used within Roberts and McMinn (1999) as guides for taxonomic references.

As a result of the “force fitting” of Antarctic taxa to European and/or American species, the “fine grained” taxonomic approach, as discussed in Vanormelingen et al. (2007), is a multi-faceted approach to diatom taxonomy. It combines LM and SEM, a larger reliance upon ecological data and a more restrictive, stringently defined morphological species concept (as seen in Mann 1999). A similar, concerted effort using the fine-grained taxonomy has been underway in both the Sub-Antarctic and Maritime Antarctic Regions, with a number of previously “cosmopolitan” taxa now being described as endemic Antarctic taxa (Zidarova et al. 2014, 2016).

Recent work has focused on revising the diatom flora of particular areas, such as the Sub-Antarctic Islands (Van de Vijver et al. 2002a) and the Maritime Antarctic (Zidarova et al. 2016). This has led to increased attention in addressing the problem of force-fitting upon Continental Antarctica, for example *Stauroneis* Ehrenberg (Van de Vijver et al. 2005) and *Eunotia* Ehrenberg (Van de Vijver et al. 2014a). Throughout East Antarctica, taxonomic revisions have focused on particular areas, such as the McMurdo Dry Valleys (Esposito et al. 2008), Bunger Hills and Lützow Holm Bay (Van de Vijver et al. 2012), and Larsemann Hills and Rauer Islands (Sabbe et al. 2003). Additionally, problematic genera often received their own focused studies, such as *Muelleria* (Frenguelli) Frenguelli (Spaulding and Stoermer 1997, Spaulding et al. 1999, Van de Vijver et al. 2010), *Nitzschia* Hassall (Hamsher et al. 2016), *Halamphora* (Cleve) Mereschkowsky (Van de Vijver et al. 2014b), and *Luticola* D.G.Mann (Kohler et al. 2015).

Diatoms in the Antarctic Realm: Ecology

Antarctic Realm diatoms occupy numerous habitats across both freshwater and terrestrial ecosystems (Jones 1996, Van de Vijver and Beyens 1999). These habitats include the sediments and benthic microbial mats of streams, pools and lakes (Ohtsuka et al. 2006, Gibson et al. 2006, Spaulding et al. 2010). Freshwater diatoms may exploit meltwater upon sea ice (Meguro et al. 1992), as well as cryoconite holes on glacial surfaces (Stanish et al. 2013). Terrestrial diatoms persist in soils with other algae as soil crusts (Borchhardt et al. 2017) as well as upon bryophytes (Zidarova et al. 2014).

The factors controlling diatom communities within Antarctica depend both on the type of community investigated, as well as the geographic location. Some present-day taxa from the

Antarctic Peninsula are absent within Continental Antarctica, and this maybe be through dispersal limitation or dynamic shifts in ranges, possibly brought about by geographic isolation, changing climate or extinction, as evidenced by sediment cores (Vyverman et al. 2007, 2010). Smaller scale studies have investigated local factors controlling diatom community structure. Within the Sub-Antarctic island of Ile de la Possession (Crozet Archipelago), terrestrial (soil) diatoms communities were structured by available moisture, phosphate and sulfate content (Van de Vijver et al. 2002b). Moss diatom community structure determined by water availability has been demonstrated in other Sub-Antarctic localities such as Prince Edward Islands, Heard Island, South Georgia and Kerguelen (Van de Vijver et al. 2004, 2008, Vinocur and Maidana 2010). Diatom communities on James Ross Island, located in the northern Weddell Sea off the Antarctic Peninsula, were structured by conductivity and nutrients, with clear distinctions between lake, seepage, and stream habitats (Kopalová et al. 2013). Moss diatom communities from the aforementioned localities in the Maritime Antarctic also appeared structured by water availability (Kopalová et al. 2014). However, there is a distinct gap in the ecological literature of terrestrial epiphytic diatoms associated with bryophytes and other vegetation within Continental Antarctica, despite the wealth of historic floristic surveys (Kellogg and Kellogg 2002).

Within the Maritime Antarctic Region, lake diatom communities on Livingston Island were structured by salinity and nutrient inputs from animal sources (Kopalová and Van de Vijver 2013). In the Continental Antarctic Region, benthic lake communities appear largely structured by salinity with the Rauer Islands (Hodgson et al. 2001) and Bunger Hills (Gibson et al. 2006). Elsewhere within East Antarctica, silicate and alkalinity within the Vestfold Hills (Roberts and McMinn 1999) and salinity and phosphate within the Windmill Islands (Roberts et al. 2001) have been reported to structure diatom communities.

Though much work has been done to revise the Continental Antarctic diatom flora, there are still gaps within the literature that need to be addressed due to their historical relevance to the study of Antarctic diatoms. These floristic and ecological data become especially pertinent as whole datasets are now being used within meta-analysis style publications akin to Terauds et al (2012) and Terauds and Lee (2016), and larger multidisciplinary reviews (see Convey et al. 2014, Convey and Peck 2019), which seek to inform larger themes of Antarctic microbial diversity, biogeography, and as an extension, microbial conservation upon the continent.

References

Abrantes, F., Lopes, C., Mix, A. and Pisias, N., 2007. Diatoms in southeast Pacific surface sediments reflect environmental properties. *Quaternary Science Reviews*, *26*(1–2), pp. 155–169.

Andersen, R.A., 1992. Diversity of eukaryotic algae. *Biodiversity & Conservation*, *1*(4), pp. 267–292.

Antonelli, M., Wetzel, C.E., Ector, L., Teuling, A.J. and Pfister, L., 2017. On the potential for terrestrial diatom communities and diatom indices to identify anthropic disturbance in soils. *Ecological Indicators*, *75*, pp. 73–81.

Armbrust, E.V., Berges, J.A., Bowler, C., Green, B.R., Martinez, D., Putnam, N.H., Zhou, S., Allen, A.E., Apt, K.E., Bechner, M. and Brzezinski, M.A., 2004. The genome of the diatom *Thalassiosira pseudonana*: ecology, evolution, and metabolism. *Science, 306*(5693), pp.79–86

Barkia, I., Li, C., Saari, N. and Witkowski, A., 2019. Nitzschia omanensis sp. nov., a new diatom species from the marine coast of Oman, characterized by valve morphology and molecular data. *FOTTEA*, *19*(2), pp.175–184.

Baas-Becking, LGM. 1934. *Geobiologie of inleiding tot de milieukunde* (No. 18–19). WP Van Stockum & Zoon, The Hague

Benito, X., Fritz, S.C., Steinitz- Kannan, M., Tapia, P.M., Kelly, M.A. and Lowell, T.V., 2018. Geo- climatic factors drive diatom community distribution in tropical South American freshwaters. *Journal of Ecology*, *106*(4), pp.1660–1672.

Blanco, S., Cejudo- Figueiras, C., Álvarez- Blanco, I., van Donk, E., Gross, E.M., Hansson, L.A., Irvine, K., Jeppesen, E., Kairesalo, T., Moss, B. and Nõges, T., 2014. Epiphytic diatoms along environmental gradients in western European shallow lakes. *CLEAN-Soil, Air, Water*, *42*(3), pp.229–235.

Blanco, S., Doucet, M., Fernández-Montiel, I., Gabilondo, R. and Bécares, E., 2017. Changes in the soil diatom community induced by experimental CO2 leakage. *International Journal of Greenhouse Gas Control*, *61*, pp.104–110.

Borchhardt, N., Schiefelbein, U., Abarca, N., Boy, J., Mikhailyuk, T., Sipman, H.J. and Karsten, U., 2017. Diversity of algae and lichens in biological soil crusts of Ardley and King George Islands, Antarctica. *Antarctic Science*, *29*(3), pp. 229–237.

Brazner, J.C., Danz, N.P., Trebitz, A.S., Niemi, G.J., Regal, R.R., Hollenhorst, T., Host, G.E., Reavie, E.D., Brown, T.N., Hanowski, J.M. and Johnston, C.A., 2007. Responsiveness of Great Lakes wetland indicators to human disturbances at multiple spatial scales: a multi-assemblage assessment. *Journal of Great Lakes Research*, *33*, pp.42–66.

Brooks, S.T., Jabour, J., Van Den Hoff, J. and Bergstrom, D.M., 2019. Our footprint on Antarctica competes with nature for rare ice-free land. *Nature Sustainability*, *2*(3), pp.185–190.

Brzezinski, M.A., Jones, J.L., Bidle, K.D. and Azam, F., 2003. The balance between silica production and silica dissolution in the sea: Insights from Monterey Bay, California, applied to the global data set. *Limnology and Oceanography*, *48*(5), pp.1846–1854.

Burki, F., 2014. The eukaryotic tree of life from a global phylogenomic perspective. *Cold Spring Harbor perspectives in biology*, *6*(5), p.a016147.

Burki, F., Roger, A.J., Brown, M.W. and Simpson, A.G., 2020. The new tree of eukaryotes. *Trends in ecology & evolution*, *35*(1), pp.43–55.

Carey, J.C. and Fulweiler, R.W., 2012. The terrestrial silica pump. *PLoS One*, *7*(12):e52932.

Chong, C.W., Pearce, D.A. and Convey, P., 2015. Emerging spatial patterns in Antarctic prokaryotes. *Frontiers in Microbiology*, *6*(1058), pp.1–14

Chown, S.L. and Convey, P., 2007. Spatial and temporal variability across life's hierarchies in the terrestrial Antarctic. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *362*(1488), pp.2307–2331.

Chown, S.L. and Brooks, C.M., 2019. The state and future of Antarctic environments in a global context. *Annual Review of Environment and Resources*, *44*, pp.1–30.

Convey, P., 2007. Influences on and origins of terrestrial biodiversity of the sub-Antarctic islands. In: *Papers and Proceedings of the Royal Society of Tasmania*, *141*(1), pp.83–93.

Convey, P. and Stevens, M.I., 2007. Antarctic biodiversity. *Science*, *317*(5846), pp.1877–1878.

Convey, P., Gibson, J.A., Hillenbrand, C.D., Hodgson, D.A., Pugh, P.J., Smellie, J.L. and Stevens, M.I., 2008. Antarctic terrestrial life-challenging the history of the frozen continent?. *Biological Reviews*, *83*(2), pp.103–117.

Convey, P., Stevens, M.I., Hodgson, D.A., Smellie, J.L., Hillenbrand, C.D., Barnes, D.K., Clarke, A., Pugh, P.J., Linse, K. and Cary, S.C., 2009. Exploring biological constraints on the glacial history of Antarctica. *Quaternary Science Reviews*, *28*(27–28), pp.3035–3048.

Convey, P., 2010. Terrestrial biodiversity in Antarctica-Recent advances and future challenges. *Polar Science*, *4*(2), pp.135–147.

Convey, P., Chown, S.L., Clarke, A., Barnes, D.K., Bokhorst, S., Cummings, V., Ducklow, H.W., Frati, F., Green, T.A., Gordon, S. and Griffiths, H.J., 2014. The spatial structure of Antarctic biodiversity. *Ecological Monographs*, *84*(2), pp.203–244.

Convey, P. and Peck, L.S., 2019. Antarctic environmental change and biological responses. *Science Advances*, *5*(11), p.eaaz0888.

Cox, E.J., 1995. Studies on the diatom genus *Navicula* Bory. VII. The identity and typification of *Navicula gregaria* Donkin, *N. cryptocephala* Kütz. and related taxa. *Diatom Research*, *10*(1), pp.91–111.

Cox, E.J., 1999. Variation in patterns of valve morphogenesis between representatives of six biraphid diatom genera (Bacillariophyceae). *Journal of Phycology*, *35*(6), pp.1297–1312.

Cox, E.J., 2012. Ontogeny, homology, and terminology—wall morphogenesis as an aid to character recognition and character state definition for pennate diatom systematics 1. *Journal of Phycology*, *48*(1), pp.1–31.

Cox, E.J., 2015. Coscinodiscophyceae, Mediophyceae, Fragilariophyceae, Bacillariophyceae (Diatoms). *Syllabus of Plant Families. Adolf Engler's Syllabus der Pflanzenfamilien, 13th Edition.*, *2*(1), pp.64–103.

Davies, B.J., Hambrey, M.J., Smellie, J.L., Carrivick, J.L. and Glasser, N.F., 2012. Antarctic Peninsula ice sheet evolution during the Cenozoic Era. *Quaternary Science Reviews*, *31*, pp.30–66.

Dodd, J.J., 1987. *The illustrated flora of Illinois: diatoms*. Southern Illinois University Press. Carbondale, 477pp.

Economo, E.P., Narula, N., Friedman, N.R., Weiser, M.D. and Guénard, B., 2018. Macroecology and macroevolution of the latitudinal diversity gradient in ants. *Nature communications*, *9*(1), pp.1–8.

Esposito, R.M.M., Spaulding, S.A., Mcknight, D.M., Van De Vijver, B., Kopalová K., Lubinski, D., Hall, B. and Whittaker, T., 2008. Inland diatoms from the McMurdo Dry Valleys and James Ross Island, Antarctica. *Botany*, *86*, pp.1378–1392.

Field, C.B., Behrenfeld, M.J., Randerson, J.T. and Falkowski, P., 1998. Primary production of the biosphere: integrating terrestrial and oceanic components. *Science*, *281*(5374), pp. 237–240.

Fierer, N. and Jackson, R.B., 2006. The diversity and biogeography of soil bacterial communities. *Proceedings of the National Academy of Sciences*, *103*(3), pp.626–631.

Finlay, B.J., 2002. Global dispersal of free-living microbial eukaryote species. *Science, 296*(5570), pp.1061–1063.

Fountain, A.G., Lyons, W.B., Burkins, M.B., Dana, G.L., Doran, P.T., Lewis, K.J., McKnight, D.M., Moorhead, D.L., Parsons, A.N., Priscu, J.C. and Wall, D.H., 1999. Physical controls on the Taylor Valley ecosystem, Antarctica. *Bioscience*, *49*(12), pp.961–971.

Futuyma, D. J. 2002. Evolution. 3rd Edition. Sinauer Associates, MA, USA. 656pp.

Geider, R.J., Delucia, E.H., Falkowski, P.G., Finzi, A.C., Grime, J.P., Grace, J., Kana, T.M., La Roche, J., Long, S.P., Osborne, B.A. and Platt, T., 2001. Primary productivity of planet earth: biological determinants and physical constraints in terrestrial and aquatic habitats. *Global Change Biology*, *7*(8), pp.849–882.

Gibbs, S.P., 1992. The evolution of algal chloroplasts. In: *Origins of plastids*, pp.107–121. Springer, Boston, MA.

Gibson, J.A., Roberts, D. and Van de Vijver, B., 2006. Salinity control of the distribution of diatoms in lakes of the Bunger Hills, East Antarctica. *Polar Biology*, *29*(8), pp.694–704.

Gordon, A.L., 1971. Antarctic polar front zone. *Antarctic Oceanology I, Antarctic Research Series*, *15*, pp.205–221.

Hale, M.S. and Mitchell, J.G., 2001. Functional morphology of diatom frustule microstructures: hydrodynamic control of Brownian particle diffusion and advection. *Aquatic Microbial Ecology*, *24*(3), pp.287–295

Hamsher, S., Kopalová, K., Kociolek, J.P., Zidarova, R. and Van de Vijver, B., 2016. The genus *Nitzschia* on the South Shetland Islands and James Ross Island. *Fottea, 16*(1), pp.79–102.

Hanson, C.A., Fuhrman, J.A., Horner-Devine, M.C. and Martiny, J.B., 2012. Beyond biogeographic patterns: processes shaping the microbial landscape. *Nature Reviews Microbiology*, *10*(7), pp.497–506.

Hodgson, D.A., Vyverman, W. and Sabbe, K., 2001. Limnology and biology of saline lakes in the Rauer Islands, eastern Antarctica. *Antarctic Science, 13*(3), pp.255–270.

Holdgate M.W. 1970. Antarctic Ecology. Academic Press, London. 998pp.

Holdgate, M.W., 1977. Life sciences-Terrestrial ecosystems in the Antarctic. *Philosophical Transactions of the Royal Society of London. B, Biological Sciences*, *279*(963), pp.5–25.

Hervé, V., Derr, J., Douady, S., Quinet, M., Moisan, L. and Lopez, P.J., 2012. Multiparametric analyses reveal the pH-dependence of silicon biomineralization in diatoms. *PloS one*, *7*(10), p.e46722.

Hughes, K.A., 2010. How committed are we to monitoring human impacts in Antarctica?. *Environmental Research Letters*, *5*(4), p.041001.

Hughes, K.A., Pertierra, L.R., Molina-Montenegro, M.A. and Convey, P., 2015. Biological invasions in terrestrial Antarctica: what is the current status and can we respond?. *Biodiversity and Conservation*, *24*(5), pp.1031–1055.

Jahn, R., Abarca, N., Gemeinholzer, B., Mora, D., Skibbe, O., Kulikovskiy, M., Gusev, E., Kusber, W.H. and Zimmermann, J., 2017. *Planothidium lanceolatum* and *Planothidium frequentissimum* reinvestigated with molecular methods and morphology: four new species and the taxonomic importance of the sinus and cavum. *Diatom Research*, *32*(1), pp.75–107.

Jahn, R., Kusber, W.H., Skibbe, O., Zimmermann, J., Van, A.T., Buczkó, K. and Abarca, N., 2019. *Gomphonella olivacea* (Bacillariophyceae)-a new phylogenetic position for a well-known taxon, its typification, new species and combinations. *Plant Ecology and Evolution*, *152*(2), pp.219–247.

Jones, V.J. 1996. The diversity, distribution and ecology of diatoms from Antarctic inland waters. *Biodiversity & Conservation 5*(11), pp.1433–1449.

Kaczmarska, I., Poulíčková, A., Sato, S., Edlund, M.B., Idei, M., Watanabe, T. and Mann, D.G., 2013. Proposals for a terminology for diatom sexual reproduction, auxospores and resting stages. *Diatom Research*, *28*(3), pp.263–294.

Keck, F., Franc, A. and Kahlert, M., 2018. Disentangling the processes driving the biogeography of freshwater diatoms: A multiscale approach. *Journal of Biogeography, 45*(7), pp.1582–1592

Kellogg, T.B. and Kellogg, D.E. (2002) Non-marine and littoral diatoms from Antarctic and subantarctic regions. Distribution and updated taxonomy. *Diatom monographs* 1, A.R.G Gantner Verlag K.G., 795 pp.

Kelly, M.G., Cazaubon, A., Coring, E., Dell'Uomo, A., Ector, L., Goldsmith, B., Guasch, H., Hürlimann, J., Jarlman, A., Kawecka, B. and Kwandrans, J., 1998. Recommendations for the routine sampling of diatoms for water quality assessments in Europe. *Journal of applied Phycology*, *10*(2), p.215.

Kociolek, J.P., Kopalová, K., Hamsher, S.E., Kohler, T.J., Van de Vijver, B., Convey, P. and McKnight, D.M., 2017. Freshwater diatom biogeography and the genus *Luticola*: an extreme case of endemism in Antarctica. *Polar Biology*, *40*(6), pp.1185–1196.

Kociolek, P.J., Williams, D.M., Stepanek, J., Liu, Q., Liu, Y., You, Q., Karthick, B. and Kulikovskiy, M., 2019. Rampant homoplasy and adaptive radiation in pennate diatoms. *Plant Ecology and Evolution*, *152*(2), pp.131–141.

Kohler, T.J., Kopalová, K., Van De Vijver, B. and Kociolek, J.P. 2015. The genus *Luticola* D.G.Mann (Bacillariophyta) from the McMurdo Sound Region, Antarctica, with the description of four new species. *Phytotaxa, 208*(2), pp.103–134.

Kopalová, K. and Van de Vijver, B., 2013. Structure and ecology of freshwater benthic diatom communities from Byers Peninsula, Livingston Island, South Shetland Islands. *Antarctic science*, *25*(2), pp.239–253.

Kopalová, K., Nedbalová, L., Nývlt, D., Elster, J. and Van de Vijver, B., 2013. Diversity, ecology and biogeography of the freshwater diatom communities from Ulu Peninsula (James Ross Island, NE Antarctic Peninsula). *Polar Biology*, *36*(7), pp.933–948.

Kopalová, K., Ochyra, R., Nedbalová, L. and Van de Vijver, B., 2014. Moss-inhabiting diatoms from two contrasting Maritime Antarctic islands. *Plant Ecology and Evolution*, *147*(1), pp.67–84.

Kulikovskiy, M.S., Andreeva, S.A., Gusev, E.S., Kuznetsova, I.V. and Annenkova, N.V., 2016a. Molecular phylogeny of monoraphid diatoms and raphe significance in evolution and taxonomy. *Biology bulletin*, *43*(5), pp.398–407.

Kulikovskiy, M., Lange-Bertalot, H., Annenkova, N., Gusev, E. and Kociolek, J.P., 2016b. Morphological and molecular evidence support description of two new diatom species from the genus *Ulnaria* in Lake Baikal. *Fottea, Olomouc*, *16*(1), pp.34–42.

Litchman, E. and Nguyen, B.L., 2008. Alkaline phosphatase activity as a function of internal phosphorus concentration in freshwater phytoplankton. *Journal of Phycology*, *44*(6), pp.1379–1383.

Livermore, R., Hillenbrand, C.D., Meredith, M. and Eagles, G., 2007. Drake Passage and Cenozoic climate: an open and shut case?. *Geochemistry, Geophysics, Geosystems*, *8*(1), pp.1–11.

Lewis, A.R., Marchant, D.R., Ashworth, A.C., Hedenäs, L., Hemming, S.R., Johnson, J.V., Leng, M.J., Machlus, M.L., Newton, A.E., Raine, J.I. and Willenbring, J.K., 2008. Mid-Miocene cooling and the extinction of tundra in continental Antarctica. *Proceedings of the National Academy of Sciences*, *105*(31), pp.10676–10680.

Lowe, R.L., 1974. *Environmental requirements and pollution tolerance of freshwater diatoms* (Vol. 1). National Environmental Research Center, Office of Research and Development, US Environmental Protection Agency, *EPA–670/4–74–005*, 333pp.

Mann, D.G., 1999. The species concept in diatoms. *Phycologia*, *38*(6), pp.437–495.

Mann, D.G. and Vanormelingen, P., 2013. An inordinate fondness? The number, distributions, and origins of diatom species. *Journal of eukaryotic microbiology*, *60*(4), pp.414–420.

Medlin, L., Kooistra, W.H.C.F. and Schmid, A.M., 2000. A review of the evolution of the diatoms-a total approach using molecules, morphology and geology. In: *The origin and early evolution of the diatoms: fossil, molecular and biogeographical approaches. A. Witkowski & J. Sieminska [eds.], Polish Academy of Sciences, Krakow, Poland,* pp. 13–35.

Medlin, L.K. and Kaczmarska, I., 2004. Evolution of the diatoms: V. Morphological and cytological support for the major clades and a taxonomic revision. *Phycologia*, *43*(3), pp.245–270.

Medlin, L.K., 2015. A timescale for diatom evolution based on four molecular markers: reassessment of ghost lineages and major steps defining diatom evolution. *Vie et milieu-life and environment*, *65*(4), pp.219–238.

Medlin, L.K., 2016. Evolution of the diatoms: major steps in their evolution and a review of the supporting molecular and morphological evidence. *Phycologia*, *55*(1), pp.79–103.

Medlin, L.K., 2018. Mini review: diatom species as seen through a molecular window. *Brazilian Journal of Botany*, *41*(2), pp.457–469.

Meguro, H., Fukushima, H. and Matsuda, T., 1992. Distribution of the two types of ice diatom communities in the Antarctic. *Journal of marine systems*, *3*(1–2), pp.163–168.

Mittelbach, G.G., Schemske, D.W., Cornell, H.V., Allen, A.P., Brown, J.M., Bush, M.B., Harrison, S.P., Hurlbert, A.H., Knowlton, N., Lessios, H.A. and McCain, C.M., 2007. Evolution and the latitudinal diversity gradient: speciation, extinction and biogeography. *Ecology letters*, *10*(4), pp.315–331.

Nakov, T., Beaulieu, J.M. and Alverson, A.J., 2019. Diatoms diversify and turn over faster in freshwater than marine environments. *Evolution*, *73*, pp.2497–2511

Nelson, D.M., Tréguer, P., Brzezinski, M.A., Leynaert, A. and Quéguiner, B., 1995. Production and dissolution of biogenic silica in the ocean: revised global estimates, comparison with regional data and relationship to biogenic sedimentation. *Global Biogeochemical Cycles*, *9*(3), pp.359–372.

Neustupa, J., Veselá, J. and Šťastný, J., 2013. Differential cell size structure of desmids and diatoms in the phytobenthos of peatlands. *Hydrobiologia*, *709*(1), pp.159–171.

Ohtsuka, T., Kudoh, S., Imura, S. and Ohtani, S., 2006. Diatoms composing benthic microbial mats in freshwater lakes of Skarvsnes ice-free area, East Antarctica. *Polar Bioscience, 20,* pp.113–130

Pankow, H., Haendel, D. and Richter, W., 1991. Die Algenflora der Schirmacheroase (Ostantarktika). *Nova Hedwigia*, *Beihefte 103*, pp.1–195.

Pappas, J., Kociolek, P. and Stoermer, E.F., 2014. Quantitative morphometric methods in diatom research. *Nova Hewigia, Beiheft 143*, pp.281–306

Pianka, E.R., 1966. Latitudinal gradients in species diversity: a review of concepts. *The American Naturalist*, *100*(910), pp.33–46.

Pickard, J. and Seppelt, R.D., 1984. Phytogeography of Antarctica. *Journal of Biogeography*, *11*(2), pp.83–102.

Pinseel, E., Harper, M., Wolfe, A.P., Lewis, A.R., Dickinson, W., Ashworth, A.C., Sabbe, K., Van de Vijver, B., Verleyen, E. and Vyverman, W., 2016. The Miocene freshwater diatom flora of the Antarctic Continent. In: *24th International Diatom symposium*, pp. 122–122.

Pinseel, E., Kulichová, J., Scharfen, V., Urbánková, P., Van de Vijver, B. and Vyverman, W., 2019. Extensive Cryptic diversity in the terrestrial diatom *Pinnularia borealis* (Bacillariophyceae). *Protist*, *170*(2), pp.121–140.

Pinseel, E., Janssens, S.B., Verleyen, E., Vanormelingen, P., Kohler, T.J., Biersma, E.M., Sabbe, K., Van de Vijver, B. and Vyverman, W., 2020. Global radiation in a rare biosphere soil diatom. *Nature Communications*, *11*(1), pp.1–12.

Potapova, M.G. and Charles, D.F., 2002. Benthic diatoms in USA rivers: distributions along spatial and environmental gradients. *Journal of biogeography*, *29*(2), pp.167–187.

Potapova, M. and Charles, D.F., 2003. Distribution of benthic diatoms in US rivers in relation to conductivity and ionic composition. *Freshwater biology*, *48*(8), pp.1311–1328.

Poulíčková, A., Hájková, P., Krenková, P. and Hájek, M., 2004. Distribution of diatoms and bryophytes on linear transects through spring fens. *Nova Hedwigia*, *78*(3–4), pp.411–424.

Poulíčková, A. and Mann, D.G., 2019. Diatom Sexual Reproduction and Life Cycles. In: *Diatoms: Fundamentals and Applications*, pp.245–272.

Raes, E.J., Bodrossy, L., van de Kamp, J., Bissett, A. and Waite, A.M., 2018. Marine bacterial richness increases towards higher latitudes in the eastern Indian Ocean. *Limnology and Oceanography Letters*, *3*(1), pp.10–19.

Reynolds, C.S., 1984. *The ecology of freshwater phytoplankton*. Cambridge University Press. 384pp.

Roberts, D. and McMinn, A., 1999. Diatoms of the saline lakes of the Vestfold Hills, Antarctica. *Bibliotheca Diatomologica*, *44*, pp.1–82.

Roberts, D., McMinn, A., Johnston, N., Gore, D.B., Melles, M. and Cremer, H., 2001. An analysis of the limnology and sedimentary diatom flora of fourteen lakes and ponds from the Windmill Islands, East Antarctica. *Antarctic Science*, *13*(4), pp.410–419.

Ross, R., Cox, E.J., Karayeva, N.I., Mann, D.G., Paddock, T.B.B., Simonsen, R. and Sims, P.A., 1979. An amended terminology for the siliceous components of the diatom cell. *Nova Hedwigia, Beiheft, 64*, pp. 513–533

Round, F.E., Crawford, R.M. and Mann, D.G., 2007. *Diatoms: biology and morphology of the genera*. Cambridge university press. 747pp.

Ruck, E.C. and Theriot, E.C., 2011. Origin and evolution of the canal raphe system in diatoms. *Protist*, *162*(5), pp.723–737.

Sabbe, K., Verleyen, E., Hodgson, D.A., Vanhoutte, K. and Vyverman, W., 2003. Benthic diatom flora of freshwater and saline lakes in the Larsemann Hills and Rauer Islands, East-Antarctica. *Antarctic Science*, *15*(2), pp.227–248.

Schlosser, E., Manning, K.W., Powers, J.G., Duda, M.G., Birnbaum, G. and Fujita, K., 2010. Characteristics of high- precipitation events in Dronning Maud Land, Antarctica. *Journal of Geophysical Research: Atmospheres*, *115*(D14107), pp.1–14.

Selkirk, P.M., 2007. The nature and importance of the sub-Antarctic. In: *Papers and Proceedings of the Royal Society of Tasmania*, *141*(1), pp.1–6.

Sims, P.A., Mann, D.G. and Medlin, L.K., 2006. Evolution of the diatoms: insights from fossil, biological and molecular data. *Phycologia*, *45*(4), pp.361–402.

Soininen, J., Paavola, R. and Muotka, T., 2004. Benthic diatom communities in boreal streams: community structure in relation to environmental and spatial gradients. *Ecography*, *27*(3), pp.330–342.

Soininen, J., 2007. Environmental and spatial control of freshwater diatoms—a review. *Diatom research*, *22*(2), pp.473–490.

Souffreau, C., Vanormelingen, P., Verleyen, E., Sabbe, K. and Vyverman, W., 2010. Tolerance of benthic diatoms from temperate aquatic and terrestrial habitats to experimental desiccation and temperature stress. *Phycologia*, *49*(4), pp.309–324.

Souffreau, C., Vanormelingen, P., Sabbe, K. and Vyverman, W., 2013a. Tolerance of resting cells of freshwater and terrestrial benthic diatoms to experimental desiccation and freezing is habitat dependent. *Phycologia*, *52*(3), pp.246–255.

Souffreau, C., Vanormelingen, P., Van de Vijver, B., Isheva, T., Verleyen, E., Sabbe, K. and Vyverman, W., 2013b. Molecular evidence for distinct Antarctic lineages in the cosmopolitan terrestrial diatoms *Pinnularia borealis* and *Hantzschia amphioxys. Protist, 164*(1), pp.101–115

Sorhannus, U., 2007. A nuclear-encoded small-subunit ribosomal RNA timescale for diatom evolution. *Marine Micropaleontology*, *65*(1–2), pp.1–12.

Spaulding, S.A. and Stoermer, E.F., 1997. Taxonomy and distribution of the genus *Muelleria* Frenguelli. *Diatom research*, *12*(1), pp.95–113

Spaulding, S.A., Kociolek, J.P. and Wong, D., 1999. A taxonomic and systematic revision of the genus *Muelleria* (Bacillariophyta). *Phycologia*, *38*(4), pp.314–341.

Spaulding, S.A., Van de Vijver, B., Hodgson, D.A., McKnight, D.M., Verleyen, E. and Stanish, L., 2010. Diatoms as indicators of environmental change in Antarctic and subantarctic freshwaters. In: *The diatoms: applications for the environmental and earth sciences*, pp.267–283.

Stanish, L.F., Bagshaw, E.A., McKnight, D.M., Fountain, A.G. and Tranter, M., 2013. Environmental factors influencing diatom communities in Antarctic cryoconite holes. *Environmental Research Letters*, *8*(4), pp.045006.

Sterner, R.W. and Elser, J.J., 2002. *Ecological stoichiometry: the biology of elements from molecules to the biosphere*. Princeton university press. 464pp.

Stevenson, R.J., Bothwell, M.L., Lowe, R.L. and Thorp, J.H., 1996. *Algal ecology: Freshwater benthic ecosystem*. Academic press. 753pp.

Telford, R.J., Vandvik, V. and Birks, H.J.B., 2006. Dispersal limitations matter for microbial morphospecies. *Science*, *312*(5776), pp.1015–1015.

Terauds, A., Chown, S.L., Morgan, F., J. Peat, H., Watts, D.J., Keys, H., Convey, P. and Bergstrom, D.M., 2012. Conservation biogeography of the Antarctic. *Diversity and Distributions*, *18*(7), pp.726–741.

Terauds, A. and Lee, J.R., 2016. Antarctic biogeography revisited: updating the Antarctic Conservation Biogeographic Regions. *Diversity and Distributions*, *22*(8), pp.836–840.

Tréguer, P., Bowler, C., Moriceau, B., Dutkiewicz, S., Gehlen, M., Aumont, O., Bittner, L., Dugdale, R., Finkel, Z., Iudicone, D. and Jahn, O., 2018. Influence of diatom diversity on the ocean biological carbon pump. *Nature Geoscience*, *11*(1), pp.27–37.

Tyler, P.A. 1996. Endemism in freshwater algae, with special reference to the Australian region. In: *Biogeography of freshwater algae* (Ed. J. Kristiansen). *Hydrobiologia* 336: 127–135. Springer, Dordrecht.

van Kerckvoorde, A., Trappeniers, K., Nijs, I. and Beyens, L., 2000. Terrestrial soil diatom assemblages from different vegetation types in Zackenberg (Northeast Greenland). *Polar Biology*, *23*(6), pp.392–400.

Van de Vijver, B. and Beyens, L., 1999. Freshwater diatoms from Ile de la Possession (Crozet Archipelago, sub-Antarctica): an ecological assessment. *Polar Biology*, *22*(3), pp.178–188.

Van de Vijver, B., Frenot, Y. and Beyens, L., 2002a. Freshwater diatoms from Ile de la Possession (Crozet Archipelago, Subantarctica). *Bibliotheca Diatomologica* 46, pp.1–412.

Van de Vijver, B., Ledeganck, P. and Beyens, L., 2002b. Soil diatom communities from Ile de la Possession (Crozet, sub-Antarctica). *Polar biology*, *25*(10), pp.721–72

Van de Vijver, B., Beyens, L., Vincke, S. and Gremmen, N.J., 2004. Moss-inhabiting diatom communities from Heard Island, sub-Antarctic. *Polar biology, 27*(9), pp.532–543.

Van de Vijver, B., Gremmen, N.J. and Beyens, L., 2005. The genus *Stauroneis* (Bacillariophyceae) in the Antarctic region. *Journal of Biogeography*, *32*(10), pp.1791–1798.

Van de Vijver, B., Gremmen, N. and Smith, V., 2008. Diatom communities from the sub-Antarctic Prince Edward Islands: diversity and distribution patterns. *Polar biology*, *31*(7), pp.795–808.

Van de Vijver, B., Mataloni, G., Stanish, L. and Spaulding, S.A., 2010. New and interesting species of the genus *Muelleria* (Bacillariophyta) from the Antarctic region and South Africa. *Phycologia, 49*(1), pp.22–41.

Van de Vijver, B., Tavernier, I., Kellogg, T.B., Gibson J., Verleyen, E., Vyverman, W. and Sabbe, K., 2012. Revision of type materials of Antarctic diatom species (Bacillariophyta) described by West & West (1911), with the description of two new species. *Fottea, 12*(2), pp.149–169.

Van de Vijver, B., de Haan, M. and Lange-Bertalot, H., 2014a. Revision of the genus *Eunotia* (Bacillariophyta) in the Antarctic Region. *Plant Ecology and Evolution*, *147*(2), pp.256–284.

Van de Vijver, B., Kopalová, K., Zidarova, R. and Levkov, Z., 2014b. Revision of the genus *Halamphora* (Bacillariophyta) in the Antarctic Region. *Plant Ecology and Evolution, 147*(3), pp.374–391.

Vanormelingen, P., Verleyen, E. and Vyverman, W., 2007. The diversity and distribution of diatoms: from cosmopolitanism to narrow endemism. In: *Protist Diversity and Geographical Distribution*, pp.159–171.

Vellend, M., 2010. Conceptual synthesis in community ecology. *The Quarterly review of biology*, *85*(2), pp.183–206.

Verleyen, E., Hodgson, D.A., Sabbe, K. and Vyverman, W., 2004. Late Quaternary deglaciation and climate history of the Larsemann Hills (East Antarctica). *Journal of Quaternary Science*, *19*(4), pp.361–375.

Verleyen, E., Vyverman, W., Sterken, M., Hodgson, D.A., De Wever, A., Juggins, S., Van de Vijver, B., Jones, V.J., Vanormelingen, P., Roberts, D. and Flower, R., 2009. The importance of dispersal related and local factors in shaping the taxonomic structure of diatom metacommunities. *Oikos*, *118*(8), pp.1239–1249.

Veselá, J. and Johansen, J.R., 2009. The diatom flora of ephemeral headwater streams in the Elbsandsteingebirge region of the Czech Republic. *Diatom research*, *24*(2), pp.443–477.

Vilmi, A., Tolonen, K.T., Karjalainen, S.M. and Heino, J., 2017. Metacommunity structuring in a highly-connected aquatic system: effects of dispersal, abiotic environment and grazing pressure on microalgal guilds. *Hydrobiologia*, *790*(1), pp.125–140.

Vinocur, A. and Maidana, N.I., 2010. Spatial and temporal variations in moss-inhabiting summer diatom communities from Potter Peninsula (King George Island, Antarctica). *Polar Biology*, *33*(4), pp.443–455.

Vyverman, W., Verleyen, E., Sabbe, K., Vanhoutte, K., Sterken, M., Hodgson, D.A., Mann, D.G., Juggins, S., Vijver, B.V.D., Jones, V. and Flower, R., 2007. Historical processes constrain patterns in global diatom diversity. *Ecology*, *88*(8), pp.1924–1931.

Vyverman, W., Verleyen, E., Wilmotte, A., Hodgson, D.A., Willems, A., Peeters, K., Van de Vijver, B., De Wever, A., Leliaert, F. and Sabbe, K., 2010. Evidence for widespread endemism among Antarctic micro-organisms. *Polar Science*, *4*(2), pp.103–113.

Werner, D. Ed., 1977. *The Biology of Diatoms*. Botanical Monographs 13. Univ. of California Press. 498pp

West, W. and West, G.S. 1911. Freshwater algae. *British Antarctic Expedition (1907–1909) Science Report, Biology 1*, pp.263–298.

Wetzel, R. G. 2001. Limnology: Lake and River Ecosystems. 3rd Edition. San Diego, CA. Academic Press. 1006pp.

Wiens, J.J. and Donoghue, M.J., 2004. Historical biogeography, ecology and species richness. *Trends in ecology & evolution*, *19*(12), pp.639–644.

Winder, M., Reuter, J.E. and Schladow, S.G., 2009. Lake warming favours small-sized planktonic diatom species. *Proceedings of the Royal Society B: Biological Sciences*, *276*(1656), pp.427–435.

Wood, R.J., Mitrovic, S.M., Lim, R.P., Warne, M.S.J., Dunlop, J. and Kefford, B.J., 2019. Benthic diatoms as indicators of herbicide toxicity in rivers-A new SPEcies At Risk (SPEARherbicides) index. *Ecological Indicators*, *99*, pp.203–213.

Yeung, L.Y., Berelson, W.M., Young, E.D., Prokopenko, M.G., Rollins, N., Coles, V.J., Montoya, J.P., Carpenter, E.J., Steinberg, D.K., Foster, R.A. and Capone, D.G., 2012. Impact of diatom- diazotroph associations on carbon export in the Amazon River plume. *Geophysical Research Letters*, *39*(L18609), pp.1–6.

Zidarova, R., Levkov, Z. and Van de Vijver, B., 2014. Four new *Luticola* taxa (Bacillariophyta) from Maritime Antarctica. *Phytotaxa*, *170*(3), pp.155–168.

Zidarova R., Kopalová K. and Van de Vijver B., 2016: Diatoms from the Antarctic Region. I: Maritime Antarctica. *Iconographia Diatomologica*. 24. 509pp.

Zorzal- Almeida, S., Soininen, J., Bini, L.M. and Bicudo, D.C., 2017. Local environment and connectivity are the main drivers of diatom species composition and trait variation in a set of tropical reservoirs. *Freshwater Biology*, *62*(9), pp.1551–1563.

Chapter 2

Sabbea gen. nov., a new diatom genus (Bacillariophyta) from continental Antarctica

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Sabbea gen. nov., a new diatom genus (Bacillariophyta) from continental Antarctica

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Abstract

The non-marine diatom flora of the Antarctic Continent includes several endemic taxa recorded over the past 100 years. One of these taxa, *Navicula adminensis* D.Roberts & McMinn*,* was described from the Vestfold Hills, East Antarctica. Detailed light and scanning electron microscopy observations have shown that based on its morphological features, the species does not belong to the genus *Navicula sensu stricto*. To determine the most closely related genera to *N. adminensis*, the morphological features of *Adlafia*, *Kobayasiella*, *Envekadea*, *Stenoneis*, *Berkeleya*, *Climaconeis,* and *Parlibellus* were compared with those of *N. adminensis*. Although each of these genera shows one or more similar features, none of them accommodates the salient morphological characteristics of *N. adminensis*. Therefore, a new genus, *Sabbea gen. nov.*, is herein described, and *Navicula adminensis* is formally transferred to the new genus as *Sabbea adminensis comb. nov*. The genus *Sabbea* is characterized by uniseriate striae composed of small, rounded areolae occluded externally by individual hymenes, a rather simple raphe structure with straight, short proximal ends and short terminal raphe fissures, open girdle bands with double perforation and a very shallow mantle.

Keywords: Bacillariophyta, Cape Royds, East Antarctica, McMurdo Dry Valleys, new genus, Vestfold Hills

Introduction

At the beginning of the 20th century, British, Belgian, Danish, and German expeditions into the Antarctic provided the world with the first glimpses of diatoms from continental Antarctica (Holmboe 1902, Van Heurck 1909, West & West 1911, Fritsch 1912, 1917, Carlson 1913, Brown 1920). These primary works were later expanded upon by other authors, whom either examined intraspecific variation within a selection of these pennate diatoms (such as Kobayashi 1963, 1965), or published detailed floras of particular regions (e.g., Fukushima 1963, 1966, Cremer *et al*. 2003). Yet, many of these reported diatoms were still identified as European or cosmopolitan taxa. In 2002, Kellogg and Kellogg compiled a list of all non-marine diatom records within the Antarctic Region based on data reported in over 300 publications, and found the majority belonged to cosmopolitan taxa. Given that recent taxonomic revisions of the diatom flora from the sub-Antarctic islands and the Maritime Antarctic Region have indicated that the cosmopolitan nature of non-marine Antarctic diatoms is overestimated (Van de Vijver *et al.* 2002, Zidarova *et al.* 2016, and references therein) and originates as a result of 'force-fitting' species into American or European names (Jones 1996, Tyler 1996, Sabbe *et al.* 2003), it is likely that the same holds true for diatoms of the Antarctic continental Region as well.

Many more recent works have revealed new diatom species endemic to continental Antarctica which have been historically overlooked or misidentified as cosmopolitan/European taxa. For example, Esposito *et al.* (2008) described four new species from the McMurdo Dry Valleys, and Van de Vijver *et al.* (2012) described *Luticola pseudomurrayi* Van de Vijver & Tavernier *in* Van de Vijver *et al.* (2012: 164) and *Chamaepinnularia gibsonii* Van de Vijver *in* Van de

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Vijver *et al.* (2012: 166) from the Bunger Hills and Lützow Holm Bay, both situated in East Antarctica. Revisions of problematic genera have also been treated, as in the case of *Muelleria* (Frenguelli 1924: 256) Frenguelli (1945: 172, Spaulding & Stoermer 1997, Spaulding *et al.* 1999, Van de Vijver *et al.* 2010), *Nitzschia* Hassall (1845: 435, Hamsher *et al.* 2016), *Halamphora* (Cleve 1895: 117) Levkov (2009: 165, Van de Vijver *et al.* 2014), and *Luticola* D.G.Mann *in* Round *et al.* (1990: 670, Kohler *et al.* 2015). These studies collectively suggest that the endemic diversity of continental Antarctica is similarly underestimated with more species awaiting description, bringing results in line with those observed for the Maritime Antarctic and Sub-Antarctic Islands.

Despite this recent progress, problematic taxa still remain in areas of high scientific significance, such as the McMurdo Sound Region and the Vestfold Hills of East Antarctica. In 1911, W. and G.S. West reported a small diatom species they identified as *Navicula perlepida* Grunow (1884: 474) from the lakes at Cape Royds, Ross Island. However, it was not illustrated, and given the only modest written description, it is difficult to say for certain what diatom they saw in their microscope. Despite this, a diatom presumed to be the same species is still reported from Ross Island (Sakaeva *et al.* 2016) and the adjacent McMurdo Dry Valleys (Whittaker *et al.* 2008) in modern times and is known to be accommodated by the wrong genus, though the correct one remains in doubt (Esposito *et al.* 2008). Across the continent, Roberts & McMinn, in a series of publications, analyzed the diatom flora from the saline lakes of the Vestfold Hills, developed transfer functions for salinity, and described two *Navicula* species (Roberts & McMinn 1999 and references therein). One of these, *N. adminii* D.Roberts & McMinn (1999: 27), was described from the sediments of Lake Admin (Vestfold Hills). The species is characterized by lightly silicified valves, a simple raphe system and an extremely fine striation pattern not discernible in light microscopy (LM). The description of the new species was accompanied by several scanning electron microscopy (SEM) observations, showing a strong similarity to those later published in Esposito *et al.* (2008) from McMurdo Sound. Given that this taxon is distributed in regions of particular scientific interest, as well as its potential historic and ecological indicator value, we here investigate the taxonomic placement and ecology of this *Navicula* s.l. species. As a first step, Van de Vijver & Kusber (2018) corrected the erroneous typification (holotype and isotype originating from different lakes) and changed the name to *N. adminensis* (Van de Vijver & Kusber 2018: 1). In this work, a re-analysis of the type material of Roberts & McMinn (1999) under LM (and in combination with their published SEM pictures), together with new and published SEM observations from Ross Island and the McMurdo Dry Valleys, has resulted in new observational data on *N. adminensis* that challenge its placement within the genus *Navicula* Bory (1822: 128) as it was redefined by Cox (1979). Since the combination of morphological features observed in *N. adminensis* is unique and is not found in any described genus worldwide, a new genus, *Sabbea* Van de Vijver, Bishop & Kopalová *gen. nov.*, is proposed for this species.

Materials & Methods

Site descriptions

Samples from the Vestfold Hills and the McMurdo Sound Region of the Antarctic Continent were investigated in the present study. Table 1 lists all samples with some measured physico-chemical data.

The Vestfold Hills (68°25'–68°40'S, 77°50'–78°35'E) form an ice-free area along the Ingrid Christensen Coast, Princess Elizabeth Land, eastern Antarctica. The Vestfold Hills contain over 300 lakes, ranging in salinity from fresh to hypersaline, across an area of 400 km^2 (Roberts & McMinn 1999). They display a marked influence from the sea, and consequently salinity and silicate appear to structure the diatom flora (Roberts & McMinn, 1996). In a study of the Vestfold Hills lakes Roberts & McMinn (1999) reported on samples collected from surface sediments (0–2cm) from the deepest point of the lakes (n=33). Admin Lake, which has a maximum depth of 6 m, is located at an elevation of nearly 9 m above sea level (Roberts & McMinn 1999, Gibson 1999). Sediment sub-samples were then prepared in triplicate for diatom analysis. One of the sets of replicate microscope slides (n=30) was used in the current analysis. From these, slide "AD-3", from Admin lake was used to examine the population of *N. adminensis* from the type locality. Unfortunately, the original material, as well as the first and second replicate slide collections, no longer remain (A. McMinn, pers. comm.), which means that the holotype slide is lost and therefore, a lectotype slide must be designated (Turland et al. 2018, article 9.3).

The McMurdo Sound Region is located in Victoria Land, East Antarctica, and includes the area between the Transantarctic Mountains and the Ross Sea. Ross Island is 2,460 km^2 in area and surrounded by the Ross Sea and McMurdo Sound. Cape Royds, situated on western Ross Island, is an ice-free, coastal area (~13 km^2) between Mt. Erebus and the Ross Sea. Five permanent, generally ice-covered lakes are found at Cape Royds along with more than

TABle 1. Examined populations of *Navicula adminensis*. Data compiled from Roberts & McMinn 1999 and MCM LTER (http://huey.colorado.edu/diatoms/)

Sample ID/Accession Number	Locality	Lake ID	Sample type	Collection Date	South	East	pH	Salinity range (%)	Specific conductance (µ)
AD-3 (BR-collection)	Vestfold Hills	Admin Lake	Benthic sediments	Nov/Dec-1992	68°27.2	78°16.5	na	14.8 - 17.5	na
2488 (INSTAAR Diatom coll.)	Cape Royds	Blue Lake, north lobe	Benthic microbial mat	24-Jan-2013	77°32’ 38.4”	166°10’ 35.87”	6.7	na	820
2462 (INSTAAR Diatom coll.)	Cape Royds	Clear Lake	Benthic microbial mat	24-Jan-2013	77°32’ 31.85”	166°9’ 41.15”	7.4	na	845
2464 (INSTAAR Diatom coll.)	Cape Royds	Clear Lake	Benthic microbial mat	24-Jan-2013	77°32’ 31.85”	166°9’ 41.15”	7.4	na	845
359 (INSTAAR Diatom coll.)	McMurdo Dry Valleys	Lake Fryxell	Benthic sediments (16 cm depth)	1-Jan-2003	77°37’ 0”	163°11’ 0”	7.8 - 8.3†	na	160 - 3900‡
364 (INSTAAR Diatom coll.)	McMurdo Dry Valleys	Lake Fryxell	Benthic sediments (50 cm depth)	1-Jan-2003	77°37’ 0”	163°11’ 0”	7.8 - 8.3†	na	160 - 3900‡
390 (INSTAAR Diatom coll.)	McMurdo Dry Valleys	Lake Fryxell	Benthic sediments (111 cm depth)	1-Jan-1999	77°37’ 0”	163°11’ 0”	7.8 - 8.3†	na	160 - 3900‡

† pH measured up to 7 m water column depth by Lawrence and Hendy (1985)

‡ Specific conductance measured from 5 m - 7 m water column depth by Aiken et al. (1996)

10 ephemeral ponds. Of these, Blue Lake, which is the farthest from the sea, is characterized by north (0.4 km^2) and south (0.6 km^2) lobes. Benthic mat samples and water chemistry from Cape Royds lakes were collected in January 2013 (Sakaeva *et al.* 2016) as part of the McMurdo Dry Valleys Long-Term Ecological Research (MCM LTER) project. From the aforementioned data, 3 benthic mat populations from 2 lakes on Cape Royds were investigated: 2 from Clear Lake (INSTAAR, Univ. of Colorado accession numbers : 2462 & 2464) and 1 from Blue Lake (north lobe) (INSTAAR, Univ. of Colorado accession number: 2488).

The McMurdo Dry Valleys (~4,800 km^2) is the largest ice-free region of Antarctica. In Taylor Valley, Lake Fryxell (7.8 km^2) is 6.5 km inland from McMurdo Sound, up to 20 m deep, fed by glacial meltwater, and is ice-covered year-round, with near-shore "moat" regions becoming ice-free during the summer. Three samples originated from the F2 core from Lake Fryxell (INSTAAR, Univ. of Colorado accession numbers: 259, 364, and 390, respectively), analyzed by Whitaker *et al.* (2008) for inferring Holocene lake levels in Lake Fryxell. Furthermore, Esposito *et al.* (2008) examined 2 diatom specimens (INSTAAR, Univ. of Colorado accession numbers: 364 and 390, respectively), under both LM and SEM, in an effort to describe the diatom flora of the McMurdo Dry Valleys.

Sample preparation and analyses

Blue lake (INSTAAR, Univ. of Colorado accession number: 2488) and Clear Lake (INSTAAR, Univ. of Colorado accession numbers: 2462 and 2464) samples were prepared for LM observation following the method described in van der Werff (1955). Small parts of the sample were cleaned by adding 37% H_2O_2 and heating to 80°C for about 1h. The reaction was completed by addition of $KMnO_4$. Following digestion and centrifugation (three times 10 minutes at 3,700 x g), cleaned material was diluted with distilled water to avoid excessive concentrations of diatom valves on the slides. Cleaned diatom material was mounted in Naphrax®. The slides were analyzed using an Olympus BX53 bright field microscope and the Olympus UC30 Imaging System. Samples and slides are stored at the BR-collection (Botanic Garden Meise, Belgium). For SEM analyses, specifically the Blue Lake samples, parts of the oxidized suspensions were filtered through a 1-µm Isopore™ polycarbonate membrane filter (Merck Millipore). The stubs were sputter-coated with a Gold-Palladium layer of 20 nm and studied on a ZEISS Ultra SEM microscope at 3 kV (Natural History Museum London, UK).

Diatom terminology follows Ross *et al.* (1979) (stria/areola structure) and Round *et al.* (1990) (raphe structure). The morphology of the new genus was compared with the ultrastructure of similar genera described worldwide: *Adlafia* Lange-Bertalot *in* Moser *et al.* (1998: 87) (Moser *et al.* 1998, Lange-Bertalot 2001), *Navicula*, *Kobayasiella* Lange-Bertalot *in* Lange-Bertalot & Genkal (1999: 272) (Lange-Bertalot 1996, 1999) *Envekadea* Van de Vijver *et al. in* Gligora *et al.* (2009: 136) (Gligora *et al.* 2009), *Climaconeis* Grunow (1862: 107) (Cox 1982, Prasad *et al.* 2000, Prasad 2003), *Berkeleya* Greville (1827: 294) (Cox 1975), *Stenoneis* Cleve (1894: 123) (Poulin 1990) and *Parlibellus* E.J.Cox (1988: 19) (Cox 1988).

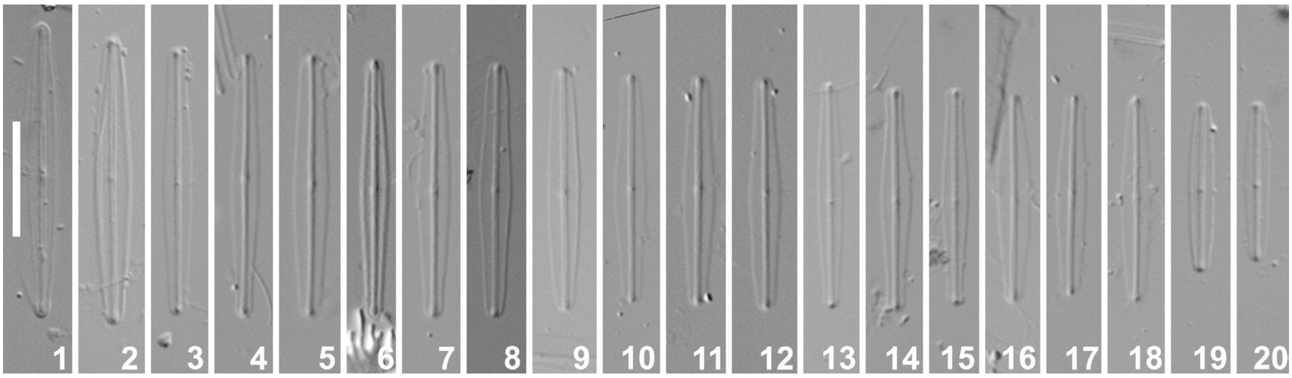
Results

***Navicula adminensis* D.Roberts *et* McMinn *in* Van de Vijver *et* Kusber (2018)** (Figs 1–29)

Replaced name: *Navicula adminii* D.Roberts & McMinn (1999)

LM (Figs 1–20):—Valves very weakly silicified, often not well-visible in LM. Valves linear-lanceolate with rhombic-convex margins and protracted, broadly rounded, often weakly subcapitate apices. Longer specimens usually with more elongated apices. Valve dimensions from the type population at Admin Lake within the Vestfold Hills: (n=50): length 14–30 µm, width 2–3 µm. Raphe-sternum clearly visible with the raphe positioned in the middle of the sternum. Proximal raphe ends hardly visible. Transapical striae not discernible in LM. **SeM (Figs 21–29):**—Frustules very thin. Girdle composed of several, open copulae, each with a double row of rounded to transapically elongated poroids (Figs 21, 22). Striae parallel to very weakly radiate throughout, composed of very small, rounded areolae, 70–80 in 10 µm (Figs 21, 24). Striae continuing without interruption from valve face onto a very shallow mantle. Around the apices, short striae composed of 1–2 areolae continuing without interruption (Fig. 26). Areolae, ca. 110 in 10 µm, covered externally by small hymenes (Fig. 23). When eroded, areolae showing a relatively large range in pore diameter (Fig. 25). External raphe branches straight, located on a weakly thickened raphe-sternum. On both sides of the raphe-sternum forming very weakly raised ribs (Figs 25, 26). Proximal raphe ends close to each other, straight, simple (Fig. 25). Terminal raphe fissures absent (Fig. 26). Internally, raphe fissures running on a raised raphe-sternum (Fig. 27).

Proximal raphe ends straight, simple (Fig. 28). Distal raphe ends terminating in very weakly developed helictoglossae (Fig. 29). Virgae usually broader than the striae (Fig. 28).



FIguReS 1–20. *Sabbea adminensis* (D.Roberts & McMinn) Van de Vijver, Bishop & Kopalová *nov. comb.* All valves were imaged from the Vestfold Hills type population on slide "AD-3". LM photographs of valves in diminishing size range. Scale bar represents 10 µm.

Remarks:—Three benthic mat populations from 2 lakes on Cape Royds were investigated: two from Clear Lake and one from Blue Lake. Table 2 shows valve length and valve width ranges for the investigated populations. From Clear Lake, (INSTAAR, Univ. of Colorado accession 2462) (*n* = 20) valve length ranged from 19.7 to 25.9 µm (x̄ = 23 ± 2 µm) and mid-breadth from 2.0 to 3.1 µm (x̄ = 2.8 ± 0.3 µm), and (INSTAAR, Univ. of Colorado accession 2464) (*n* = 18) valve length ranged from 17.5 to 24 µm (x̄ = 20 ± 1.6 µm) and mid-breadth from 2.1 to 3.1 µm (average 2.5 ± 0.3 µm). Valve dimensions from a benthic mat population from Blue Lake (north lobe), (INSTAAR, Univ. of Colorado accession 2488) (*n* = 21), ranged from valve length 18.0 to 26.6 µm (average 20.8 ± 2.6 µm) and mid-breadth from 2.6 to 3.9 µm (average 3.2 ± 0.4 µm). Three sediment core sections taken from Lake Fryxell within the McMurdo Dry Valleys were investigated: 16 cm and 50 cm deep from a 170 cm core and 111 cm deep from a 175 cm core. At 16 cm (Accession 3559, *n*=10), valve length measured 13.8–23.4 µm (x̄ = 17 ± 3.4 µm) and mid-breadth measured 2.4–3.2 µm (x̄ = 2.7 ± 0.3 µm). At 50 cm (Accession 364, *n*=20), valve length measured 9.7–19.4 µm (x̄ = 14 ± 2.8 µm) and mid-breadth measured 2.2–3.1 µm (x̄ = 2.6 ± 0.3 µm). At 111 cm (Accession 390, *n*=12), valve length measured 10.0–23.7 µm (x̄ = 14 ± 3.8 µm) and mid-breadth measured 1.9 – 3.6 µm (x̄ = 2.6 ± 0.4 µm).

TABle 2. Habitat conditions and population morphometrics for examined populations.

				Valve length (µ)		Valve width (µ)	
Sample ID	Locality	Lake ID	Valves measured	Range	Mean ±sd	Range	Mean ±sd
AD-3	Vestfold Hills	Admin Lake	76	18.8–28.4	21.8 ±2.9	2.1–3.2	2.7 ±0.4
2488	Cape Royds	Blue Lake, north lobe	21	18.0–26.6	20.8 ±2.6	2.6–3.9	3.2 ±0.4
2462	Cape Royds	Clear Lake	20	19.7–25.9	23.0 ±2.0	2.0–3.1	2.8 ±0.3
2464	Cape Royds	Clear Lake	18	17.5–24.0	20.0 ±1.6	2.1–3.1	2.5 ±0.3
359	McMurdo Dry Valleys	Lake Fryxell	10	13.8–23.4	17.0 ±3.4	2.4–3.2	2.7 ±0.3
364	McMurdo Dry Valleys	Lake Fryxell	20	9.7–19.4	14.0 ±2.8	2.2–3.1	2.6 ±0.3
390	McMurdo Dry Valleys	Lake Fryxell	12	10.0–23.7	14.0 ±3.8	1.9–3.6	2.6 ±0.4

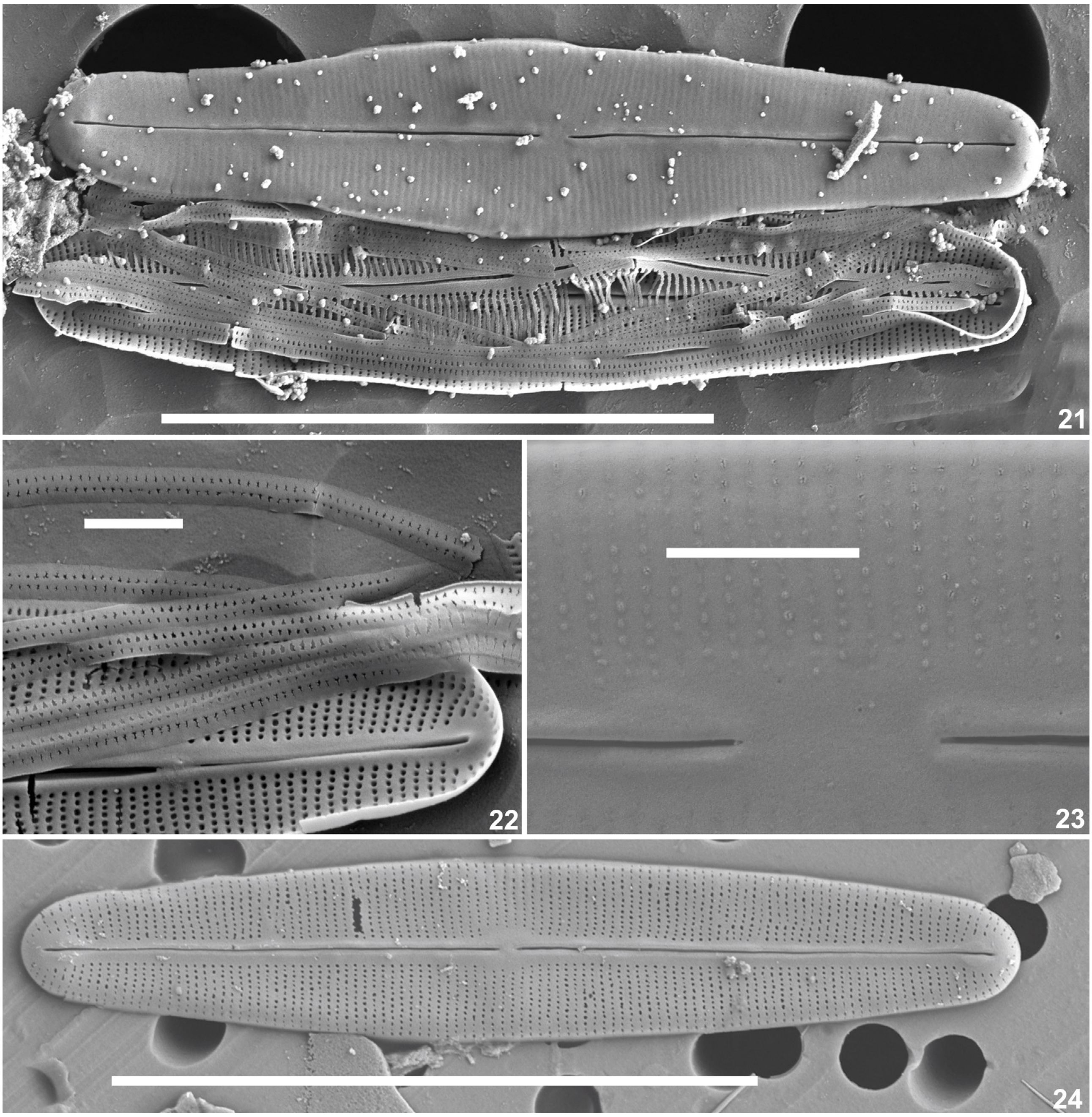
Typification: Unfortunately, the holotype and paratype slides are lost. Moreover, also the original unmounted material, used to prepare the holotype slide from, was destroyed. However, an additional set of slides, prepared from the original material of the Vestfold Hills study was kept for counting purposes. One slide (AD-3) of this set was prepared from the same original material as the (lost) holotype slide. Therefore, this slide is officially designated here as lectotype slide. As there is no original material left, an additional sample containing the population that was used for the SEM analysis from Blue Lake (accession 2488) is added as epitype.

Lectotype (designated here): BR-4555 (Meise Botanic Garden, Belgium, slide AD-3, Admin Lake, Vestfold Hills, Antarctic Continent)

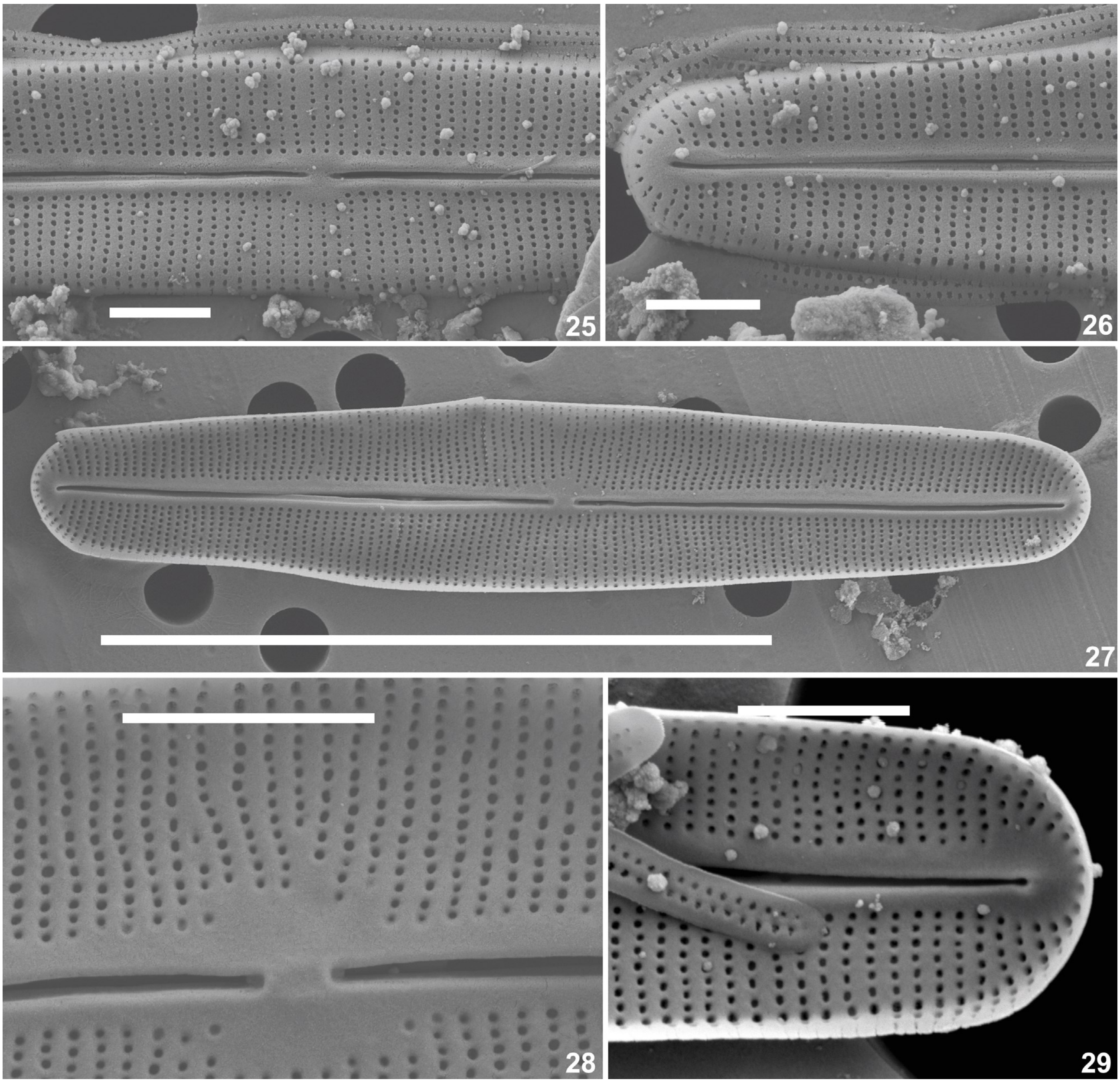
Epitype (designated here): BR-4556 (Meise Botanic Garden, Belgium, sample accession 2488, Blue Lake, McMurdo Sound, Antarctic Continent)

ecology & Distribution:—*Navicula adminensis,* as *Navicula adminii,* has been reported from the Vestfold Hills, Bunger Hills, and the McMurdo Sound Region (Roberts & McMinn 1999, Roberts *et al.* 2000, Gibson *et al.* 2006, Sakaeva *et al.* 2016). From the McMurdo Dry Valleys, specifically Taylor Valley, Esposito *et al.* (2008) reported this taxon as *N. lineola* var. *perlepida* (Grunow 1884: 474) Cleve (1894: 107) (although under the invalidly published name *N. perlepida*), suggesting the taxon was erroneously placed in *Navicula* and needing further work (Esposito *et al*. 2008, Whittaker *et al*. 2008).

Within the Vestfold and Bunger Hills, *N. adminensis* was reported across a wide salinity gradient in 24 and 10 lakes, respectively, despite the classification of its type locality, Admin Lake, as hyposaline. However, Sakaeva *et al.* (2016) also reported *N. adminensis* at lower salinity levels in Blue Lake and Clear Lake on Ross Island and from the partially ice-free Picture Pond in Taylor Valley within the McMurdo Sound Region.



FIguReS 21–24. *Sabbea adminensis* (D.Roberts & McMinn) Van de Vijver, Bishop & Kopalová *nov. comb.* Figures taken from Blue Lake, Cape Royds, Ross Island, Antarctic Continent (INSTAAR, Univ. of Colorado accession numbers: 2488). Fig. 21. Scanning electron micrograph of an entire frustule with girdle bands. Note the external areola hymenes, the shallow mantle, the simple raphe and the girdle bands with double perforation. Fig. 22. SEM detail of the girdle bands clearly showing the two rows of pores per copula. Fig. 23. SEM external detail of the areolae with partly eroded external hymenes. Fig. 24. SEM external view of an entire valve showing the eroded uniseriate striae with small areolae. Scale bar represents 10 µm for figs 21, 24 and 1 µm for figs 22 & 23.



FIguReS 25–29. *Sabbea adminensis* (D.Roberts & McMinn) Van de Vijver, Bishop & Kopalová *nov. comb.* Figures taken from Blue Lake, Cape Royds, Ross Island, Antarctic Continent (INSTAAR, Univ. of Colorado accession number: 2488). Fig. 25. SEM external detail of the central area with the short, straight proximal raphe endings, the narrow, weakly raised ridges next to the raphe and the uniseriate striae. Fig. 26. SEM external detail of the valve apex showing the absence of the terminal raphe fissures. Fig. 27. SEM internal view of an entire valve. Fig. 28. SEM internal detail of the central area with the short, straight proximal raphe endings. Fig. 29. SEM external detail of the valve apex showing an only weakly developed helictoglossa. Scale bar represents 10 µm for fig. 27 and 1 µm for figs 25, 26, 28 & 29.

Discussion

The first record of *Navicula adminensis* is found in West & West (1911), reported as *N. perlepida*. The species was originally described by Grunow in 1884 from Franz Joseph Land (Grunow 1884) and later recombined by Cleve to *N. lineola* var. *perlepida* (Cleve 1894). Unfortunately, apart from some basic data on length and width, the only information given in West & West (1911, p. 282) is the high similarity between the Antarctic population and specimens from the Arctic. Later authors (Esposito *et al.* 2008, Van de Vijver *et al.* 2012) suggested, based on valve outline and the fine morphological structure, that *Navicula adminensis* could in fact be conspecific with *Navicula lineola* var. *perlepida*. Given the very fine structure, only scanning electron microscope observations could resolve the conspecificity question. Unfortunately, unmounted material was no longer available from the Grunow collection in Vienna (Austria) (A. Igersheim, pers. comm.). In literature, only a few published images are available from the var. *perlepida* (other than Antarctic populations that are considered belonging to *Navicula adminensis*). Hustedt (1961) showed a few line-drawings that unfortunately did not provide conclusive morphological information. Witkowski *et al.* (2000) discussed the species in his Baltic diatom monograph and illustrated both *N. lineola* and its variety *perlepida* (plate 156, figs15–16 and 12–14 resp.).

The most interesting record was found in Poulin & Cardinal (1982) who published several SEM pictures (figs 63–65). In their description the presence of a transapical fascia in the central area bordered by a few scattered areolae was explicitly mentioned. Moreover, the striae become denser toward the valve apices. Valve dimensions of the observed specimens show a valve length of 30–52 µm, a valve width of 3–5 µm and a stria density of 35–38 in 10 µm increasing to 39–42 in 10 µm near the apices. All these observations are in contrast with the morphology as recorded for *N. adminensis*: a fascia has never been observed in any of the reported populations, the stria density is uniform throughout the entire valve and reaches almost 80 in 10 µm. The population studied in Poulin & Cardinal (1982) originated from Manitounuk Sound in the southeastern Hudson Bay (Canada), relatively far away from the type locality of the species near Franz Joseph Land (Grunow 1884). Although there is no conclusive evidence that both Arctic populations represent the same species, the observed LM morphology in Poulin & Cardinal (1982) shows no differences with the species described by Grunow. However, the Arctic populations differ markedly from *N. adminensis* making conspecificity between *N. lineola* var. *perlepida* and *N. adminensis* unlikely.

Whether all Antarctic records of *N. lineola* var. *perlepida* should be considered to be *N. adminensis*, remains a question that can only be solved by careful re-examination of the material, as most of the published records did not present LM or SEM images. Whittaker *et al.* (2008) found *Navicula lineola* var. *perlepida* to be dominant within layers of a sediment core associated with increased carbonate concentrations in Lake Fryxell (Taylor Valley, McMurdo Dry Valleys). Although the species was unfortunately not imaged in the publication, its presence was later confirmed by one of the co-authors (S. Spaulding, pers. comm.). Esposito et al. (2008) illustrated the species from the McMurdo region, naming it also *N. lineola* var. *perlepida*. The latter authors presented detailed SEM observations that showed a clear conspecificity with the population from Admin Lake that was used for the description of *N. adminensis* (Roberts & McMinn 1999).

In 1979, Cox typified the genus *Navicula* based on *N. tripunctata* (O.F.Müller 1786: 52) Bory (1827: 563). The main morphological features of *Navicula* s.s. include a typical lineolae-structure of the striae, a boat-shaped valve outline, two rectangular, plate-like plastids, internal raphe branches located on the side of an axial costa, external terminal raphe fissures deflected to the same (secondary) side and indistinct or weakly curved proximal raphe pores. It is clear that *N. adminensis* shows an entirely different set of morphological characters, making its placement within the genus *Navicula* s.s. no longer possible. A transfer to another, more suitable and taxonomically discrete genus is therefore necessary.

The presence of *N. adminensis* in both hyper- and hypo-saline lakes, but with an accompanying diatom flora of both marine and freshwater species (based upon re-investigation of Vestfold Hills material used in Roberts & McMinn, 1999), make a comparison with both similar marine and freshwater genera necessary. Only a few freshwater genera share some of the morphological features of *N. adminensis*: *Adlafia*, *Envekadea* and *Kobayasiella*. In the marine realm, especially in the family Berkeleyaceae, the genera *Stenoneis*, *Climaconeis*, *Parlibellus* and *Berkeleya* should be considered as holding the possible closest relationship to *N. adminensis*. Table 3 presents all these genera together with their discriminating features. Based on the table, it is clear that almost all mentioned genera show some resemblance to *N. adminensis,* but none sufficiently adequate to host the species.

The genera *Envekadea*, *Adlafia* and *Kobayasiella* show a superficial resemblance when only considering the morphological features visible in light microscopy. All three genera contain species with very fine areolae making the striae hardly visible in LM. Unlike *N. adminensis*, all three genera have an entirely different raphe structure with deflected or even hooked terminal raphe fissures (*N. adminensis* lacks terminal raphe fissures) and internally with well-developed helictoglossae, unlike the weakly-developed helictoglossae in *N. adminensis*. The striae in *Kobayasiella* are composed of one transapically elongated areola and the raphe has an umbilicus, visible as a slight 'notch', at about one third to halfway along the straight raphe (Vanhoutte *et al.* 2004), a feature never observed in *N. adminensis*. Almost all *Adlafia* species show a typical striation pattern with radiate striae becoming convergent near the apices, whereas the striae in *N. adminensis* are parallel throughout the entire valve. *Envekadea*, containing mostly brackish water species, has a very distinct sigmoid raphe system, rather large areolae arranged in radiate striae and well-developed helictoglossae. All three genera can therefore be excluded as a host genus for *N. adminensis*.

TABle 3. Discriminating features of cell morphology and ecology acoss genera similar to *Sabbea*

	Envekadea	***Adlafia***	***Kobayasiella***	***Stenoneis***	***Climaconeis***	***Berkeleya***	***Parlibellus***	***Sabbea***
Valve size (μ)	25-52	<25 (40)	relative small	variable	variable	variable	variable	<60 μ
Valve outline	linear-lanceolate with (sub)- capitate apices	linear to linear-lanceolate, protracted, subcapitate or rostrate apices	linear to elliptic-lanceolate, protracted, subcapitate or rostrate apices	linear, bluntly rounded, sometimes protracted apices	narrowly linear, linear-lanceolate or lunar with slight capitate apices	linear to linear-lanceolate with slightly capitate apices	lanceolate, or linear, with bluntly or acutely rounded apices	linear with parallel margins and weakly protracted to broadly rounded apices
Raphe	straight, filiform	filiform, weakly curved	filiform, umbilicus present	straight, filiform	straight, filiform	short, straight, filiform	straight	straight
Proximal raphe endings	greatly expanded, forming conical depressions, straight	indistinct	indistinct	expanded, straight	simple to slightly expanded, sometimes deflected to the ventral margin	straight, weakly expanded	simple, or slightly expanded, short terminal fissures turned towards same side	simple, slightly expanded into pores or hooked, usually towards secondary side
Proximal internal endings	very slightly deflected to one side	clearly deflected, indistinct	T-shaped, straight	turned to one side	simple	straight	simple, or fissure continuing into narrow rib-or helictoglossa-like structure	straight, unexpanded
Terminal raphe fissures	very short terminating in expanded, golfclub-like pores bent to opposite directions, giving the raphe a sigmoid look	deflected to the same side	strongly deflected or hooked to the same side	more-or-less absent, terminating in expanded pores, deflected slightly to the same side	terminal fissures absent	straight or slightly deflected to the secondary side	very short, turned towards the same side of the valve	absent (endings very short)

...continued on the next page

TABle 3. (Continued)

	Envekadea	*Adlafia*	*Kobayasiella*	*Stenoneis*	*Climaconeis*	*Berkeleya*	*Parlibellus*	*Sabbea*
Striation pattern	very dense, radiate in the centre, then abruptly convergent close to the apices	very dense, clearly radiate, ad the apices convergent,	radiate in the centre, then abruptly convergent close to the apices	equistant, rather parallel to convergent, usually faint in LM,large hyaline zone in the central area	equistant, rather parallel to convergent, a stauros is present in some species	fairly dense, parallel to convergent near the poles	somewhat more distantly spaced at center	parallel throughout the entire valve
Striae	uniseriate, continuing over the face/mantle junction	uniseriate, continuing without interruption from face to mantle	presence of a hyaline ridge at the face/ mantle junction	uniseriate, rather disorderly	uniseriate, continuing over the face/mantle junction	uniseriate	uniseriate	uniseriate
Areolae	large, rectangular to polygonal pores, usually occluded externally by porous hymenes	simple, small rounded poroids, occluded externally by hymenes	transapically elongated, finely hymenated	small, round poroids, usually occluded externally by hymenes	small round to oval poroids, closed internally by hymenes	simple round poroids closed internally by hymenes	small round poroids occluded by hymenes; one or few centrally located but appear not to penetrate to valve interior	small, rounded, externally occluded by individual hymenes
Girdle structure	2-3 non-porous bands	2 bands each with double row of poroids	2 bands with one or two rows of poroids	not studied	numerous bands with 2 rows of poroids	5 open bands with two rows of round/oval poroids	many open bands with two transverse rows of poroids	several open copulae with double perforations
Plastids	one, H-shaped in valve view	unknown	one, H-shaped, asymmetrical	unknown	4-20 H-shaped plastids	one consisting of 2 girlde-appressed plates	2 butterfly shaped; lying one each side against girdle	???
Habitat	freshwater-marine	freshwater	freshwater	marine	marine	brackish-marine	brackishmarine	freshwater- brackish

The marine genus *Climaconeis* shows the greatest similarity to *N. adminensis*, especially considering the linear-shaped valve outline (Cox 1982) and the fine structure of the striae, not visible in LM. The genus is characterized by having finely areolated striae, a simple raphe structure with straight external raphe branches lacking terminal raphe fissures and distinct proximal raphe ends (Cox 1982, Round *et al.* 1990). The fine striae are a feature shared with *N. adminensis,* although near the central area the striation pattern differs in most *Climaconeis* species which have shortened and often radiate striae. However, several differences exclude the placement of *N. adminensis* in *Climaconeis*. Several (though not all) *Climaconeis* species, having a typical scalariform valvocopula, bear 'craticular bars' growing from both sides of the valvocopula and interdigitating in near the valve middle. Unfortunately, some *Climaconeis* species seem to lack this feature such as *C. delicatula* (Cleve 1894: 144) E.J.Cox (1982: 166) making this criterion less decisive in excluding *N. adminensis* from *Climaconeis*. Prasad (2003) discussed the morphology and taxonomy of the genus *Climaconeis* and presented a table with all known species and their morphological features. It is clear that the presence of the craticular bars is randomly distributed in the genus.

A more diagnostic character is that *Climaconeis* species show a very typical, large, prominent helictoglossa at the apices (see for instance Round *et al.* 1990, p. 521 fig. g), a feature found in all *Climaconeis* species worldwide (Cox 1982, Prasad *et al.* 2000, Reed & Williams 2002, Prasad 2003). This type of helictoglossa is never observed in *N. adminensis,* which only shows a very faint helictoglossa. The areolae in *Climaconeis* are closed internally by hymenes whereas in *N. adminensis*, the areolae are covered externally. Internally, the raphe in *Climaconeis* is located in a well-developed raphe-sternum, often accompanied by raised ribs, a feature not observed in any of the investigated *N. adminensis* populations.

Besides *Climaconeis*, three other genera were placed in the Berkeleyaceae family. The genus *Stenoneis* contains species with a characteristic striation pattern, showing irregular hyaline areas where areolae are lacking; this has never been observed in *N. adminensis* (Round *et al.* 1990, Poulin 1990). The proximal raphe endings in *Stenoneis* are always expanded and clearly visible, even in LM, usually appearing as two thickened structures next to the raphe endings in the central area (see Poulin 1990, figs 15 & 22). Internally, the raphe sternum is well-developed with two prominent longitudinal ribs on both sides of the raphe (Round *et al.* 1990). The distal raphe endings terminate on clear helictoglossae. None of these characteristics has ever been seen in *N. adminensis*. The only feature shared with *Stenoneis* is the presence of external hymenes covering the areolae (Poulin 1990) but this is insufficient to include *N. adminensis* in *Stenoneis*. The third genus in the Berkeleyaceae, *Berkeleya*, has a different raphe structure with deflected proximal and terminal raphe endings, the internal hymenes covering the areolae and the well-developed helictoglossae. In most *Berkeleya* species, the raphe-sternum has a unique structure with only half of it being continuous and the other interrupted near the central area (Round *et al.* 1990, p. 519, fig. g). Finally, *Parlibellus* contains species with a more lanceolate valve outline, typical hooked external terminal raphe fissures, hymenes covering the areolae internally, a well-developed central nodule and differences in stria structure with the central striae more spaced. The mantle in most *Parlibellus* species is rather high, unlike *N. adminensis* that has a very low mantle (Cox 1988).

In conclusion, it is clear that *N. adminensis* cannot be placed into any of the genera discussed above. Expanding the original genus description of the most closely related genus, *Climaconeis*, with the features observed in *N. adminensis*, could potentially be a solution, although it would require drastically modifying the characterization of some features, such as the helictoglossa and the internal hymens, and this would create a genus that is so broad that a lot of other species would fit likewise in there. Molecular evidence could lend another perspective, possibly linking the species to one of the already described genera, but up to now all attempts to culture *N. adminensis* have been unsuccessful.

Therefore, a new genus, Sabbea Van de Vijver, Bishop & Kopalová *gen. nov.*, is proposed to accommodate species with a very simple raphe structure lacking external terminal raphe fissures and having only a very faint helictoglossae, uniseriate striae with occluded externally by hymenes, a low valve mantle and doubly perforated girdle bands.

Formal description

Sabbea **Van de Vijver, Bishop & Kopalová *gen. nov.***

Valves linear with a low mantle. Girdle composed of several, open copulae, each with a double row of rounded to transapically elongated poroids. Raphe sternum well-developed with the raphe positioned in the middle of the sternum. Raphe straight, simple with straight, non-expanded proximal raphe ends. Terminal raphe fissures absent. Internally, helictoglossae only weakly developed to almost absent. Striae very fine, not discernible in LM, uniseriate, parallel, composed of small, rounded areolae, externally occluded by small hymenes.

Type:—*Sabbea adminensis* (D.Roberts & McMinn) Van de Vijver, Bishop & Kopalová *comb. nov.*

etymology:—the genus is named in honor of our dear friend and colleague Prof. dr. Koen Sabbe (Ghent University, Belgium) for his outstanding contributions to diatom science and the International Society for Diatom Research

New combination

Sabbea adminensis* (D.Roberts & McMinn) Van de Vijver, Bishop & Kopalová *comb. nov.

Basionym: *Navicula adminensis* Roberts & McMinn 1999 Bibliotheca Diatomologica 44, p. 27, plate 4, figs 2–4.

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References

Bory de Saint-Vincent, J.B.M. & Coll. (Eds.) (1822) *Dictionnaire Classique d'Histoire Naturelle Paris*. Vols. 1–17. Rey & Gravier, libraires-éditeurs; Baudouin Frères, libraires-éditeurs. Available from: https://archive.org/details/dictionnaireclas01bory/page/n6 (Accessed 23 Sept. 2019)

Bory de Saint Vincent, J.B.M. (1827) *Encyclopédie Méthodique, Histoire Naturelle Des Zoophytes ou Animaux Rayonnés*. Paris, pp. 563–565. Available from: https://archive.org/details/bub_gb_Y-thEeccPd8C/page/n6 (Accessed 23 Sept. 2019)

Carlson, G.W.F. (1913) Süsswasseralgae aus der Antarktis, Südgeorgien und den Falkland Inseln. *Wissenschaftliche Ergebnisse der Schwedischen Südpolar-Expedition 1901-1903, unter leitung von dr. Otto Nordenskjøld*: 4 (Botanique): 1–94. Available from: http://digital.slv.vic.gov.au (Accessed 23 Sept. 2019)

Cleve, P.T. (1894) Synopsis of the Naviculoid Diatoms, Part I. *Kongliga Svenska-Vetenskaps Akademiens Handlingar* 26: 1–194. Available from: https://ia800204.us.archive.org (Accessed 23 Sept. 2019)

Cleve, P.T. (1895) Synopsis of the Naviculoid Diatoms, Part II. *Kongliga Svenska-Vetenskaps Akademiens Handlingar* 27: 1–219.

Cox, E.J. (1975) Further studies on the genus *Berkeleya* Grev. *British Phycological Journal* 10: 205–217. https://doi.org/10.1080/00071617500650191

Cox, E.J. (1979) Taxonomic studies on the diatom genus *Navicula* Bory. The typification of the genus. *Bacillaria* 2: 137–153.

Cox, E.J. (1982) Taxonomic studies on the diatom genus *Navicula* Bory. IV. *Climaconeis* Grun., a genus including *Okedenia inflexa* (Bréb.) Eulenst. ex De Toni and members of *Navicula* sect. *Johnsonieae* sensu Hustedt. *British Phycological Journal* 17: 147–168. https://doi.org/10.1080/00071618200650161

Cox, E.J. (1988) Taxonomic studies on the diatom genus *Navicula* Bory. V. The establishment of *Parlibellus* gen. nov. for some members of *Navicula* sect. Microstigmaticae. *Diatom Research* 3: 9–38. https://doi.org/10.1080/0269249X.1988.9705014

Cremer, H., Roberts, D., McMinn, A., Gore, D. & Melles, M. (2003) The Holocene Diatom Flora of Marine Bays in the Windmill Islands, East Antarctica. *Botanica Marina* 46: 82–106. https://doi.org/10.1515/BOT.2003.010

Esposito, R.M.M., Spaulding, S.A., McKnight, D.M., Van de Vijver, B., Kopalová, K., Lubinski, D., Hall, B. & Whittaker, T. (2008) Inland diatoms from the McMurdo Dry Valleys and James Ross Island, Antarctica. *Botany* 86: 1378–1392. https://doi.org/10.1139/b08-100

Frenguelli, J. (1924) Resultados de la Primera Expedición a Tierra del Fuego (1921) - Diatomeas de Tierra del Fuego. *Anales de la Sociedad Cientifica Argentina* 97: 87–118, 231–266.

Frenguelli, J. (1945) El Platense y sus diatomeas, Las diatomeas del Platense. *Revista del Museo de La Plata (Nueva Serie), Seccioìn*

Paleontologiìa 3: 77–221.

Fritsch, F.E. (1912) Freshwater algae. *In*: *Natural History. London. British Museum. National Antarctic Expedition 1901–1904. v.6 (Zoology & Botany)*. 60 pp.

Fritsch, F.E. (1917) Freshwater algae. British Antarctic ("Terra Nova") Expedition, 1910. *Natural History Report* 1–17.

Fukushima, H. (1963) Diatoms from Bybog Osane (Antarctic Continent) and Ongul Kalven Island. *Antarctic Record* 17: 56–58.

Fukushima, H. (1966) Diatoms from Molodezhnaya Station and Mirny Station Antarctica. *Antarctic Record* 27: 13–17.

Gibson, J.A.E. (1999) The meromictic lakes and stratified marine basins of the Vestfold Hills, East Antarctica. *Antarctic Science* 11 (2): 175-192.
https://doi.org/10.1017/s0954102099000243

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

Gligora, M., Kralj, K., Plenković-Moraj, A., Hinz, F., Acs, E., Grigorszky, I., Cocquyt, C. & Van de Vijver, B. (2009) Observations on the diatom *Navicula hedinii* Hustedt (Bacillariophyceae) and its transfer to a new genus *Envekadea* Van de Vijver et al. gen. nov. *European Journal of Phycology* 44: 123–138.
https://doi.org/10.1080/09670260802389783

Greville, R.K. (1827) *Scottish Cryptogamic Flora, or colored figures and descriptions of cryptogamic plants, belonging chiefly to order Fungi. Edinburgh and London. Volume 5*. pp. 241–301.

Grunow, A. (1862) Die österreichischen Diatomaceen nebst Anschluss einiger neuen Arten von andern Lokalitäten und einer kritischen Uebersicht der bisher bekannten Gattungen und Arten. Erste Folge. Epithemieae, Meridioneae, Diatomeae, Entopyleae, Surirelleae, Amphipleureae. Zweite Folge. Familie Nitzschieae. *Verhandlungen der Kaiserlich-Königlichen Zoologisch-Botanischen Gesellschaft in Wien* 12: 315–472, 545–588.
https://doi.org/10.5962/bhl.title.64361

Hamsher, S., Kopalová, K., Kociolek, J.P., Zidarova, R. & Van de Vijver, B. (2016) The genus *Nitzschia* on the South Shetland Islands and James Ross Island. *Fottea* 16: 79–102.
https://doi.org/10.5507/fot.2015.023

Hassall, A.H. (1845) *A history of the British Freshwater Algae (including descriptions of the Diatomaceae and Desmidiaceae) with upwards of one hundred Plates. I. Text.* Taylor, Walton, and Maberly, London, 462 pp.
https://doi.org/10.5962/bhl.title.22609

Holmboe, J.D. (1902) IV. *Navicula mutica* Kütz. Aus dem antarktischen Festlande. *Nyt Magazin for Naturvidenskaberne, Christiana* 40: 221–222.

Hustedt, F. (1961) Die Kieselalgen Deutschlands, Österreichs und der Schweiz unter Berücksichtigung der übrigen Länder Europas sowie der angrenzenden Meeresgebiete. *In*: Rabenhorst, L. (Ed.) *Kryptogamen Flora von Deutschland, Österreich und der Schweiz*. Vol. 7. Teil 3, Lief. 1. Akademische Verlagsgesellschaft m.b.h. Leipzig, pp. 1–160.

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

Kellogg, T.B. & Kellogg, D.E. (2002) Non-marine and littoral diatoms from Antarctic and subantarctic regions. Distribution and updated taxonomy. *Diatom monographs* 1: 1–795.

Ko-Bayashi, T. (1963) Variations on some pennate diatoms from Antarctica (Part 1): III. Variations of *Navicula muticopsis* Van Heurck var. *muticopsis* f. *murrayi* (W. & G.S. West) Ko-Bayashi. *Japanese Antarctic Research Expedition 1956-1962, Scientific Reports Series E* 18: 1–20.

Ko-Bayashi, T. (1965) Variations on some pennate diatoms from Antarctica. *Japanese Antarctic Research Expedition (JARE) 1956-1962 Scientific Reports Series E* 24: 1–28.

Kohler, T.J., Kopalová, K., Van de Vijver, B. & Kociolek, J.P. (2015) The genus *Luticola* D.G.Mann (Bacillariophyta) from the McMurdo Sound Region, Antarctica, with the description of four new species. *Phytotaxa* 208: 103–134.
https://doi.org/10.11646/phytotaxa.208.2.1

Konfirst, M.A., Sjunneskog, C., Scherer, R.P. & Doran, P.T. (2011) A diatom record of environmental change in Fryxell Basin, Taylor Valley, Antarctica, late Pleistocene to present. *Journal of Paleolimnology* 46: 257–272.
https://doi.org/10.1007/s10933-011-9537-6

Lange-Bertalot, H. (1996) *Kobayasia* gen. et spec. nov. *Iconographia Diatomologica* 4: 278–287.

Lange-Bertalot, H. & Genkal, S.I. (1999) Diatoms from Siberia I. *Iconographia Diatomologica* 6: 272–275.

Lange-Bertalot, H. (2001) *Navicula* sensu stricto, 10 genera separated from *Navicula* sensu lato, *Frustulia*. *Diatoms of Europe* 2: 1–526.

Levkov, Z. (2009) *Amphora sensu lato. Diatoms of Europe* 5: 1–916.

Moser, G., Lange-Bertalot, H. & Metzeltin, D. (1998) Insel der Endemiten Geobotanisches Phänomen Neukaledonien (Island of endemics New Caledonia - a geobotanical phenomenon). *Bibliotheca Diatomologica* 38: 1–464.

Müller, O.F. (1786) *Diatomaceen (Vibrio paxillifer, V. bipunctatus, V. tripunctatus, Gonium pulvinatum). Animalcula infusoria fluviatilia et marina quae detexit, systematice, descripsit et ad vivum delineare curavit O.F. Muller.* Havniae, LVI + 367 pp.

Poulin, M. & Cardinal, A. (1982) Sea ice diatoms from Manitounuk Sound, southeastern Hudson Bay (Quebec, Canada). II. Naviculaceae, genus *Navicula*. *Canadian Journal of Botany* 60: 2825–2845.
https://doi.org/10.1139/b82-343

Poulin, M. (1990) Sea Ice diatoms (Bacillariophyceae) of the Canadian Arctic. I. The genus *Stenoneis*. *Journal of Phycology* 26: 156–167.
https://doi.org/10.1111/j.0022-3646.1990.00156.x

Prasad, A.K.S.K., Riddle, K.A. & Nienow, J.A. (2000) Marine diatom genus *Climaconeis* (Berkeleyaceae, Bacillariophyta): two new species, *Climaconeis koenigii* and *C. colemaniae*, from Florida Bay, USA. *Phycologia* 39: 199–211.
https://doi.org/10.2216/i0031-8884-39-3-199.1

Prasad, A.K.S.K. (2003) Fine structure and taxonomy of two species of the marine diatom genus *Climaconeis* (Berkeleyaceae, Bacillariophyta): *C. silvae* sp. nov. and *C. riddleae* sp. nov. from the Caribbean Sea and Florida bay, USA. *Hidrobiológica* 12: 9–22.

Reid, G. & Williams, D.M. (2002) The marine diatom genus *Climaconeis* (Berkeleyaceae, Bacillariophyta): two new species from Abu Dhabi, United Arab Emirates. *Diatom Research* 17: 309–318.
https://doi.org/10.1080/0269249x.2002.9705550

Roberts, D. & McMinn, A. (1996) Relationships between surface sediment diatom assemblages and water chemistry gradients in saline lakes of the Vestfold Hills, Antarctica. *Antarctic Science* 8: 331–341.
https://doi.org/10.1017/s0954102096000508

Roberts, D. & McMinn, A. (1999) Diatoms of the saline lakes of the Vestfold Hills, Antarctica. *Bibliotheca Diatomologica* 44: 1–83.

Roberts, D., McMinn, A. & Zwartz, D. (2000) An initial palaeosalinity history of Jaw Lake, Bunger Hills based on a diatom–salinity transfer function applied to sediment cores. *Antarctic Science* 12: 172–176.
https://doi.org/10.1017/S0954102000000225

Ross, R., Cox, E.J., Karayeva, N.I., Mann, D.G., Paddock, T.B.B., Simonsen, R. & Sims, P.A. (1979) An amended terminology for the siliceous components of the diatom cell. *Nova Hedwigia Beiheft* 64: 513–533.

Round, F.E., Crawford, R.M. & Mann, D.G. (1990) *The Diatoms. Biology and Morphology of the Genera*. Cambridge University Press, Cambridge, 747 pp.

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

Sakaeva, A., Sokol, E.R., Kohler, T.J., Stanish, L.F., Spaulding, S.A., Howkins, A., Welch, K.A., Lyons, W.B., Barrett, J.E. & McKnight, D.M. (2016) Evidence for dispersal and habitat controls on pond diatom communities from the McMurdo Sound Region of Antarctica. *Polar Biology* 39: 2441–2456.
https://doi.org/10.1007/s00300-016-1901-6

Spaulding, S.A. & Stoermer, E.F. (1997) Taxonomy and distribution of the genus *Muelleria* Frenguelli. *Diatom Research* 12: 95–115.
https://doi.org/10.1080/0269249x.1997.9705405

Spaulding, S.A., Kocielek, J.P. & Wong, D. (1999) A taxonomic and systematic revision of the genus *Muelleria* (Bacillariophyta). *Phycologia* 38 (4:) 314–341.
https://doi.org/10.2216/i0031-8884-38-4-314.1

Turland, N.J., Wiersema, J.H., Barrie, F.R., Greuter, W., Hawksworth, D.L., Herendeen, P.S., Knapp, S., Kusber, W.-H., Li, D.-Z., Marhold, K., May, T.W., McNeill, J., Monro, A.M., Prado, J., Price, M.J. & Smith, G.F. (Eds.) (2018) International Code of Nomenclature for algae, fungi, and plants (Shenzhen Code) adopted by the Nineteenth International Botanical Congress Shenzhen, China, July 2017. *Regnum Vegetabile* 159. [Glashütten: Koeltz Botanical Books]
https://doi.org/10.12705/Code.2018

Tyler, P.A. (1996) Endemism in freshwater algae, with special reference to the Australian region. *Hydrobiologia* 336: 127–135.
https://doi.org/10.1007/BF00010826

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

Van de Vijver, B., Mataloni, G., Stanish, L. & Spaulding, S.A. (2010) New and interesting species of the genus *Muelleria* (Bacillariophyta) from the Antarctic region and South Africa. *Phycologia* 49: 22–41.
https://doi.org/10.2216/09-27.1

Van de Vijver, B., Tavernier, I., Kellogg, T.B., Gibson, J., Verleyen, E., Vyverman, W. & Sabbe, K. (2012) Revision of type materials of Antarctic diatom species (Bacillariophyta) described by West & West (1911), with the description of two new species. *Fottea* 12: 149–169.
https://doi.org/10.5507/fot.2012.012

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

Van de Vijver, B. & Kusber, W.-H. (2018) Correction of the typification of *Navicula adminii* Roberts & McMinn (Bacillariophyceae). *Notulae algarum* 65: 1.

Van der Werff, A. (1955) A new method for cleaning and concentrating diatoms and other organisms. *Verhandlungen der Internationalen Vereinigung für theoretische und angewandte Limnologie* 12: 276–277.
https://doi.org/10.1080/03680770.1950.11895297

Van Heurck, H. (1909) Diatomées. *In:* Résultats du Voyage du S.Y. Belgica en 1897-1898-1899. Rapports Scientifiques. Botanique. Antwerpen: Imprimerie J.-E. Buschmann. Botanique 6: 1–129.

Vanhoutte, K., Verleyen, E., Vyverman, W., Chepurnov, V. & Sabbe, K. (2004) The freshwater diatom genus *Kobayasiella* (Bacillariophyta) in Tasmania, Australia. *Australian Systematic Botany* 17: 483–496.
https://doi.org/10.1071/sb03035

West, W. & West, G.S. (1911) Freshwater algae. *British Antarctic Expedition (1907-1909) Science Report, Biology* 1: 263–298.

Whittaker, T.E., Hall, B.L., Hendy, C.H. & Spaulding, S.A. (2008) Holocene depositional environments and surface-level changes at Lake Fryxell, Antarctica. *The Holocene* 18: 775–786.
https://doi.org/10.1177/0959683608091797

Witkowski, A. Lange-Bertalot, H. & Metzeltin, D. (2000) Diatom flora of marine coasts I. *Iconographia Diatomologica* 7: 1–925.

Zidarova, R., Kopalová, K. & Van de Vijver, B. (2016) Diatoms from the Antarctic Region. Maritime Antarctica. *Iconographia Diatomologica* 24: 1–504.

Chapter 3

A re-investigation of lake sediment diatoms from the Vestfold Hills, Antarctica, using an updated, fine-grained taxonomy

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A RE-INVESTIGATION OF LAKE SEDIMENT DIATOMS FROM THE VESTFOLD HILLS, ANTARCTICA, USING AN UPDATED, FINE-GRAINED TAXONOMY

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Abstract: The non-marine diatom flora of the Antarctic continent is currently being revised as recent work within the Maritime and Sub-Antarctic regions has unveiled a number of new endemic species. The under reporting of endemic species is partially due to the historic "force-fitting" of Antarctic species into European names. Within East Antarctica, the Vestfold Hills are an extensively studied area known for their diversity of lakes spanning a gradient in salinity, and the *Diatoms of the saline lakes of the Vestfold Hills, Antarctica* by Roberts & McMinn (1999) has been one of the primary resources for identifying Continental Antarctic diatoms for over two decades. To determine if improved taxonomic resolution alters the ecological interpretation of these lakes, 30 prepared lakes sediment samples first examined by Roberts & McMinn (1999) were re-analyzed using an updated, fine-grained taxonomic approach. Canonical correspondence analysis (CCA) with forward model selection was used to determine which lake variables structured diatom communities. Permutational analysis of variance was then used to analyze categorical lake parameters. Our analyses confirm the work of Roberts & McMinn (1999), which described the role of salinity and alkalinity in structuring Vestfold Hills diatom communities. Thus, increased taxonomic resolution did not change the original ecological interpretation. However, the revised flora of the Vestfold Hills features 37 species endemic to the Antarctic Region, including members of *Luticola, Sabbea* and *Halamphora,* among others. In total, 183 taxa across 38 genera were observed, in contrast to the 67 taxa reported in the original work. The revised flora, now with a larger proportion of endemic species, may improve our understanding of the diatom community in general, and has wider implications for both conservation and overall biodiversity estimates of Antarctica. More widely applied, these data can be incorporated into larger studies of Antarctic microbial biogeography and biodiversity.

Keywords: *Antarctica, diatoms, Vestfold Hills, fine-grained taxonomy, East Antarctica, lake sediments*

Introduction

Microbial biogeography has undergone a paradigm shift away from the Baas-Becking (Baas-Becking 1934), or Ubiquity, hypothesis stating that "Everything is everywhere but the environment selects" (Finlay 2002). A major tenet of this theory assumes unlimited dispersal of microbes, due to small body sizes and vast populations. A number of difficulties have been raised in attempting to test this hypothesis, including differences in taxonomic resolution between groups, (e.g. bacterial, algal and ciliates) (Martiny et al. 2006), as well their respective differences in size, physiology/metabolism, and dispersal ability (Carbonero et al. 2014, van der Gast 2015). Works focused on elucidating global trends in microbial biodiversity, with component datasets throughout Antarctica, and East Antarctica in particular, have suggested a "regionalization" on the continent, with a number of endemic taxa (Vyverman et al. 2010) due to constraints upon "historic processes" such as colonization, extinction and migration (Vyverman et al. 2007, Verleyen et al. 2009, De Wever et al. 2009).

As a whole, the Antarctic Biogeographical Region comprises the Sub-Antarctic, Maritime Antarctic, and the Continental Antarctic sub-regions. Continental Antarctica is separated by the so-called "Gressit Line", akin to the Wallace line of southeast Asia demarcating marked changes in fauna (Futuyma 2013). On Antarctica, the Gressit Line separates the continent from the peninsula based upon levels of ice cover, climatic regime and biota present, among other criteria (Chown & Convey, 2007). Indeed, the presence of ice is pervasive as ice-free areas account for less than 1% of Antarctica's surface area (Chown et al. 2015). Using these ice free "islands", and overlaying GIS data layers featuring fauna and flora data, Terauds et al. (2012) initially described 15 distinct Antarctic Conservation Biogeographical Regions (ACBRs). This was later increased to 16 ACBRs in Terauds and Lee (2016), with the formation of another ACBR within East Antarctica. However, their study revealed a lack of coverage and limited incorporation of the Antarctic microflora. More specifically, there is a lack of Continental Antarctic diatoms. This omission is due, in part, to an incomplete knowledge of the taxonomy and ecology of Antarctic diatoms. Namely, this concerns issues associated with overly broad morphological species concepts and species force-fitting (Jones 1996). Indeed, at present there is no standardized diatom flora for Antarctica.

Historically, taxonomic coverage has been limited to inconsistent species lists (Jones 1996). Kellogg & Kellogg (2002) compiled over 300 publications featuring non-marine diatom taxa within the Antarctic Region, including extensive records throughout East Antarctica, and noted an overwhelming dominance of cosmopolitan species. Recent works throughout the Maritime and Sub-Antarctic regions have revealed a higher degree of endemic taxa than originally thought (Van de Vijver et al. 2002, Zidarova et al. 2016 and references therein). Attention has been brought to investigating Continental Antarctica through the investigation of problematic taxa in the genera *Muelleria* (Frenguelli) Frenguelli (Spaulding & Stoermer 1997, Spaulding et al. 1999, Van de Vijver et al. 2010) and *Halamphora* (Cleve) Levkov (Van de Vijver et al. 2014). Other studies re-examined particular regions or localities such as the McMurdo Sound Region in Victoria Land (Esposito et al. 2008), Bunger Hills (Gibson et al. 2006), Larsemann Hills and Rauer Islands (Sabbe et al. 2003), and Skarvsnes (Ohtsuka et al. 2006). Finally, other studies re-analyzed historic materials. A clear example of the latter was the reinvestigation and partial revision of West & West's (1911) work on Shackleton's materials from Ross Island (Van de Vijver et al. 2012). Based on this revision and applying a more fine-grained morphological taxonomy, the authors described *Luticola pseudomurrayi* Van de Vijver et Tavernier (in Van de Vijver et al. 2012: 164) and *Chamaepinnularia gibsonii* Van de Vijver (in Van de Vijver et al. 2012: 166) from the Bunger Hills and Lützow Holm Bay, both situated in East Antarctica.

Despite this progress, there are still areas in East Antarctica, such as the Vestfold Hills, that have not yet been re-investigated. Given its historical importance to the Australian Antarctic Division (AAD) as the site of Davis station, the Vestfold Hills has long been a base for biodiversity studies in East Antarctica for terrestrial lithic algae, mosses and lichens (Seppelt et al. 1988), bacteria (Line 1988), and terrestrial, sub-lithic green algae (Broady 1981). The presence of the station ensures the possibility that the area can be monitored for the long term, as the effects of human disturbance, exacerbated by climate change, are expected to increase concurrently with traffic between ACBRs (Hughes et al. 2019). However, the impact this is likely to have upon diatom communities is unknown, due in part to an incomplete understanding of the communities themselves and concomitant exclusion (and/or limited inclusion) from works evaluating biodiversity management and preservation (Hughes et al. 2016, Wauchope et al. 2019). The first step in mediating this is to accurately assess the flora.

Roberts & McMinn (1999) published a non-marine diatom flora of the Vestfold Hills, comprising an overview of their previous publications (1996) that developed a diatom transfer function for salinity to use throughout the numerous saline-influenced lakes in the area. Despite progress in understanding Antarctic diatom taxonomy and ecology throughout East Antarctica, these records have not been revisited. In the present study, we apply a ‘fine-grained’ taxonomic approach based on a narrower species concept (Mann 1999), to re-analyze samples from 30 lakes within the Vestfold Hills, East Antarctica. In the present study, our research aims were to first survey the diversity of the diatom flora and compare the results with the original species list, and then apply statistical approaches to evaluate if ‘modernizing’ the diatom flora could lead to changes in ecological interpretation. Given the aforementioned results in other areas of East Antarctica, we expect to observe a greater species richness and a larger number of endemic Antarctic species compared to the original assessment. We expect this result due to the application of narrower morphological species concept in response to the broad, “force-fitting” concepts previously used (Tyler 1996). We expect that the revised, fine-grained flora will aid in interpreting the complexity of the Vestfold Hills lake ecosystems as described in Roberts & McMinn (1999).

Materials and methods

Study area

Occurring as an outcrop in East Antarctica into Prydz Bay, the Vestfold Hills (68˚25’–68 40’S, 77˚50’–78˚35’E) form an ice-free area along the Ingrid Christensen Coast, Princess Elizabeth Land as part of the Australian Antarctic Territory, bordered to the south by the Sørsdal Glacier (Fig. 1). The Vestfold Hills feature over 300 lakes, ranging in salinity from fresh to hypersaline, across an area of 400 km^2 (Roberts & McMinn 1999). Formed in part by glacial retreat and concomitant isostatic rebound, the lakes occur across an elevational gradient, displaying marked influence from both the sea and glacial meltwater (Gibson 1999). A “typical” meromictic lake of the Vestfold Hills is described in Gibson & Burton (1996) as ice covered for at least part of the year with well-defined limnetic layers that may be mixed by seasonal differences in heat and/or salinity regimes.

Here, we adopt the categories proposed in Gibson (1999) to divide the studied lakes into three geographical groups: Long Peninsula, Broad Peninsula, and Mule Peninsula (Fig. 1). The Long Peninsula group includes the largest number of lakes within the study at 13, with two of the three freshwater lakes (Table 1). The Long Peninsula group also has eight hypersaline lakes, the largest in the study, and three hyposaline lakes. The Broad Peninsula group is situated between the northernmost Long Peninsula group and the southernmost Mule Peninsula group of lakes. The Broad group does not possess any freshwater lakes but has seven hypersaline and four hyposaline lakes, including the most alkaline lake in the study, Lake Collerson (CO). The Mule Peninsula group has six lakes, the least amount amongst groups, but

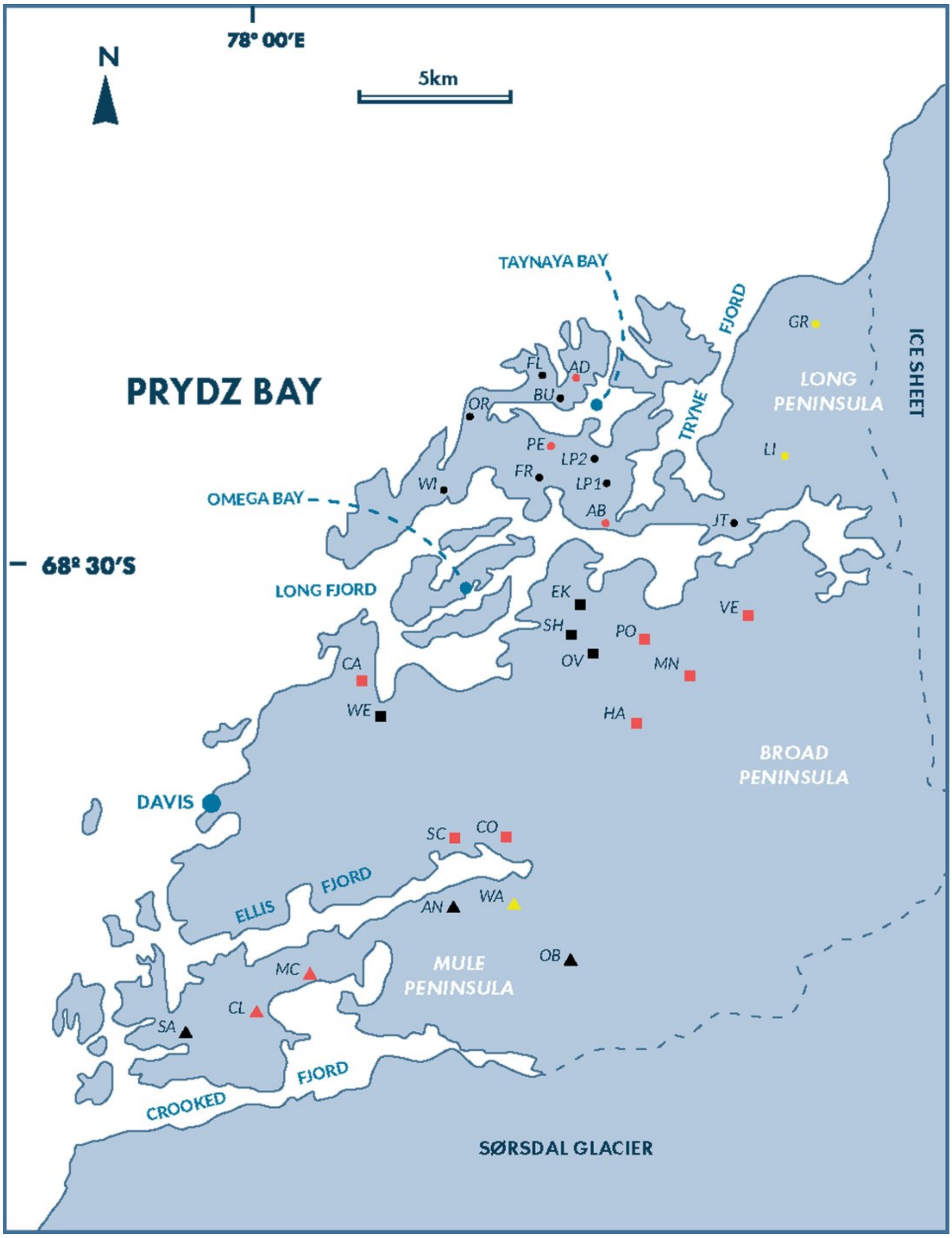


Figure 1. The location of the lakes of the Vestfold Hills within Prydz Bay, East Antarctica (adapted from Roberts & McMinn 1996). Lake locations are denoted by their respective lake sample code. Long, Broad, and Mule lake groups are denoted by shape: circle, square and triangle, respectively. Lake salinity categories are show with color: fresh (yellow), hyposaline (red) and hypersaline (black)

also the last of the freshwater lakes. The Mule Peninsula group also has the deepest, and most saline lakes, Clear Lake (CL) and South Angle lake (SA), respectively, in the study.

Table 1. Lake codes alongside qualitative and quantitative water chemistry metadata from Roberts & McMinn (1996, 1999). Species Richness was calculated for the current study. Lake Group has been adapted from Gibson (1999). Samples denoted with "#" were collected with an Ekman Grab Corer. The remainder were sampled with a Glew corer.

Lakes Name	Lake Code	Group	Elevation (m)	Maximum Depth (m)	Salinity Minimum (‰)	Salinity Maximum (‰)	Mixing Status
Abraxas	AB	Long	13.11	23	15.36	22.85	meromictic
Admin	AD	Long	0.95	6	14.84	17.53	holomictic
Burch	BU	Long	-0.07	7	135.02	167.83	meromictic
Fletcher	FL	Long	0.36	12	65.3	100.01	meromictic
Franzmann	FR#	Long	NA	8.5	71.16	96.02	meromictic
Grace	GR#	Long	NA	3	0.57	1.17	holomictic
Johnstone	JT#	Long	NA	9.8	155.8	167.42	meromictic
Lichen	LI#	Long	NA	26	0.5	0.61	holomictic
LP1	LP1	Long	7.51	4.9	73.94	127.38	meromictic
LP2	LP2	Long	7.51	1.8	132.77	170.22	holomictic
Organic	OR#	Long	2.75	7	138.78	177.07	meromictic
Pendant	PE	Long	3.045	18.4	13.53	36.6	meromictic
Williams	WI	Long	1.165	7	46.56	134.31	meromictic
Camp	CA#	Broad	NA	7.4	15.56	18.58	uncertain
Collerson	CO	Broad	4.99	8.2	7.74	9.33	holomictic
Hand	HA	Broad	9.55	29	4.9	5.59	meromictic
McNeil	MN	Broad	27.3	3.8	8.35	11.05	holomictic
Pointed	PO#	Broad	5.52	5	5.04	5.14	holomictic
Vereteno	VE#	Broad	0.96	25	3.65	3.75	holomictic
Weddell	WE	Broad	NA	6	58.91	72.61	holomictic
Scale	SC	Broad	NA	10.6	16.29	32.39	meromictic
Shield	SH#	Broad	-6.915	33	71.31	154.14	meromictic
Ekho	EK#	Broad	-1.405	39	46.13	149.14	meromictic
Oval	OV#	Broad	-28.44	16	142.86	175.31	meromictic
Oblong	OB#	Mule	-2.89	14.8	148.43	178.05	meromictic
Anderson	AN	Mule	3.5	21	57.24	144.05	meromictic
Clear	CL	Mule	-8.28	60.5	8.73	13.84	meromictic
McCallum	MC	Mule	-1.71	32	10.05	23.92	meromictic
South Angle	SA	Mule	-0.385	20	104.64	181.54	meromictic
Watts	WA	Mule	NA	29.5	2.24	2.4	holomictic

Table 1. Continued.

Lakes Name	Lake Category	Oxycline Depth (m)	Minimum Salinity Above Oxycline (‰)	Maximum Salinity Above Oxycline (‰)
Abraxas	hyposaline	17.5	17.3	22.9
Admin	hyposaline	NA	NA	NA
Burch	hypersaline	5	147.2	166.5
Fletcher	hypersaline	7.5	65.3	90.7
Franzmann	hypersaline	3.5	71.2	72.9
Grace	fresh	NA	NA	NA
Johnstone	hypersaline	7.5	163.9	167.4
Lichen	fresh	NA	NA	NA
LP1	hypersaline	3	88.4	127.4
LP2	hypersaline	NA	NA	NA
Organic	hypersaline	4	175	177.1
Pendant	hyposaline	10	13.5	18.1
Williams	hypersaline	5.5	104.05	134.3
Camp	hyposaline	4	18.2	18.6
Collerson	hyposaline	NA	NA	NA
Hand	hyposaline	NA	NA	NA
McNeil	hyposaline	NA	NA	NA
Pointed	hyposaline	NA	NA	NA
Vereteno	hyposaline	NA	NA	NA
Weddell	hypersaline	NA	NA	NA
Scale	hyposaline	5	16.3	27.6
Shield	hypersaline	17.5	71.3	133.4
Ekho	hypersaline	14	46.1	77
Oval	hypersaline	11	142.2	174.4
Oblong	hypersaline	5.5	171.1	178.1
Anderson	hypersaline	3.5	121.6	144.1
Clear	hyposaline	30	8.7	12.5
McCallum	hyposaline	19.5	10.1	23.9
South Angle	hypersaline	4	104.6	162.1
Watts	fresh	NA	NA	NA

Table 1. Continued.

Lakes Name	Salinity (‰ at 2 m)	NO_3 (μmol L $^{-1}$)	PO_4 (μmol L $^{-1}$)	SiO_2 (μmol L $^{-1}$)	Na (mg L $^{-1}$)	K (mg L $^{-1}$)
Abraxas	15.8	<0.10	0.08	36.04	3560	237
Admin	14.8	<0.10	0.91	186.76	4470	340
Burch	138	<0.10	2.76	134.61	52830	3130
Fletcher	65.3	0.42	1.27	91.35	25090	1130
Franzmann	71.4	15.06	3.36	133.31	23880	1070
Grace	1.1	<0.10	0.79	3.49	132	7.1
Johnstone	157	<0.10	0.26	90.7	62610	3820
Lichen	0.5	<0.10	0.14	5	9.8	1.4
LP1	74.1	<0.10	0.11	147.89	26590	1180
LP2	140	<0.10	0.24	139.54	59380	3290
Organic	142	<0.10	16	68.74	67640	4870
Pendant	13.6	<0.10	0.61	118.54	4250	296
Williams	46.9	0.95	0.21	49.29	12960	1370
Camp	16.4	<0.10	0.29	99	4500	360
Collerson	8.6	<0.10	0.99	98.97	2600	174
Hand	5.5	<0.10	0.08	117.91	880	87
McNeil	8.8	<0.10	0.1	122.65	3050	195
Pointed	5.1	<0.10	0.18	54.81	1410	430
Vereteno	3.7	<0.10	0.1	17.95	1050	205
Weddell	59.5	0.11	0.13	153.16	17540	2240
Scale	16.3	<0.10	0.16	79.15	4500	435
Shield	77.5	<0.10	0.19	101.6	23410	1240
Ekho	52	0.13	0.35	41.74	13210	1940
Oval	143	<0.10	0.94	122.07	52830	2900
Oblong	165	<0.10	0.21	113.53	65520	4620
Anderson	62.9	1.45	0.12	104.27	16890	1150
Clear	10.7	<0.10	0.26	107.92	2370	148
McCallum	14.5	<0.10	0.15	84.06	2750	184
South Angle	138	<0.10	0.45	142.38	49180	2760
Watts	2.3	<0.10	0.18	9.68	610	105

Table 1. Continued.

Lakes Name	Mg (mg L $^{-1}$)	Ca (mg L $^{-1}$)	Cl (mg L $^{-1}$)	SO_4 (mg L $^{-1}$)	Alkalinity as $CaCO_3$ (mg L $^{-1}$)	Species Richness
Abraxas	690	76	6150	1076	50	18
Admin	740	182	7400	1788	67.5	25
Burch	15020	2310	92700	3320	80	10
Fletcher	6380	1010	35100	5720	52.5	27
Franzmann	6090	1080	35700	6460	92.5	44
Grace	28	8.3	275	17.7	10	16
Johnstone	18000	2750	105300	4010	165	16
Lichen	1.6	2.5	18	3.2	12.5	12
LP1	7870	530	45300	2610	215	16
LP2	17400	1950	102500	4130	187.5	12
Organic	20080	3190	116400	4100	197.5	16
Pendant	870	178	7400	1320	60	21
Williams	3180	570	25550	1910	65	29
Camp	1140	115	8200	520	75	26
Collerson	560	16	4600	84	237.5	14
Hand	320	13	2200	8.8	67.5	17
McNeil	930	50	5850	448	82.5	21
Pointed	460	22	2950	81	107.5	50
Vereteno	270	38	1950	207	40	17
Weddell	4460	430	33500	3485	130	19
Scale	1500	22	9200	122	245	23
Shield	6680	790	40300	2750	70	27
Ekho	3360	430	26100	1975	80	16
Oval	15020	1730	89700	89700	165	24
Oblong	19490	2460	117800	2460	157.5	36
Anderson	5490	500	33500	1740	90	47
Clear	540	24	4400	458	120	23
McCallum	540	20	4800	390	162.5	31
South Angle	14430	1810	89700	2400	160	18
Watts	215	25	1200	187	42.5	23

Diatom Analysis

Surface sediments (0–2 cm) from the deepest sections of 33 lakes in the Vestfold Hills were collected using a Glew corer or Eckman grab sampler during the November to December field seasons in 1992 and 1994 (Roberts & McMinn 1999). In the original study, three slides were prepared for each lake, with 400 diatom valves counted on each. These data were then combined for a total of 1200 valves per lake. In the present study, a total of 30 slides containing prepared lake sediments (Table 1), originating as the third set of replicates from Roberts & McMinn (1999), were analyzed. The first and second replicates, as well as the corresponding unprepared sediments have been either lost or destroyed. Four hundred diatom valves per sample were counted in random transects. In four lake samples it was not possible to reach 400 counted valves even after scanning the entire slide: Watts (WA, 71 valves), Vereteno (VE, 171 valves), Abraxas (AB, 173 valves) and Weddell (WE, 209 valves). Despite the low count data for the four lakes, they were included in the analysis. Light Microscopy (LM) was performed using an Olympus BX43 light microscope equipped with Differential Interference Contrast (Nomarski) optics at 1000x magnification. Images were taken using an Olympus PD27 Color camera with CellSens Entry 1.15 software.

Lake environmental data such as salinity, nitrate (NO_3), phosphate (PO_4), silicate (SiO_2), sodium (Na), potassium (K), magnesium (Mg), calcium (Ca), chloride (Cl), sulfate (SO_4), alkalinity as $CaCO_3$, and mixing status, among others, were compiled by Roberts & McMinn (1999) and displayed through a series of tables in their original publication. Briefly, water samples were taken from a depth of 2 m, except from Watts and Pointed lakes, which were taken from the surface. Samples were frozen at –20° C, then returned and analyzed at the Institute of Antarctic and Southern Ocean Studies, University of Tasmania. Water sample analysis protocols and descriptions of field methods and equipment are described within Roberts & McMinn (1996). Taxonomic affiliations and biogeographic data have been compiled from the following: Medlin & Hasle (1990), Cox (1995), Roberts & McMinn (1996, 1999), Witkowski et al. (2000), Lange-Bertalot (2001), Kellogg & Kellogg (2002), Cremer at al. (2003), Sabbe et al. (2003), Ohtsuka et al. (2006), Al-Handal & Wulff (2008a, 2008b), Van de Vijver at al. (2002, 2010, 2012, 2014), Kohler et al. (2015) and Zidarova et al. (2016). In the event of ambiguous or uncertain taxa, images were taken and corresponding measurements of valve length, valve width at mid-valve and stria density per 10 ∝m were made. When the identity of a taxon could not be confirmed based on the existing literature, the designations “cf.” or “sp.” were added alongside a proposed generic and/or species identification.

Statistical Analysis

Raw diatom count data were transformed into relative abundance (%) per sample that were used for subsequent statistical analyses. All species remained throughout the analyses despite their relative abundance. This contrasts Roberts & McMinn (1999), where a taxon was included if its abundance was greater than or equal to 2% in any single sample.

A permutational multivariate analysis of variance (PERMANOVA, Anderson 2001) test was used to determine if the communities were significantly different based upon categorical data classifications, such as lake salinity category, mixing status, and their combined effects. Significance was designated at $\alpha = 0.05$, and was performed using the *vegan* package, version 2.5–6 (Oksanen et al. 2019) in the R console, version 3.5.0 (R core team 2018).

Principal components analysis (PCA) was used to explore large-scale relationships between diatom species distributions and lake salinity categories, classified as either fresh, hyposaline, or hypersaline. To investigate how differences in lake environments structure diatom communities, relative abundance data were analyzed roughly following Roberts & McMinn (1996) in CANOCO (ver. 5). Roberts & McMinn (1999) referred to Robert &

McMinn (1996) regarding the details of the statistical analyses presented in their later (1999) study. Due to the differences in software versions between the original and present analysis, Šmilauer & Lepš (2014) was consulted to ensure agreement between methods. Environmental variables were $\log_{(10)}$ transformed prior to analysis. Within the original analysis performed by Roberts & McMinn (1996), NO_3 and PO_4 were removed. Here, we chose to include them. In the case of nitrate concentration, a number of values are shown as " <0.10 µmol l^{-1} ". For these, we substituted values with half the detection limit (0.05 µmol l^{-1}). For phosphate, we performed a series of CCA analyses with phosphate values, and although two lakes with elevated concentrations (Franzmann (FR) and Anderson (AN), respectively) exhibited higher influence (measured as leverage) within the analysis. As in Roberts & McMinn (1996), we chose to include these lakes. Roberts & McMinn (1996) reported that once an "outlier" lake sample with elevated phosphate levels was removed, the subsequent lakes with the next highest value for phosphate then in turn became the "outlier". We performed this analysis and despite the leverage values for each lake, subsequent effects to the model overall was negligible. Additionally, omission of phosphate and nitrate yielded negligible differences in subsequent CCA and forward model selection.

Species abundance data and their responses to environmental variables are often nonlinear, making unimodal models more effective in analyzing these data (ter Braak 1996). A preliminary DCA was performed to investigate gradient lengths, measured in standard deviations, as this will aid in determining if unimodal or linear methods should be used. A gradient length above four standard deviations suggests that response variables exhibit a unimodal response along the gradient (ter Braak & Šmilauer 2012). In the current analysis, gradient lengths for the first four axes were 5.91, 4.34, 2.76, and 2.85, respectively, making unimodal techniques more appropriate. As such, a series of constrained, canonical correspondence analysis (CCA) were performed to investigate how individual lake chemistry measurements affect diatom community structure. The results of a preliminary CCA using all lake chemistry variables yielded strong correlations between salinity and a number of other cations. As performed in Roberts & McMinn (1996), variables were separated into active and passive environmental variables as determined by their relationships in the correlation matrix and a high variance inflation factors (VIFs). Passive variables possess inflated VIFs (much larger than 20) and are strongly correlated with other variables. As such, they contribute little additional information in the ordination (ter Braak & Šmilauer, 2012). In the present analysis, variables possessing VIF's larger than 20 were removed from the analysis, and included Cl, Ca, K, Mg and Na. The remaining active environmental variables were salinity, SiO_2, SO_4, alkalinity, NO_3 and PO_4. Following this, a CCA with forward model selection, undergoing 9999 permutations of an unrestricted Monte Carlo test was performed.

Results & Discussion

Diatom community composition

A total of 183 taxa (including species, varieties and forms) from 38 genera were observed across all lake ecologies (fresh, hyposaline and hypersaline) in the present study. Fifty-eight taxa were identified to species level (including variety and forms), including 19 marine and 39 freshwater taxa. One hundred fifteen taxa could be confidently identified to the genus level, while ten taxa could not be assigned to a genus or species. Within Roberts & McMinn (1999), 67 species across 26 genera were observed. We report "freshwater" and "marine" species based upon observational and distribution data from the literature, where available. We report 37 taxa, including forms and varieties, in the present study that are endemic to the Antarctic region. Roberts & McMinn (1999) provide distribution data for the taxa they encountered but specifically state three species (*Eucampia antarctica* (Castracane) Manguin, *Fragilariopsis curta* (Van Heurck) Hasle, and *Chamaepinnularia cymatopleura* (W. et G.S.West) Cavacini, then described as *Pinnularia cymatopleura*) as endemic to the Antarctic region. Table 2 lists the observed taxa in full, across all analyses, alongside their distribution data.

The majority of taxa belonged to the following genera: *Navicula* Bory (38 taxa), *Nitzschia* Hassall (20 taxa), and *Planothidium* Round & Bukhtiyarova (16 taxa). Species richness ranged from 10 to 50 per lake with a median value of 21. The lakes with the largest species richness were Pointed Lake (50), Anderson Lake (47), and Franzmann Lake (44). We recorded 41 taxa above 0.5% relative abundance and only 25 taxa occurred at a relative abundance larger than 1%. The most abundant taxa were *Sabbea adminensis* (D.Roberts & McMinn) Van de Vijver, Bishop and Kopalová (14% of all valves counted), *Navicula* Bory sp. 2 (8.2%), and *Navicula* Bory sp. 3 (5.4%). The top ten most important taxa accounted for 50% of all counted valves. Taxa with a relative abundance >1% comprise 77% of all counted valves. Selected taxa are shown in Figs. 2–66.

A principal components analysis (PCA) comparing species abundance data with lake salinity categories (fresh, hyposaline, and hypersaline), shows that each lake category features characteristic taxa, namely *Navicula* sp. 2 (Nav_Ma3) and *Navicula* sp. 3 (Nav_Ma4) in hypersaline lakes (Fig. 67). While lake salinity categories appear distinct, there was overlap between all three categories, suggesting that a subset of species can occur in lakes with a range of salinities (Fig. 67). Initial data exploration by PCA revealed distinct groupings of hyper- and hypo-saline lakes by their respective salinity category, with the smallest group (fresh, n=3) in the study grouping clustered most closely together, while the former groups display a wide breadth in their classification **(**Fig. 67**)**. A number of individual species showed distinct preferences. For example, *Sabbea adminensis* (Nav_adm) is associated with both hyposaline and hypersaline lakes, as its type locality Admin Lake (AD) appears closely situated near the saline lake grouping. This is also seen with *Halamphora vyvermaniana* Van de Vijver,

Table 2. Current taxonomic placement and distribution data compiled for the flora of the Vestfold Hills. Distribution designations follow the conventions: SA: Sub-Antarctic, MA: Maritime Antarctic, CA: Continental Antarctica, C: Cosmopolitan Freshwater, Marine: Marine species, CircAnt: Circum-Antarctic marine waters, NCW/SCW: Northern and Southern Cold Waters, Marine. Taxonomic groupings "MRN" refer to the small, presumably marine *Navicula* taxa while "GRP" refers to the artificial grouping of *Navicula phyllepta* -like species. Taxa endemic to the Antarctic Region are denoted with "Endemic".

Code	**Taxon**	**Distribution**	**Current taxonomic status vs. Roberts & McMinn (1999)**	**Notes**	**Taxon Group**	**Endemic**
Ach_tay	*Achnanthes taylorensis* D.E.Kellogg, Stuiver, T.B.Kellogg & G.H.Denton	MA/CA	Present & Revised	Plate 1. Figs 3–4 as *Achnanthes brevipes* Agardh in Roberts & McMinn (1999)	–	Endemic
Ast_sp1	*Astartiella* A.Witkowski, Lange-Bertalot & Metzeltin sp1	–	Not Present	–	–	–
Ast_lik	*Astartiella* A.Witkowski, Lange-Bertalot & Metzeltin cf. sp1	–	–	–	–	–
Amp_ant	*Amphora antarctica* Hustedt	CircAnt	Present&Unchecked (Revisions)	–	–	Endemic
Amp_spd	*Amphora* Ehrenberg ex Kützing sp1	–	–	–	–	–
Amp_ma1	*Amphora* Ehrenberg ex Kützing sp2	–	–	–	–	–
Amp_ma2	*Amphora* Ehrenberg ex Kützing sp3	–	–	–	–	–
Ber_sp1	*Berkeleya* Greville sp1	–	*Berkeleya adeliensis* Medlin was identified in Roberts & McMinn Plate 2, Figs 1–3 (1999) but the taxon observed here could not be identified to species level	–	–	–
Cat_sp1	*Catenula* Mereschkowsky sp1	–	*Genus not originally identified in Roberts & McMinn (1999)	–	–	–
Cat_sp2	*Catenula* Mereschkowsky sp2	–	*	–	–	–
Cat_sp3	*Catenula* Mereschkowsky sp3	–	*	–	–	–
Cnt_pck	Centric sp1	–	–	–	–	–
Cnt_fpc	Centric sp2	–	–	–	–	–
Cnt_spy	Centric sp3	–	–	–	–	–
Cnt_hup	Centric sp4	–	–	–	–	–
Cnt_phu	Centric sp5	–	–	–	–	–
Cnt_cnt	Centric sp6	–	–	–	–	–
Tha_ant	*Thalassiosira antarctica Comber*	NCW/SCW	Present&Unchecked (Revisions)	–	–	–
Coc_cos	*Cocconeis costata* Gregory	C–Marine	Present&Unchecked (Revisions)	–	–	–
coc_pin	*Cocconeis pinnata* Gregory	C–Marine	Present&Unchecked (Revisions)	–	–	–
Coc_sp1	*Cocconeis* Ehrenberg sp1	–	–	–	–	–

Table 2. Continued

Code	Taxon	Distribution	Current taxonomic status vs. Roberts & McMinn (1999)	Notes	Taxon Group	Endemic
Cha_cel	*Chaetoceros Ehrenberg* vegetative cells	–	Present&Unchecked(Revisions)	–	–	–
Cha_ufo	*Chaetoceros Ehrenberg* resting spores	–	Present&Unchecked(Revisions)	–	–	–
Chm_sp1	*Chamaepinnularia* Lange-Bertalot & Krammer sp1	–	Not Present	–	–	–
Chm_cym	*Chamaepinnularia cymatopleura* (W. et G.S.West) Cavacini	CA	Present & Revised	–	–	Endemic
Cra_lae	*Craspedostauros laevissimum* (W. et G.S.West) Sabbe	CA	Present & Revised	–	–	Endemic
Sub_lik	*Craticula* cf. *submolesta* (Hustedt) Lange-Bertalot var 1	–	Not Present. Possibly lumped within other Navicula taxa	–	–	–
Sub_lk2	*Craticula* cf. *submolesta* (Hustedt) Lange-Bertalot var 2	–	Not Present. Possibly lumped within other Navicula taxa	–	–	–
Cra_ant	*Craticula antarctica* Van de Vijver & Sabbe	MA/CA	Not Present	–	–	Endemic
Ant_Lik	*Craticula* cf. *antarctica* Van de Vijver & Sabbe	–	–	–	–	–
Dip_spl	*Diploneis splendida* Cleve	C–Marine	Present&Unchecked (Revisions)	–	–	–
Euc_ant	*Eucampia antarctica* (Castracane) Mangin	SCW	Present&Unchecked (Revisions)	–	–	Endemic
Enc_sp1	*Entomoneis* Ehrenberg sp1	–	Genus present in both	–	–	–
Eun_sp1	*Eunotia* Ehrenberg sp1	–	*Genus not originally identified in Roberts & McMinn (1999)	–	–	–
Eun_sp2	*Eunotia* Ehrenberg sp2	–	*Genus not originally identified in Roberts & McMinn (1999)	–	–	–
Fop_cur	*Fragilariopsis curta* (Van Heurck) Hustedt	CA–Marine	Present&Unchecked (Revisions)	–	–	Endemic
Fop_cyl	*Fragilariopsis cylindrus* (Grunow ex Cleve) Helmcke & Krieger	CA–Marine	Present&Unchecked (Revisions)	–	–	Endemic
Fop_per	*Fragilariopsis peragalloi* (Hasle) Cremer	CA–Marine	Not Present	–	–	Endemic
Fop_rho	*Fragilariopsis rhombica* (O'Meara) Hustedt	CA–Marine	Not Present	–	–	Endemic
Fop_sub	*Fragilariopsis sublinearis* (Van Heurck) Heiden & Kolbe	CA–Marine	Not Present	–	–	Endemic

Table 2. Continued

Code	Taxon	Distribution	Current taxonomic status vs. Roberts & McMinn (1999)	Notes	Taxon Group	Endemic
Fop_van	*Fragilariopsis vanheurckii* (Peragallo) Hustedt	CA–Marine	Not Present	–	–	Endemic
Fop_bg1	*Fragilariopsis* Hustedt sp1	–	–	–	–	–
Gom_lit	*Gomphonemopsis littoralis* (Hendey) Medlin	C–Marine	Not Present	–	–	–
Gom_cfl	*Gomphonemopsis* cf. *littoralis* (Hendey) Medlin	–	–	–	–	–
Gom_sp1	*Gomphonema* Ehrenberg sp1	–	–	–	–	–
Gom_sp2	*Gomphonema* Ehrenberg sp2	–	–	–	–	–
Gom_sp3	*Gomphonema* Ehrenberg sp3	–	–	–	–	–
Gom_sp4	*Gomphonema* Ehrenberg sp4	–	–	–	–	–
Hal_vyv	*Halamphora vyvermaniana* Van de Vijver, Kopalová, Zidarova & Levkov	CA	Not Present	*On Plate 1. Fig 5 (Roberts & McMinn 1999) as *Amphora veneta* Kützing.	–	Endemic
Hal_lat	*Halamphora lateantarctica* Van de Vijver, Kopalová, Zidarova & Levkov	CA	Not Present	*	–	Endemic
Hal_sp1	*Halamphora* (Cleve) Levkov sp1	–	–	–	–	–
Hal_sp2	*Halamphora* (Cleve) Levkov sp2	–	–	–	–	–
Hal_sp3	*Halamphora* (Cleve) Levkov sp3	–	–	–	–	–
Hal_sp4	*Halamphora* (Cleve) Levkov sp4	–	–	–	–	–
Hal_sp5	*Halamphora* (Cleve) Levkov sp5	–	–	–	–	–
Hal_xxx	*Halamphora* (Cleve) Unidentifiable valve	–	–	–	–	–
Hnz_sp1	*Hantzschia* cf. *amphioxys* (Ehrenberg) Grunow	–	–	–	–	–
Hum_sp1	*Humidophila australis* (Van de Vijver & Sabbe) R.L.Lowe, Kociolek, J.R.Johansen, Van de Vijver, Lange-Bertalot & Kopalová	MA/CA	Not Present	–	–	Endemic
Lut_mut	*Luticola muticopsis* (Van Heurck) D.G.Mann	SH	Present & Revised	*Luticola D.G.Mann taxa were grouped as Navicula mutica Kützing/muticopsis Van Heurck. See Plate 5. Figs 1–6 (Roberts & McMinn 1999)	–	–

Table 2. Continued

Code	Taxon	Distribution	Current taxonomic status vs. Roberts & McMinn (1999)	Notes	Taxon Group	Endemic
Mut_lik	*Luticola* cf. *muticopsis* (Van Heurck) D.G.Mann	–	–	–	–	–
Lut_sp1	*Luticola* D.G.Mann sp1	–	–	–	–	–
Lut_olg	*Luticola olegsakharovii* Levkov & Van de Vijver	MA	Not Present	*	–	Endemic
Lut_psu	*Luticola pseudomurrayi* Van de Viver & Tavernier	CA	Not Present	*	–	Endemic
Lut_gau	*Luticola* cf. *gaussii* (Heiden) D.G.Mann	–	–	*	–	–
Lut_trn	*Luticola* cf. *transantarctica* Kohler & Kopalová	–	–	*	–	–
Lut_aus	*Luticola austroatlantica* Van de Vijver, Kopalová, Spaulding & Esposito	CA/MA	Not Present	–	–	Endemic
Mri_like	*Luticola* D.G.Mann unidentifiable valve	–	–	–	–	–
Mic_lik	*Microfissurata* Lange-Bertalot, Cantonati & Van de Vijver sp1	–	*Genus not originally identified in Roberts & McMinn (1999)	–	–	–
Mic_lik2	*Microfissurata* Lange-Bertalot, Cantonati & Van de Vijver sp2	–	*	–	–	–
Nan_shi	*Nanofrustulum shiloi* (Lee, Reimer & McEnery) Round, Hallsteinsen & Paache	Marine	Not Present	–	–	–
Nav_col	*Navicula collersonii* Roberts & McMinn	CA	Present & Unchecked (Revisions)	*Species described in Roberts & McMinn (1999)	–	Endemic
Cry_lik	*Navicula* cf. *criophila* (Castracane) Van Heurck	–	–	–	–	–
Nav_dir	*Navicula directa* (W.Smith) Ralfs	Marine	Present & Unchecked (Revisions)	*Often identified as a problematic taxa	–	–
Nav_ect	*Navicula ectoris* Van de Vijver	SA/CA	Not Present	Not originally reported; likely grouped with *N. phyllepta* Kützing	GRP	Endemic
Ect_Lik	*Navicula* cf. *ectoris* Van de Vijver 1	–	–	–	GRP	–
Ect_lk2	*Navicula* cf. *ectoris* Van de Vijver 2	–	–	–	GRP	–

Table 2. Continued

Code	Taxon	Distribution	Current taxonomic status vs. Roberts & McMinn (1999)	Notes	Taxon Group	Endemic
Nav_gre	*Navicula gregaria* Donkin	C	Questionable	See Text	GRP	–
Gre_lik	*Navicula* cf. *gregaria* Donkin	–	–	–	GRP	–
Per_like	*Navicula* cf. *perminuta* Grunow	–	–	–	–	–
Nav_phy	*Navicula phyllepta* Kützing	C	Questionable	See Text	GRP	–
Phy_lik	*Navicula* cf. *phyllepta* Kützing	–	–	–	GRP	–
Nav_sma	*Navicula phylleptosoma* Lange-Bertalot	C	Questionable	See Text	GRP	–
Sma_lik	*Navicula* cf. *phylleptosoma* Lange-Bertalot	–	–	–	GRP	–
Nav_gla	*Navicula glacei* Van Heurck	Marine	Present & Unchecked (Revisions)	–	MRN	–
Nav_spa	*Navicula* Bory sp1	–	–	*many *Navicula* taxa are represented by a single valve or fragment, small in size and likely marine	MRN	–
Nav_ma3	*Navicula* Bory sp2	–	–	*	MRN	–
Nav_ma4	*Navicula* Bory sp3	–	–	*	MRN	–
Nav_ma5	*Navicula* Bory sp4	–	–	*	MRN	–
Nav_ma6	*Navicula* Bory sp5	–	–	*	MRN	–
Nav_ma7	*Navicula* Bory sp6	–	–	*	MRN	–
Nav_ma9	*Navicula* Bory sp7	–	–	*	MRN	–
Nav_ma10	*Navicula* Bory sp8	–	–	*	MRN	–
Nav_m11	*Navicula* Bory sp9	–	–	*	MRN	–
Nav_m12	*Navicula* Bory sp10	–	–	*	MRN	–
Nav_mra	*Navicula* Bory sp11	–	–	*	MRN	–
Nav_mrb	*Navicula* Bory sp12	–	–	*	MRN	–
Nav_mrd	*Navicula* Bory sp13	–	–	*	MRN	–
Nav_mre	*Navicula* Bory sp14	–	–	*	MRN	–
Nav_mrf	*Navicula* Bory sp15	–	–	*	MRN	–
Nav_mrg	*Navicula* Bory sp16	–	–	*	MRN	–
Nav_mrh	*Navicula* Bory sp17	–	–	*	MRN	–
Nav_sal	*Navicula* cf. *salinarum* Grunow	–	Identified in Roberts & McMinn (1999) but questionable	–	GRP	–
Nav_sha	*Navicula shackletonii* W.West & G.S.West	CA	Not Present	–	–	Endemic
Nav_fmc	*Navicula* Bory sp18	–	–	–	MRN	–
Nav_sp1	*Navicula* Bory sp19	–	–	–	MRN	–

Table 2. Continued

Code	Taxon	Distribution	Current taxonomic status vs. Roberts & McMinn (1999)	Notes	Taxon Group	Endemic
Nav_sp2	*Navicula* Bory sp20	–	–	–	MRN	–
Nav_sp3	*Navicula* Bory sp21	–	–	–	MRN	–
Nav_xxx	*Navicula* Bory Unidentifiable Valve	–	–	–	–	–
Nit_xxx	*Nitzschia* Hassall Unidentifiable Valve	–	–	–	–	–
Frg_sy2	*Nitzschia* Hassall girdle view	–	–	–	–	–
Nit_gra	*Nitzschia gracilis* Hantzsch	C	Not Present	–	–	–
Gra_lik	*Nitzschia* cf. *gracilis* Hantzsch	–	–	–	–	–
Nit_com	*Nitzschia australocommutata* Hamsher, Kopalová, Kociolek, Zidarova & Van de Vijver	MA/CA	Not Present	–	–	Endemic
Nit_lec	*Nitzschia lecointei* Van Heurck	CircAnt	Present & Unchecked (Revisions)	–	–	Endemic
Lec_lik	*Nitzschia* cf. *lecointei* Van Heurck	–	–	–	–	–
Wst_like	*Nitzschia* cf. *westiorum* Kellogg et Kellogg	–	–	–	–	–
Nit_eee	*Nitzschia* Hassall sp1	–	–	–	–	–
Nit_bhx	*Nitzschia* Hassall sp2	–	–	–	–	–
Nit_ma1	*Nitzschia* Hassall sp3	–	–	–	–	–
Nit_ma2	*Nitzschia* Hassall sp4	–	–	–	–	–
Nit_sp.3	*Nitzschia* Hassall sp5	–	–	–	–	–
Nit_sp4	*Nitzschia* Hassall sp6	–	–	–	–	–
Nit_sp5	*Nitzschia* Hassall sp7	–	–	–	–	–
Nit_sp6	*Nitzschia* Hassall sp8	–	–	–	–	–
Nit_sp7	*Nitzschia* Hassall sp9	–	–	–	–	–
Nit_sp8	*Nitzschia* Hassall sp10	–	–	–	–	–
Nit_sp9	*Nitzschia* Hassall sp11	–	–	–	–	–
Nit_mda	*Nitzschia* cf. *medioconstricta* Hustedt	–	–	–	–	–
Pin_opn	*Pinnularia australomicrostauron* Zidarova, Kopalová & Van de Vijver morphotype 1	*Nominate variety MA/CA	**Present & Revised (Morphotypes were separated as in the present study)	–	–	Endemic
Pin_clo	*Pinnularia australomicrostauron* Zidarova, Kopalová & Van de Vijver morphotype 2	*	**	–	–	Endemic

Table 2. Continued

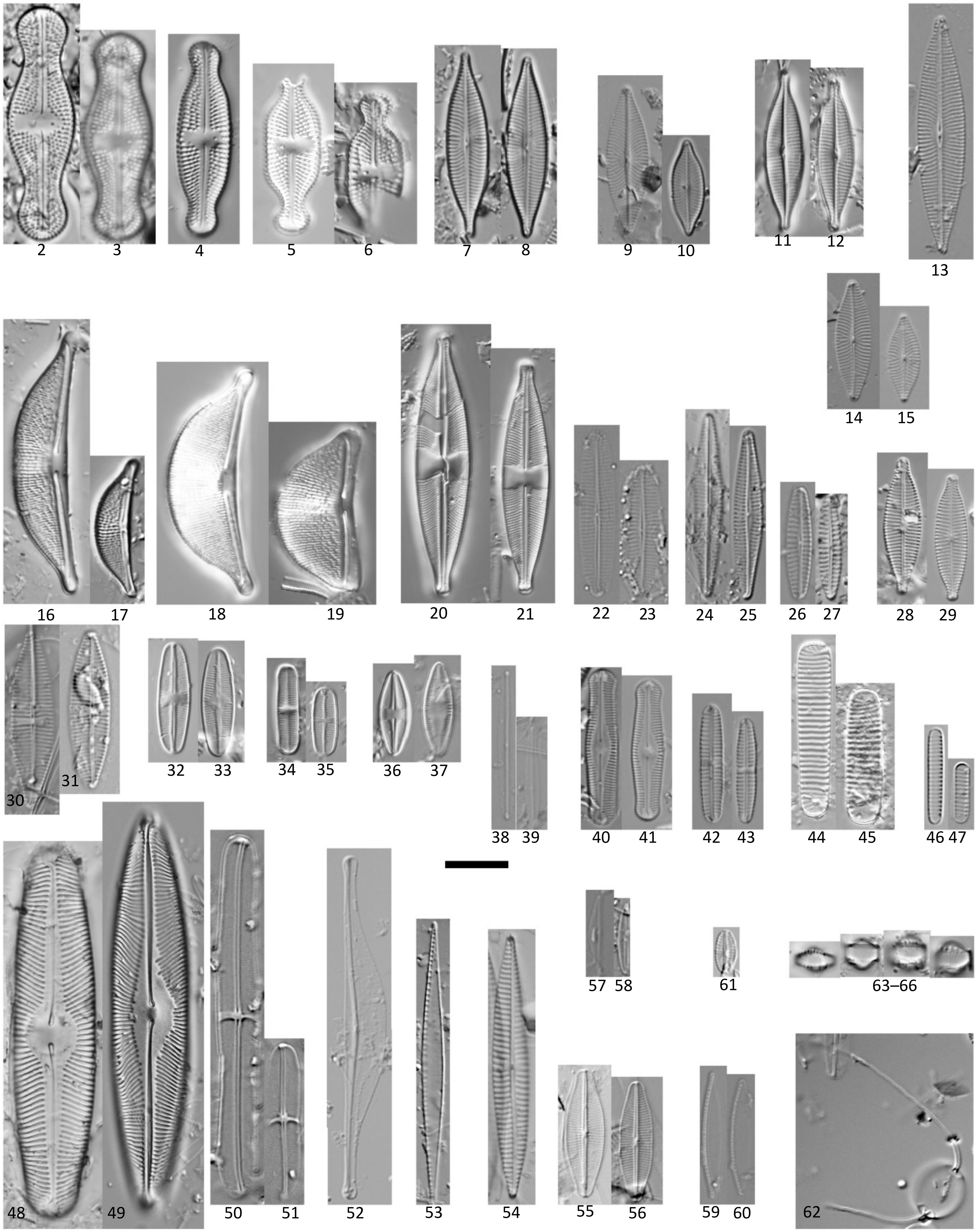
Code	Taxon	Distribution	Current taxonomic status vs. Roberts & McMinn (1999)	Notes	Taxon Group	Endemic
Pin_cl2	*Pinnularia australomicrostauron* Zidarova, Kopalová & Van de Vijver morphotype 3	*	**	–	–	Endemic
Pin_var	*Pinnularia australomicrostauron* Zidarova, Kopalová & Van de Vijver morphotype 4	*	**	–	–	Endemic
Pin_new	*Pinnularia australomicrostauron* Zidarova, Kopalová & Van de Vijver morphotype 5	*	**	–	–	Endemic
Pin_flt	*Pinnularia australomicrostauron* Zidarova, Kopalová & Van de Vijver morphotype 6	*	**	–	–	Endemic
Pin_glb	*Pinnularia australoglobiceps* Zidarova, Kopalová & Van de Vijver	SH	Present & Revised	–	–	–
Pin_lun	*Pinnularia* cf. *lundii* Hustedt	–	Present & Unchecked (Revisions)	Followed Roberts & McMinn (1999) for identifications	–	–
Pin_qbi	*Pinnularia* cf. *quadratarea* var. *bicuneata* Heiden	–	Present & Unchecked (Revisions)	Followed Roberts & McMinn (1999) for identifications	–	–
Pin_vir	*Pinnularia* cf. *viridis* (Nitzsch) Ehrenberg	–	Present & Unchecked (Revisions)	Followed Roberts & McMinn (1999) for identifications	–	–
Pin_sp1	*Pinnularia* Ehrenberg sp1	–	–	–	–	–
Pin_sp2	*Pinnularia* Ehrenberg sp2	–	–	–	–	–
Pin_sp3	*Pinnularia* Ehrenberg sp3	–	–	–	–	–
Pin_cte	*Pinnularia* Ehrenberg sp4	–	–	–	–	–
Ren_lik	*Planothidum* cf. *renei* (Lange-Bertalot & Schmidt) Van de Vijver	–	–	–	–	–
Pla_qua	*Planothidium quadripunctatum* (Oppenheim) Sabbe	MA/CA	Not Present	*This genus possibly appears, often represented by a single image discerning each species (Plate 2, Roberts & McMinn 1999)	–	Endemic

Table 2. Continued

Code	Taxon	Distribution	Current taxonomic status vs. Roberts & McMinn (1999)	Notes	Taxon Group	Endemic
Mgs_lik	*Planothidium* cf. *marginostriatum* Van de Vijver & Beyens	–	Not Present	–	–	–
Pla_dub	*Planothidium dubium* (Grunow) Round & Bukhtiyarova	C	Not Present	–	–	–
Pla_wtz	*Planothidium wetzelectorianum* Kopalová, Zidarova & Van de Vijver	MA	Not Present	–	–	Endemic
Pla_bea1	*Planothidium* Round & L.Bukhtiyarova sp1	–	–	–	–	–
Pla_bea2	*Planothidium* Round & L.Bukhtiyarova sp2	–	–	–	–	–
Pla_sp1	*Planothidium* Round & L.Bukhtiyarova sp3	–	–	–	–	–
Pla_sp2	*Planothidium* Round & L.Bukhtiyarova sp4	–	–	–	–	–
Pla_sp3	*Planothidium* Round & L.Bukhtiyarova sp5	–	–	–	–	–
Pla_sp4	*Planothidium* Round & L.Bukhtiyarova sp6	–	–	–	–	–
Pla_sp5	*Planothidium* Round & L.Bukhtiyarova sp7	–	–	–	–	–
Pla_sp6	*Planothidium* Round & L.Bukhtiyarova sp8	–	–	–	–	–
Pla_sp7	*Planothidium* Round & L.Bukhtiyarova sp9	–	–	–	–	–
Pla_sp8	*Planothidium* Round & L.Bukhtiyarova sp10	–	–	–	–	–
Bee_rap	*Planothidium* Round & L.Bukhtiyarova sp11	–	–	–	–	–
Psa_abu	*Psammothidium abundans* (Manguin) Bukhtiyarova & Round	C	Present & Revised	–	–	–
Abu_like	*Psammothidium* cf. *abundans* (Manguin) Bukhtiyarova & Round	–	–	–	–	–
Psa_con	*Psammothidium confusoneglectum* Kopalová, Zidarova & Van de Vijver	MA	Not Present	–	–	Endemic

Table 2. Continued

Code	Taxon	Distribution	Current taxonomic status vs. Roberts & McMinn (1999)	Notes	Taxon Group	Endemic
Psa_pap	*Psammothidium papilio* (D.E. Kellogg, M. Stuiver, T.B. Kellogg & G.H. Denton) Kopalová & Van de Vijver	MA/CA	Not Present	–	–	Endemic
Psa_spr	*Psammothidium superpapilio* Kopalová, Zidarova & Van de Vijver	MA	Not Present	–	–	Endemic
Psa_sub	*Psammothidium subatomoides* (Hustedt) Bukhtiyarova & Round	C	Not Present	–	–	–
Psa_sta	*Psammothidium stauroneioides* (Manguin) Buhktiyarova	SA/CA	Not Present	–	–	Endemic
Psa_inc	*Psammothidium incognitum* (Krasske) Van de Vijer	SH	Not Present	–	–	–
Pse_sp1	*Pseudostaurosira* D.M.Williams & Round sp1	–	–	–	–	–
Nav_adm	*Sabbea adminensis* (D.Roberts & McMinn) Van de Vijver, Bishop & Kopalová	CA	Genus not originally identified in Roberts & McMinn (1999)	–	–	Endemic
Nvd sem	*Sellaphora seminulum* (Grunow) D.G.Mann	C	Genus not originally identified in Roberts & McMinn (1999)	–	–	–
Sel_ant	*Sellaphora* Mereschowsky sp1	–	–	–	–	–
Lut_mri	*Sellaphora* Mereschowsky girdle view	–	–	–	–	–
Sta_sp1	*Stauroneis* Ehrenberg sp1	–	–	–	–	–
Sta_lat	*Stauroneis latistauros* Van de Vijver & Lange-Bertalot	MA/CA	Not Present	–	–	Endemic
Sta_ine	*Stauroforma inermis* Flower, Jones & Round	MA/CA	Present & Unchecked (Revisions)	Need for revision discussed in Zidarova et al. (2016)	–	–
Frg_sy1	*Synedra* Ehrenberg sp1	–	–	–	–	–
Syn_sp1	*Synedra* Ehrenberg sp3	–	–	–	–	–
Str_sp1	*Staurosira* Ehrenberg sp1	–	–	–	–	–
Tha_sp1	*Thalassionema* Grunow ex Mereschkowsky sp1	–	–	–	–	–
Try_mar	*Tryblionella marginulata* (Grunow) Mann	Marine	Present & Unchecked (Revisions)	–	–	–
Fst_xxx	Elongated Pennate Frustule *incertae sedis*	–	–	–	–	–



Figures 2–66. Common taxa of the Vestfold Hills. Figs 2–3 *Luticola psuedomurrayi*, Fig. 4 *Luticola austroatlantica*, Figs 5–6 *Luticola muticopsis*, Figs 7–8 *Navicula* cf. *salinarum*, Figs 9–10 *Navicula* cf. *ectoris*, Figs 11–12 *Navicula gregaria*, Fig. 13 *Navicula phyllepta*, Figs 14–15 *Navicula ectoris*, Figs 16–17 *Halamphora vyvermaniana*, Figs 18–19 *Halamphora lateantartica*, Figs 20–21 *Stauroneis latistauros*, Figs 22–23 *Navicula* sp. 1, Figs 24–25 *Navicula* sp. 2, Figs 26–27 *Navicula* sp. 3, Figs 28–29 *Craticula antarctica*, Figs 30–31 *Navicula glaciei*, Figs 32–33 *Psammothidium papilio*, Figs 34–35 *Psammothidium abundans*, Figs 36–37 *Psammothidium stauroneioides*, Figs 38–39 *Sabbea adminensis*, Figs 40–41 *Chamaepinnularia cymatopleura*, Figs 42–43 *Navicula collersonii*, Figs 44–45 *Fragilariopsis curta*, Figs 46–47 *Fragilariopsis cylindrus*, Fig. 48 *Pinnularia australomicrostauron* "closed fascia" morphotype, Fig. 49 *Pinnularia australomicrostauron* "new fascia" morphotype, Figs 50–51 *Craspedostauros laevissimus*, Fig. 52 *Amphora antartica*, Fig. 53 *Nitzschia lecontei*, Fig. 54 *Navicula directa*, Figs 55–56 *Astartiella* sp. 1, Figs 57–58 *Catenula* sp. 1, Figs 59–60 *Nitzschia* sp. 1, Fig. 61 *Microfissurata* sp. 1, Fig. 62 *Chaetoceros* species, Figs 63–66 *Chaetoceros* resting spores. 10µm scale bar applies to all images.

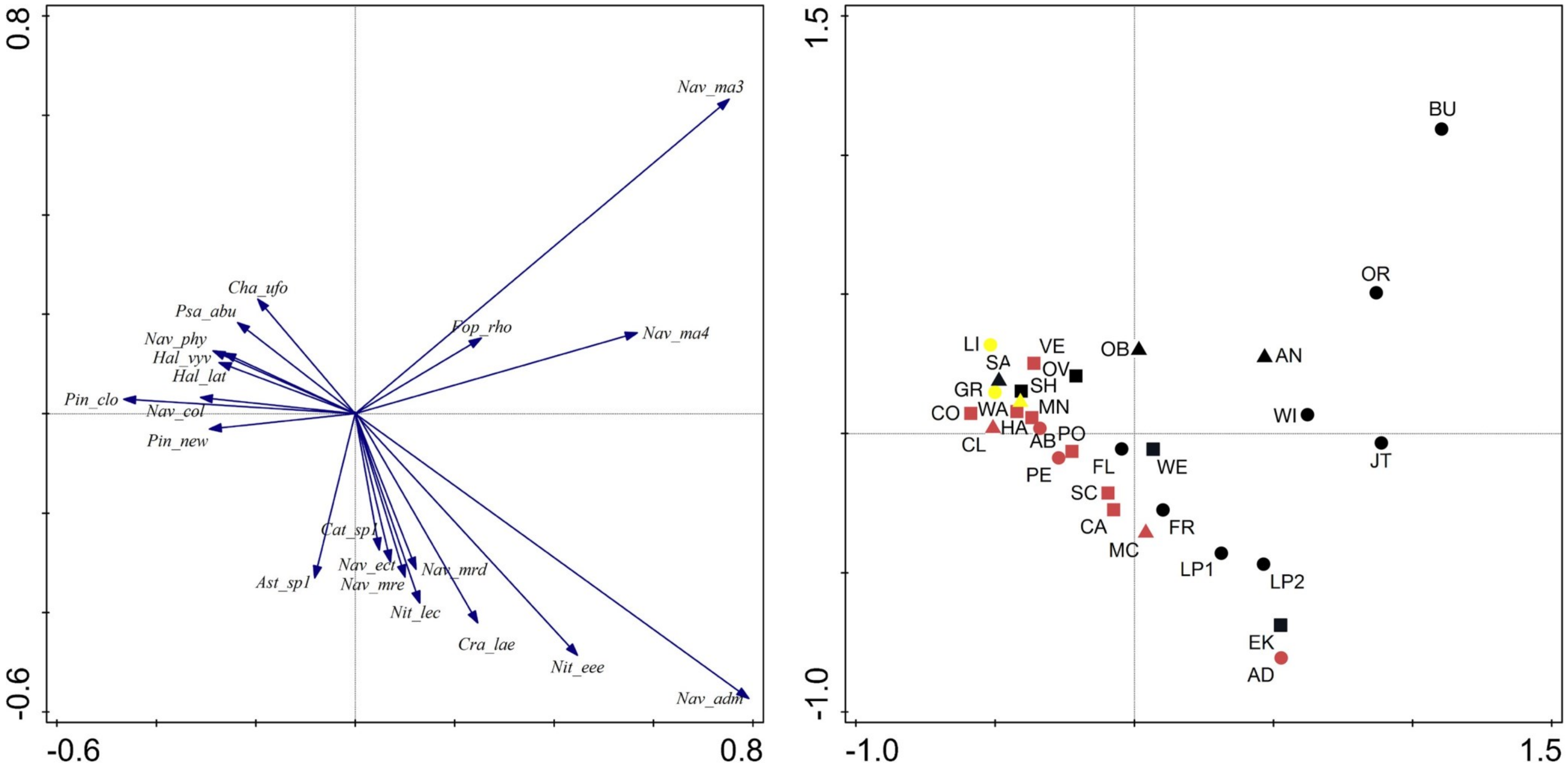


Figure 67. The results of a principal components analysis (PCA) comparing all 30 lakes present in the study against their lake salinity category (fresh, hyposaline, and hypersaline) represent by colored symbols (yellow, red, and black), respectively. Long, Broad, and Mule Lake groups are denoted by shape: circle, square and triangle, respectively. Taxon identity and codes are: *Chaetoceros* resting spores (Cha_ufo), *Psammothidium abundans* (Psa_abu), *Navicula phyllepta* (Nav_phy), *Halamphora vyvermaniana* (Hal_vyv), *Halamphora lateantartica* (Hal_lat), *Pinnularia australomicrostauron* "closed fascia" morphotype (Pin_clo), *Pinnularia australomicrostauron* "new fascia" morphotype (Pin_new), *Navicula collersonii* (Nav_col), *Astartiella* sp.1 (Ast_sp1), *Catenulla* sp.1 (Cat_sp1), *Navicula ectoris* (Nav_ect), *Navicula* sp.14 (Nav_mre), *Navicula* sp.13 (Nav_mrd), *Nitzschia lecontei* (Nit_lec), *Nitzschia* sp.1 (Nit_eee), *Craspedostauros laevissimus* (Cra_lae), *Navicula* sp.2 (Nav_Ma3), *Navicula* sp.3 (Nav_Ma4), *Sabbea adminensis* (Nav_adm), *Fragilariopsis rhombica* (Fop_rho).

Kopalová, Zidarova & Levkov (Hal_vyv) with fresh lakes, and *Navicula* sp. 2 (Nav_Ma3) with hypersaline lakes.

The results of the PERMANOVA showed that the lake salinity category was significant (*P*=0.001, r^2=0.208), but mixing status (*P*=0.595) was not. The combined effect of lake salinity category and mixing status was not significant in structuring diatom communities (*P*=0.503).

CCA with forward model selection (Fig. 68) displayed two overarching gradients present in the analysis, one with salinity and the other with alkalinity. The first two axes explain 15.08% of the variation, with axis 1 (eigenvalue=0.62) and axis 2 (eigenvalue=0.42) explaining 8.97% and 6.11%, respectively. Canonical coefficients revealed strong relationships with axis 1 (Table 3) and are comparable to data from Roberts & McMinn (1996).

Table 3. Canonical coefficients and their t values of the forward selected canonical correspondence analysis for axes 1 and 2. Results from the current analysis are shown with those values adopted from Table 4 in Roberts & McMinn (1996), denoted by "R&M".

Study	Variable	Axis 1	Axis 2	T value Axis 1	T value Axis 2
R&M	Salinity	-0.560	-0.600	-5.840	-5.830
	$Si0_2$	-0.210	0.710	-2.210	6.910
		Axis 1	**Axis 2**	**T value Axis 1**	**T value Axis 2**
Current	Salinity	-0.672	0.998	-4.795	4.272
	$Si0_2$	-0.032	-0.794	-0.343	-5.053

Forward model selection revelated a gradient on axis 1 associated with salinity and SO_4 (Fig. 68). On the left side of the graph, close to the origin, species-rich lakes such as AN (n=47) and FR (n=44) characterize the saline environment with associated taxa such as *Fragilariopsis curta* (Van Heurck) Hustedt (Fop_cur). Hyposaline lakes such as Hand (HA) (n=17) and Collerson(CO) (n=14) are characterized by taxa such as *Stauroneis latistauros* Van de Vijver & Lange-Bertalot (Sta_lat) and *Psammothidium stauroneioides* (Manguin) Bukhtiyarova (Psa_sta). The second gradient demonstrated by forward model selection occurs upon both axes 1 and 2 and is associated with alkalinity and SiO_2. Low alkalinity, low SiO_2 lakes such as Grace (GR) (n=16) and Lichen (LI) (n=12) are associated with taxa of *Halamphora* species (*H.*

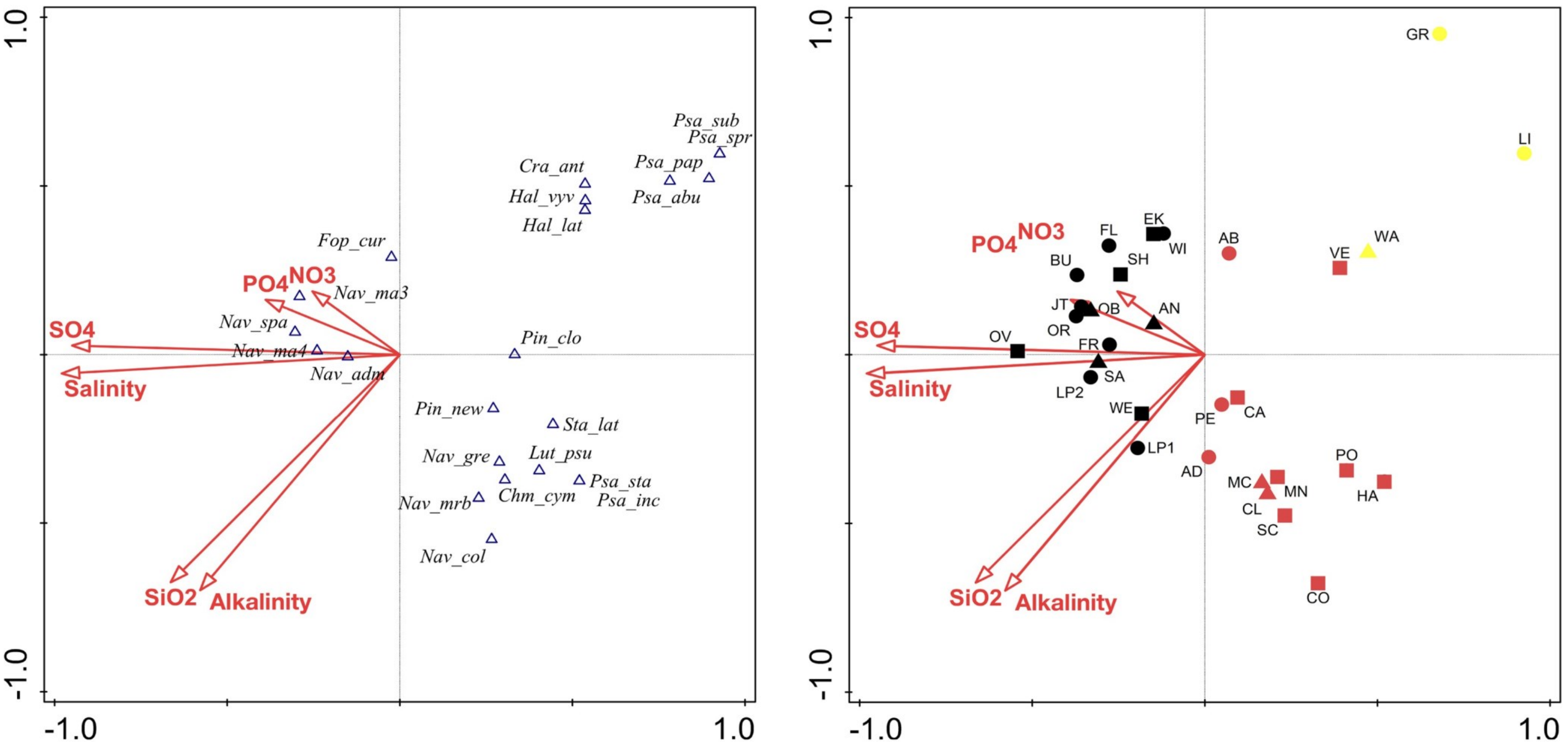


Figure 68. The results of a forward selected canonical correspondence analysis (CCA) using active lake chemistry variables of: Salinity (at 2 m depth), SiO2, SO4, Alkalinity (as CaCO3), NO3 and PO4. All 30 lakes are presented with their lake salinity category (fresh, hyposaline, and hypersaline) represented by color (yellow, red, and black), respectively. Long, Broad, and Mule Lake groups are denoted by circle, square and triangle shapes, respectively. Taxon identity and codes are: *Fragilariopsis curta* (Fop_cur), *Navicula* sp.1 (Nav_spa), *Sabbea adminensis* (Nav_adm), *Navicula* sp.2 (Nav_Ma3), *Navicula* sp.3 (Nav_Ma4), *Navicula* sp.12 (Nav_mrb), *Pinnularia australomicrostauron* "closed fascia" morphotype (Pin_clo), *Pinnularia australomicrostauron* "open fascia" morphotype (Pin_new), *Navicula collersonii* (Nav_col), *Navicula gregaria* (Nav_gre), *Chamaepinnularia cymatopleura* (Cha_cym), *Luticola psuedomurrayi* (Lut_psu), *Stauroneis latistauros* (Sta_lat), *Craticula antarctica* (Cra_lat), *Halamphora vyvermaniana* (Hal_vyv), *Halamphora lateantartica* (Hal_lat), *Psammothidium papilio* (Psa_pap), *Psammothidium abundans* (Psa_abu), *Psammothidium stauroneioides* (Psa_sta), and *Psammothidium incognitum* (Psa_inc), *Psammothidium subatomoides* (Psa_sub), *Psammothidium superpapilio* (Psa_spr).

lateantarctica Van de Vijver, Kopalová, Zidarova & Levkov (Hal_lat) and *H. vyvermaniana* (Hal_vyv) and *Psammothidium subatomoides* (Hustedt) Bukhtiyarova & Round (Psa_sub). Lakes such as Admin (AD) (n=25) and LP1 (n=16) are characteristically alkaline with *Sabbea adminensis* (Nav_adm) often being the most abundant taxa. Moderate levels of both salinity and alkalinity occur in lakes Hand(HA) (n=17) and Pointed(PO) (n=50) featuring taxa such as *Luticola pseudomurrayi* Van de Viver & Tavernier (Lut_psu) and *Chamaepinnularia cymatopleura* (Chm_cym).

Drivers of community structure

One of the aims of the present study was to recreate the CCA analysis performed by Roberts & McMinn (1996) that investigated the role of lake chemistry variables in structuring the diatom flora of 30 lakes in the Vestfold Hills. Later, this analysis went to be used to training datasets for transfer functions (Roberts & McMinn 1998, 1999) which demonstrated the importance of salinity and alkalinity in structuring diatom communities.

In this study, the results of Roberts & McMinn (1999) are once again confirmed. In our analysis, two separate gradients were observed in the CCA. The first gradient is associated with salinity, while the second is associated with alkalinity. Although difficult to make direct comparisons between CCA of the current study and those in Roberts & McMinn (1999), we see an overall similarity amongst the directionality and magnitude of the salinity and alkalinity gradients in both studies. Further inference of similarity of the CCA plots for both studies, by way of comparing axes scores, was deemed inappropriate based upon the data presented in Roberts & McMinn (1996) (Table 3) and methodological differences between the studies. The inclusion of four lakes with less than 400 valves counted per sample was compared to analyses performed without them (unshown). As the component lakes included one fresh (Watts, WA), two hyposaline (Vereteno, VE and Abraxas, AB), and one hypersaline (Weddell, WE), the CCA analyses revealed the same aforementioned results of salinity and alkalinity gradients.

Diatom taxonomic and ecological remarks

In the present study, a combination of historic and present-day records was used to determine species distributions. The revised flora of the Vestfold Hills is comprised of cosmopolitan species as well as species endemic to the Antarctic Region. The flora has typical freshwater species co-occurring alongside species shown to favor brackish and marine environments. This is the result of recent advances made in diatom taxonomy in the Antarctic Region, which has attempted to unify Antarctica under a single diatom floristic model. As such, the Vestfold Hills are noted for featuring cosmopolitan taxa, revised taxa (although present in original analysis) and those taxa absent from the original investigation (Table 2).

The reinvestigation of the Vestfold Hills, together with the larger review throughout the Antarctic Region, has identified a number of problematic naviculoid taxa, often resulting in transfer of taxa from *Navicula sensu stricto* to more appropriate genera. Sometimes this warrants the description of a new genus, as is the case with *Sabbea adminensis* (Figs 38–39). Described from Admin Lake as *Navicula adminii* D.Roberts & A.McMinn, this species is characterized by a thin, finely silicified valve that appears in 24 of the 30 lakes in the present investigation, often as a dominant member of the lake assemblage, i.e. over 50% relative abundance in Admin Lake. This taxon was also reported in the McMurdo Sound Region of Antarctica as *N. lineola* var. *perlepida* (Cleve) (Esposito et al. 2008). However, despite the issue of conspecificity between the two species being raised (Sakaeva et al. 2016 and references therein), no formal investigation of the taxa was performed at that time. In the initial re-investigation of the taxon, Van de Vijver and Kusber (2018) corrected an erroneous typification and corrected the species epithet to *N. adminensis.* Bishop et al. (2019) was able to confirm that *S. adminensis* occurred also in the McMurdo Sound Region and that given its unique morphology, differed from that of *Navicula sensu stricto*, warranting its placement in a new genus, *Sabbea* Van de Vijver, Bishop & Kopalová.

In the present study, we confirm a number of endemic Continental Antarctic taxa in the Vestfold Hills. *Craspedostauros laevissimus* (W. et G.S.West) Sabbe (Figs 50–51) (Fig. 67, Cra_lae) and *Chamaepinnularia cymatopleura* (Figs 40–41) were featured in the analysis performed by Roberts & McMinn, as *Stauroneis* sp. A on Plate 7, figs 5–7 and as *Pinnularia cymatopleura* W. & G.S.West on plate 6, figs. 4–5, respectively (1999). However, since their initial observation in the Vestfold Hills, these species have undergone taxonomic revision and transfer, discussed at length by Van de Vijver et al. (2012). *Navicula collersonii* D.Roberts & A.McMinn (Figs 42–43) (Fig.67, Nav_col) was described from Collerson lake, where it has a relative abundance over 64%, occurring in lakes Abraxas (AB), Burch (BU), Clear (CL), Hand (HA), McNeil (MN), and Weddell (WE) (Roberts & McMinn 1999). In the present analysis, we have confirmed its dominance in the type locality and three additional lakes LP 1 (LP1), McCallum (MC), and Watts (WA). Kellogg & Kellogg (2002) have also listed a questionable occurrence in the Vestfold Hills, at the Taynaya Bay Core, but this record is unavailable for verification.

Pinnularia australomicrostauron Zidarova, Kopalová & Van de Vijver was also shown by Roberts & McMinn (1999) on Plate 6. Figs 7–8 as *P. microstauron* (Ehrenberg) Cleve and *P. microstauron* var. *microstauron*, respectively, where the differences in the central fascia were the factors delimiting the separation of the species from its nominate to the varietal form. In the present analysis, we have used the “closed fascia” (Fig. 48)(Fig. 67, Pin_clo) and “new fascia” (Fig. 49)(Fig. 67, Pin_new) system. However, we have recorded four additional morphotypes based upon opened/closed fascia denoted by striae patterning around the fascia and central area, as well as overall valve characteristics such as valve length, width, shape and morphology of the apices. As Zidarova et al. (2016) also demonstrated, a number of morphotypes within this species in the Maritime Antarctic region, a more detailed examination of this taxon is needed to determine if these morphotypes are a result of phenotypic plasticity driven by environmental variables or if these morphotypes represent distinct species.

In total, from the single *N. mutica*/*N. muticopsis* taxon originally described in Roberts & McMinn (1999), we identified nine taxa (species, varieties or forms) of the genus *Luticola* D.G. Mann in the Vestfold Hills. This genus also features a large number of endemic species throughout the Antarctic region (Kociolek et al. 2017). In Roberts & McMinn (1999) Plate 5, Figs. 1–5 show what was described as the *Navicula mutica* Kützing/*muticopsis* Van Heurck group and due to the difficulty in deciphering a number of forms, all were grouped under this taxon, appearing in 25 lakes (Roberts & McMinn 1999). In our analysis, the genus *Luticola* appears in 12 of the lakes analyzed. Both the present study and Roberts & McMinn (1999) report the highest *Luticola* concentrations in Hand Lake, at 19% and 23% relative abundance per study, respectively. McNeil (MN) showed the second largest relative abundance for a *Luticola* taxon with 10% relative abundance while the remaining lakes featured individual *Luticola* species at or below 1% relative abundance per sample. However, our analysis identified this abundant taxon as *L. pseudomurrayi* (Figs 2–3) instead of within the *N. mutica/N. muticopsis* group.

The initial combination of forms and varieties into Roberts & McMinn's *N. mutica/N. muticopsis* group into what are currently a number of distinct *Luticola* species has obscured that species ecology, making it difficult to compare. The taxon group was shown to have a salinity optimum of 11% and a wide tolerance between 3–39%. In the present study, however, *L. pseudomurrayi* (Fig. 68, Lut_psu) occurs in only three lakes. It is most abundant in two hyposaline lakes, Hand (HA) and McNeil (MN), and least abundant in hypersaline Abraxas (AB), at 19% and 10%, and 1%, relative abundance respectively.*Luticola muticopsis* (Figs 5–

6) occurs at less than or equal to 1% relative abundances in a total of five lakes: one fresh lake, Grace (GR), and the remaining hypersaline McNeil (MC), Oval (OV), Organic (OR) and Scale (SC). These results would suggest that the *Luticola* taxa lumped into the *N. mutica/N. muticopsis* group in the Vestfold Hills did not feature a broad ecological (and salinity) tolerance, but instead appeared as such due to overlapping narrow, species specific environmental tolerances.

After the description of *Luticola* in 1990, *Navicula muticopsis* was transferred to the former genus as *Luticola muticopsis* (Van Heurck) D.G.Mann, a taxon that historically, but even into the present time, has served as a "catch-all" species for almost all distinctly capitate morphologies (Van de Vijver & Mataloni 2008, Kohler et al. 2015). Historic surveys throughout the entirety of the East Antarctica have shown the morphological variability of this taxon group, and associated forms and varieties for quite some time in West Ongul Island (Fukushima et al. 1974), Cape Royds (Fukushima 1962), Mirny Station, within Queen Mary Land (Fukushima 1966), the Larsemann Hills and Rauer Island group (Sabbe et al 2003).

Throughout the Antarctic Region, re-investigations have separated a number of taxa from the capitate *L. muticopsis* group, often appearing as being endemic to a particular region of Antarctica, such as *L. truncata* Kopalová & Van de Vijver on the Antarctic Peninsula (Kopalová et al. 2009) and Maritime Antarctica (Zidarova et al. 2016). Work performed in East Antarctica, particularly the McMurdo Sound Region, on the capitate, *L. muticopsis*-like group have raised a number of varieties and forms to species level. One of which is *L. austroatlantica* Van de Vijver, Kopalová, S.A.Spaulding et Esposito (Fig. 4), which was co-described from the Antarctic Peninsula (Esposito et al. 2008). Using the original species description, as well as an expanded species description detailing the morphological variability of this taxon (Kohler et al. 2015), we can confirm its presence in the Vestfold Hills. Other localities in the Vestfold Hills not featured within this study have been shown to harbor large populations of both *L.*

muticopsis and *L. austroatlantica* greater than or equal to 10% relative abundance per sample (Bishop et al., unpublished data). Finally, and most interestingly, a taxon identified based on four valves (1% relative abundance) in hypersaline South Angle Lake, *L. olegsakharovii* Zidarova, Levkov & Van de Vijver, is a rare species so far known only to occur in the area around the South Shetland Islands within the Maritime Antarctic in nutrient dense soils (Zidarova et al. 2014).

Another taxon "group" that has been difficult to investigate are those naviculoid diatoms with (sub) capitate, lanceolate forms often referred to, in one way or another, as the *N. phyllepta*-like group. This designation can often expand and contract, depending on component members of the community being investigated. For example, in Canadian Arctic communities, it is marred by the similarity, and apparent morphological flexibility, across the size range of a number of lanceolate *N. phyllepta*-like species (Campeau et al. 1999). Doubly troublesome was the terminology associated with the group, which Cox (1995) attempted to standardize.

In Roberts & McMinn (1999), Plate 5, Figs 7–8, 10, feature a number of lanceolate *Navicula* species that could be included in the *N. phyllepta* group such as *N.* cf. *salinarum* Grunow (Figs 7–8), *N.* cf. *seminulum* Grunow, and *N.* species f. Upon closer inspection of valve morphological characteristics (length, width, stria density, central area shape and terminal raphe ending structures), we were not confident to re-assign a number of taxa to the *Navicula* designations proposed in Roberts & McMinn (1999). As a consequence, we investigated type material for a number of taxa resembling the assemblages found in the Vestfold Hills flora including *N. venetiformis* Van de Vijver & Beyens, *N. phylletpa* Kützing, *N. ectoris* Van de Vijver, as well as Antarctic populations, in the Bunger Hills, of proposed *N. phyllepta.* We concluded that the nominate species of *N. phyllepta* (Fig. 13) (Fig. 67, Nav_phy), *N. phylleptosoma*, *N. gregaria* Donkin (Figs 11–12) *N. ectoris* (Fig. 67, Nav_ect) were present in the analysis. Only *N. gregaria* (Fig. 68, Nav_gr) existed at the time of publishing, as *N.*

ectoris (Figs 14–15) was described from the Sub-Antarctic region and *N. phylleptosoma* was split from *N. phyllepta* in 1999 (Lange-Bertalot 2001). In total, we include a total of 10 taxa (as species and forms, labeled as "GRP" in Table 2), including the aforementioned three taxa originally discussed in the publication by Roberts & McMinn (1999) in our definition of the *N. phyllepta*-like group. Intermediate forms of these species, such as *Navicula* cf. *ectoris* (Figs 9–10), that did not fit their respective species descriptions were kept separate in the analysis to account for possible (semi-)cryptic species/hybridization events. It is clear that this suite of *N. phyllepta*-like species requires extensive, further work (Bishop et al., unpub).

In Roberts & McMinn (1999), Plate 1, Figs 5–13 display a number of *Amphora* species, including *Amphora veneta* Kützing (Plate 1. Fig 5). When records of this taxon are compared to the distribution data in Kellogg & Kellogg (2002), it is shown to readily occur throughout the entirety of the Antarctic region, as a cosmopolitan taxon. However, Van de Vijver et al. (2014) yielded a number of revisions of taxa within the *A. veneta* complex, also identified as *Halamphora* cf. *veneta* (Kützing) Levkov in numerous records throughout the region. In the present study, we identified two taxa from the original *A. veneta* reported by Roberts & McMinn (1999): *H. lateantarctica* (Figs 18–19) and *H. vyvermaniana* (Figs 16–17). Roberts & McMinn (1999) characterized this as a typical hyposaline taxon, occurring in 21 of their 33 sampled lakes, with a salinity optimum of 6.7% and tolerance range between 1.5–29%. Together, *H. lateantarctica* and *H. vyvermaniana* co-occur in four lakes that are either fresh, Grace (GR) and Watts (WA), or hyposaline, Hand (HA) and McNeil (MN). The distribution of *Halamphora lateantarctica* is limited to these lakes. *H. vyvermaniana* occurs at their largest relative abundances in Grace (GR), Watts (WA), and Hand (HA) lakes (43%, 18%, and 17% respectively). *H. vyvermaniana* also appears in the hyposaline lakes of Abraxas (AB), McCallum (MC), McNeil (MN), Pointed (PO), and Vereteno (VE) and one hypersaline Anderson Lake (AN) where it occurs at 5% relative abundance. For this study, we did not calculate salinity optimum for species. However, salinity ranges for Grace (0.57–1.17%), Watts (2.24–2.40%) and Hand (4.90–5.59), where *H. vyvermaniana* occurs at its greatest relative abundances, strongly contrast those for Abraxas (AB), 15.36–22.85%, and McNeil (MN) 8.35–11.05%, where it occurs at <1% relative abundance. These correlations would suggest it is indeed a hyposaline taxon, but with much narrower tolerances than originally described. This appears to be the case with *H. lateantarctica* too, as within McNeil (MN) it occurs at <1% relative abundance, suggesting an even narrower tolerance to salinity than *H. vyvermaniana*.

Halamphora vyvermaniana was first described from the Vestfold Hills at Tarnya Lake though both species appear widely distributed throughout East Antarctica. The true distribution of these species is not yet known, as it is believed that a number of records attributed to *H. veneta* may be erroneous, and likely belong to another species. In the case of *H. lateantarctica,* Van de Vijver et al. (2014) confirm its presence in the Windmill Islands, Amery Oasis, and its type locality of the Bunger Hills.

Amphora antarctica Hustedt (Fig. 52) is thought to be an endemic, marine Antarctic taxon. Although not observed by Roberts & McMinn (1996, 1999), it was recorded in two hypersaline lakes, Fletcher (FL) and Oblong (OB), though only two and one valve(s) were recorded, respectively. This taxon appears to be distributed elsewhere throughout East Antarctica with confirmation in Rauer Islands (Berg et al. 2010). Cremer et al. (2003) confirmed its presence in the Windmill Islands and mentions a questionable record by Manguin (1960), where it is reported as a new species *A. barrei* Manguin. However, Kellogg & Kellogg (2002) list *A. antarctica* as a synonym of *A. barrei* and again show distribution to Adélie land and the Vestfold Hills (within Nicholson Lake, not present in the current study).

Eight *Psammothidium* taxa were found in the Vestfold Hills, though only one cosmopolitan species, then described as *Achnanthes abundans* Manguin was shown on Plate 1, Figs. 1–2 in Roberts & McMinn (1999). Bukhtiyarova & Round (1996) described the genus

Psammothidium, transferring a number of *Achnanthidium* species to *Psammothidium,* including the transfer of *P. abundans* (Figs 34–35) (Fig. 68, Psa_abu). This taxon was reported by Roberts & McMinn (1999), as *A. abundans,* in a total of five lakes Grace (GR), Johnstone (JT), Lichen (LI), Shield (SH) and Watts (WA) lakes and described as characteristic of freshwater lakes, with a "stenohaline" salinity tolerance and optimum of 0.2–2.1% and 0.6%, respectively. Our analysis shows this taxon in Anderson (AN, at <1%), Hand (HA, 1%), South Angle (SA, 5%), Shield (SH ~1.7%) Watts (WA, 5%) and, at its highest relative abundance of 66% in Lichen (LI), lakes. Our analysis suggests that this species' salinity tolerances may be larger than originally described, given its appearance in hypersaline lakes South Angle and Shield, as well as its larger geographic distribution in the Maritime Antarctic (Zidarova et al. 2016), the Bunger Hills (Gibson et al. 2006) and the Larsemann Hills and Bølingen Islands (Sabbe et al. 2003).

In addition, a number of cosmopolitan and endemic *Psammothidium* taxa were found: *P. papilio* (D.E.Kellogg, M.Stuiver, T.B.Kellogg & G.H.Denton) Kopalová & Van de Vijver (Figs 32–33), *P. subatomoides* (Hustedt) Bukhtiyarova & Round, *P. stauroneioides* (Manguin) Buhktiyarova, *P. incognitum* (Krasske) Van de Vijver (Figs 36–37) and *P. superpapilio* Kopalová, Zidarova & Van de Vijver. In certain lakes, four co-occurring species were observed. For example, *P. abundans* and *P. papilio* (Fig. 68, Psa_pap) co-occurred at both Hand (HA) and Lichen (LI) Lakes. However, in Hand Lake the aforementioned two species were observed with *P. stauroneioides* (Fig. 68, Psa_sta) and *P. incognitum* (Fig. 68, Psa_inc) whereas in Lichen Lake *P. subatomoides* (Fig. 68, Psa_sub) and *P. superpapilio* (Fig. 68, Psa_spr) were observed instead. Despite these taxa occurring along a wide environmental gradient of lakes, from fresh to hypersaline, the freshwater Lichen Lake (LI) was shown to have the largest *Psammothidium* community (*P. abundans* at 66% relative abundance and *P.*

papilio at 6%), whereas in the remainder of the lakes, these species occur at or less than 1% of the relative abundance.

Craticula antarctica Van de Vijver & Sabbe (Figs 28–29) (Fig. 68, Cra_ant) was observed in the freshwater lakes of Watts (WA) and Grace (GR) in our analysis at less that 1% relative abundance. However, this taxon has a long history throughout the East Antarctic literature deserving analysis in its own right. A taxon identified in Roberts & McMinn (1999) as *Navicula* sp. i. is shown on Plate 5. Figs 12–13 bears a resemblance to *Craticula antarctica,* falling in the lower size range of the species with measures of length, width and striae density. Comments following the species description show that in previous work, this species was described as *Navicula* cf. *gregaria,* however *N.* sp. i. was described with straight striae as opposed to the radiate striae of those on *Navicula* cf. *gregaria.* The difficulty here lies with striae patterning, as *N. gregaria* often possess radiate striae nearest the valve center, becomes parallel to convergent, finally, at the poles whereas *C. antarctica* are noted for straight to slightly radiate striae at the valve center, becoming increasingly convergent to arcuate striae, and possibly geniculate, at the poles. Overall, a lack of a complete size series in LM, and limited SEM, makes the attribution of *C. antarctica* to *N.* sp. i. all but impossible.

Within a large portion of the lakes analyzed 28 of 30, except Collerson (CO) and Hand (HA), 22 *Navicula* taxa occurred that we believe to be marine in origin (We denote these within Table 2 as “MRN”). As such, 12 of these taxa occur at less than or equal to 2% in any single lake. Only *Navicula* sp. 2 (Nav_ma3) (Figs 24–25) and *Navicula* sp. 3 (Nav_ma4) (Figs 26–27) occur within 17 of the lakes analyzed, co-occurring in 12 of the lakes, with overall relative abundances in the study of 8% and 5%, respectively. Within forward model selection (Fig. 68) both taxa are recovered along the primary axis attributed to salinity. When plotted with lake salinity categories, these taxa are recovered well situated within the saline group of lakes (Fig. 67). In particular, *Navicula* sp. 2 is recovered was observed at 72% relative abundance in Burch lake (BU), where along with *Navicula* sp. 3 it accounted for 80% combined relative abundance. *Navicula* sp. 2 is seen at its largest relative abundances within hypersaline lakes: Organic (OR, 41%), Anderson (AN, 28%), Williams (WI, 27%), Johnstone (JT, 26%). Collectively, the lakes represent some of the largest values in salinity within the study.

Some *Navicula* taxa were observed in numerous lakes despite their low overall relative abundance in the study. *Navicula* sp. 1 (Figs 22–23, 68, Nav_spa) was observed at 2% overall relative abundance in the study and occurs in a total of seven lakes. In two lakes, it co-occurs with *Navicula* sp. 2 and *Navicula* sp. 3. Some *Navicula* taxa were observed in multiple lakes despite an overall relative abundance of less than 1% in the study. For example, *Navicula* sp. 13 (Fig. 67, Nav_mrd), *Navicula* sp. 11, *Navicula* sp. 12 (Fig. 68, mrb), *Navicula* sp. 14 (Fig. 67, Nav_mre) were observed in 11, six, four, and three lakes, respectively. The remainder of the "MRN" species (10) are represented by less than 1% relative abundance in either one or two lakes, respectively. In Roberts & McMinn (1999), Plate 4. Figs 5–15 there are a number of *Navicula* taxa that bear resemblance to these "MRN" taxa, but when valve characteristics of length, width, striae density and descriptors of shape were compared, we could not confidently attribute the taxa shown to the list of "MRN" taxa. Utilizing the compiled records of Kellogg & Kellogg (2002), Van de Vijver et al. (2011) compiled a checklist of non-marine *Navicula sensu stricto* from throughout the Sub–Antarctic and Maritime Antarctic, with a total of 11 species throughout the region, with five endemic taxa, in particular from moist, terrestrial habitats.

In the current study, we see a number of presumed marine *Navicula* species alongside planktonic and/or cryophilic marine species. This is suggested by the observation of marine planktonic *Chaetoceros* cells (Fig. 62), and resting spores (Figs 63–66, Fig. 67, Cha_ufo), as well as *N. glaciei* Van Heurck (Figs 30–31)*, N. directa* (W.Smith) Ralfs (Fig. 54), *Nitzschia lecontei* (Fig. 53) and members of *Fragilariopsis* Hustedt (Figs 44–47), such as *F. rhombica*

(O'Meara) Hustedt (Fig. 67, Fop_rho). The aforementioned species are known to occur within the fjords of the Vestfold Hills (McMinn et al. 2000) and as such, we believe these species signify a strong influence from the marine environment, due to the close proximity to the sea and the dynamic, geological formation of the Vestfold Hills. As an outlet into Pyrdz Bay, flanked by the Sørsdal glacier, both glacial meltwater and sea water inundations occurred. The latter resulted in mixed benthic and planktonic marine diatom records (Harwood et al. 2000). More recently, low-lying waterbodies are influenced by the cyclical nature of sea level rise and fall in the Holocene, with resultant trapping of sea water behind sills (Zwartz et al. 1998).

The present study relies solely upon prepared LM slides. As previously stated, all other materials from the original study have been lost, making potential SEM analysis, not possible. SEM is crucial in separating semi-cryptic species groups. Oftentimes, troublesome species may be difficult or impossible to accurately identify without a complete size series in the LM. For genera such as *Luticola*, *Navicula* and *Nitzschia*, this makes proper identification difficult, and for valves at the lower size ranges and/or small taxa, such as *Nitzschia* sp. 1 (Figs 59–60, 67, Nit_eee), *Astartiella* sp.1 (Figs 55–56, 67, Ast_sp1), *Catenula* sp.1 (Figs 57–58, 67, Cat_sp1), and *Microfissurata* sp. 1 (Fig. 61), proper identification may not be possible without resolving the internal valve structures under SEM. As such, the true extent of diatom diversity and endemism in the Vestfold Hills may still be unknown, and likely remains underestimated.

Conclusions

Our results from the re-investigation of sediments from the Vestfold Hills fall in line with other aforementioned works that expand the flora of the Antarctic Region. We see that the Vestfold Hills possesses 183 taxa, including a number of endemic and cosmopolitan taxa spanning fresh, brackish and marine habitats. This is an increase from the 67 taxa reported in the original study. Overall, the number of endemic taxa in the current study increased from the previous study, from approximately 4% to 20%. Although the utilization of SEM for this study was not possible, through the use of LM we identify a number of taxa that require further, concerted work.

The revised diatom flora of the Vestfold Hills did not noticeably alter the ecological understanding of the lakes as we expected. The major gradients in the current study and Roberts & McMinn (1999) are salinity and alkalinity driven. However, our predictions of a more endemic flora were confirmed, as many taxa previously thought to be cosmopolitan have been revised to reflect their status as endemic to the Antarctic Region. Because of these revisions, we have shown a refined, narrower environmental tolerance for a number freshwater taxa belonging to *Luticola, Psammothidium* and *Halamphora*. A large number of taxa attributed to *Navicula* and *Nitzschia* occurred at much less than 1% relative abundance. There are most likely from the marine environment based upon the co-occurrence of other marine taxa such as the suite of *Fragilariopsis* species*, Chaetoceros* and several unidentified centric taxa.

Finally, this study highlights the necessity, and utility, of re-evaluating Continental Antarctic diatom records within biological collections using the current fine-grained taxonomic approach. These revised taxonomic data may be incorporated into larger studies of Antarctic microbial diversity, biogeography and conservation. When applied, these taxonomic data will be crucial in tracking the impacts of climate change and human impacts on freshwater ecosystems on the Antarctic continent.

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References

Al-Handal, A.Y. and Wulff, A., 2008a. Marine benthic diatoms from Potter Cove, King George Island, Antarctica. *Botanica Marina*, *51*(1), pp. 51–68.

Al-Handal, A.Y. and Wulff, A., 2008b. Marine epiphytic diatoms from the shallow sublittoral zone in Potter Cove, King George Island, Antarctica. *Botanica Marina*, *51*(5), pp. 411–435.

Anderson, M.J. 2001. A new method for non- parametric multivariate analysis of variance. *Austral ecology,26*(1), pp. 32–46.

Baas-Becking, LGM. 1934. *Geobiologie of inleiding tot de milieukunde* (No. 18–19). WP Van Stockum & Zoon, The Hague

Berg, S., Wagner, B., Cremer, H., Leng, M.J. and Melles, M., 2010. Late Quaternary environmental and climate history of Rauer Group, East Antarctica. *Palaeogeography, Palaeoclimatology, Palaeoecology*, *297*(1), pp.201–213.

Bishop, J., Kopalová, K., Darling, J.P., Schulte, N.O., Kohler, T.J., Mcminn, A., Spaulding, S.A., Mcknight, D.M. and Van De Vijver, B., 2019. *Sabbea* gen.nov., a new diatom genus (Bacillariophyta) from continental Antarctica. *Phytotaxa 418*(1), pp.42–56.

Broady, P.A., 1981. The ecology of sublithic terrestrial algae at the Vestfold Hills, Antarctica. *British Phycological Journal*, *16*(3), pp.231–240.

Bukhtiyarova, L. and Round, F.E., 1996. Revision of the genus *Achnanthes* sensu lato. *Psammothidium*, a new genus based on *A. marginulatum*: In memory of John Carter who contributed greatly to the discovery of many *Achnanthes* species. *Diatom research*, *11*(1), pp.1–30.

Campeau, S., Pienitz, R. and Héquette, A., 1999. Diatoms from the Beaufort Sea Coast, southern Arctic-Ocean (Canada). *Bibliotheca Diatomologica*, *42*, pp.1–244

Carbonero, F., Oakley, B.B. and Purdy, K.J., 2014. Metabolic flexibility as a major predictor of spatial distribution in microbial communities. *PLoS One*, *9*(1), p.e85105.

Chown, S.L. and Convey, P., 2007. Spatial and temporal variability across life's hierarchies in the terrestrial Antarctic. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *362*(1488), pp.2307–2331.

Chown, S.L., Clarke, A., Fraser, C.I., Cary, S.C., Moon, K.L. and McGeoch, M.A., 2015. The changing form of Antarctic biodiversity. *Nature*, *522*(7557), pp.431–438.

Cox, E.J., 1995. Studies on the diatom genus *Navicula* Bory. VII. The identity and typification of *Navicula gregaria* Donkin, *N. cryptocephala* Kütz. and related taxa. *Diatom Research*, *10*(1), pp.91–111.

Cremer, H., Roberts, D., McMinn, A., Gore, D. and Melles, M., 2003. The Holocene diatom flora of marine bays in the Windmill Islands, East Antarctica. *Botanica Marina*,*46*(1), pp.82–106.

De Wever, A., Leliaert, F., Verleyen, E., Vanormelingen, P., Van der Gucht, K., Hodgson, D.A., Sabbe, K. and Vyverman, W., 2009. Hidden levels of phylodiversity in Antarctic green algae: further evidence for the existence of glacial refugia. *Proceedings of the royal society B: Biological sciences*, *276*(1673), pp.3591–3599.

Esposito, R.M.M., Spaulding, S.A., McKnight, D.M., Van de Vijver, B., Kopalová, K., Lubinski, D., Hall, B. and Whittaker, T., 2008. Inland diatoms from the McMurdo dry valleys and James Ross Island, Antarctica. *Botany*, *86*(12), pp.1378–1392.

Finlay, B.J., 2002. Global dispersal of free-living microbial eukaryote species. *Science*, *296*(5570), pp.1061–1063.

Fukushima, H., 1962. Notes on diatom vegetation of the Kasumi Rock ice-free area, Prince Olav Coast, Antarctica. *Antarctic Record, 15*, pp. 39–52.

Fukushima, H., 1966. Diatoms from Molodezhnaya station and Mirny station, Antarctica. *Antarctic Record, 27,* pp.13–17

Fukushima, H., Watanuki, T. and Kobayashi, T., 1974. Diatoms from O-ike, West Ongul Island, Antarctica. *Antarctic Record*, *50*, pp.35–40.

Futuyma, D. J. 2013. *Evolution*. 3rd Edition. Sinauer Associates, Inc., Massachusetts. 656 pp.

Gibson, J.A.E., 1999. The meromictic lakes and stratified marine basins of the Vestfold Hills, East Antarctica. *Antarctic Science, 11*(2), pp.175–192.

Gibson, J.A.E. and Burton, H.R., 1996. Meromictic Antarctic lakes as recorders of climate change: The structures of Ace and Organic Lakes, Vestfold Hills, Antarctica. *Papers and Proceedings of the Royal Society of Tasmania 130*(2), pp. 73–78.

Gibson, J.A., Roberts, D. and Van de Vijver, B., 2006. Salinity control of the distribution of diatoms in lakes of the Bunger Hills, East Antarctica. *Polar Biology*, *29*(8), pp.694–704.

Harwood, D. M., Mcminn, A. and Quilty, P. G., 2000. Diatom biostratigraphy and age of the Pliocene Sørsdal Formation, Vestfold Hills, East Antarctica. *Antarctic Science, 12*(4), pp.443–462.

Hughes, K.A., Ireland, L.C., Convey, P. and Fleming, A.H., 2016. Assessing the effectiveness of specially protected areas for conservation of Antarctica's botanical diversity. *Conservation Biology*, *30*(1), pp.113–120.

Hughes, K.A., Convey, P., Pertierra, L.R., Vega, G.C., Aragón, P. and Olalla-Tárraga, M.Á., 2019. Human-mediated dispersal of terrestrial species between Antarctic biogeographic regions: A preliminary risk assessment. *Journal of environmental management*, *232*, pp.73–89.

Jones, J., 1996. The diversity, distribution and ecology of diatoms from Antarctic inland waters. *Biodiversity & Conservation*, *5*(11), pp.1433–1449.

Kellogg, T.B. and Kellogg, D.E. (2002) Non-marine and littoral diatoms from Antarctic and subantarctic regions. Distribution and updated taxonomy. *Diatom monographs* 1, A.R.G Gantner Verlag K.G., 795 pp.

Kociolek, J.P., Kopalová, K., Hamsher, S.E., Kohler, T.J., Van de Vijver, B., Convey, P. and McKnight, D.M., 2017. Freshwater diatom biogeography and the genus *Luticola*: an extreme case of endemism in Antarctica. *Polar Biology*, *40*(6), pp.1185–1196.

Kohler, T.J., Kopalová, K., Van De Vijver, B. and Kociolek, J.P., 2015. The genus *Luticola* D.G.Mann (Bacillariophyta) from the McMurdo Sound Region, Antarctica, with the description of four new species. *Phytotaxa, 208*(2), pp.103–134.

Kopalová, K., Elster, J., Nedbalová, L. and Van de Vijver, B., 2009. Three new terrestrial diatom species from seepage areas on James Ross Island (Antarctic Peninsula Region). *Diatom Research*, *24*(1), pp.113–122.

Lange-Bertalot H., 2001. The Genus *Navicula* Sensu Stricto: 10 Genera Separated From *Navicula* Sensu Lato *Frustulia*. In: *Diatoms of Europe* (Ed. By H. Lange-Bertalot) Vol. 2, A.R.G. Gantner Verlag K.G., Ruggell. 526 pp.

Line, M.A., 1988. Microbial flora of some soils of Mawson Base and the Vestfold Hills, Antarctica. *Polar Biology, 8*(6), pp.421–427.

Manguin, E., 1960. Les diatomées de le Terre Adélie. Campagne du "Commandant Charcot" 1949–1950. *Annales des Sciences Naturelles, Botanique*, *12*, pp.223–363.

Mann, D.G. 1999. The species concept in diatoms. *Phycologia*, *38*(6), pp.437–495.

Martiny, J.B.H., Bohannan, B.J., Brown, J.H., Colwell, R.K., Fuhrman, J.A., Green, J.L., Horner-Devine, M.C., Kane, M., Krumins, J.A., Kuske, C.R. and Morin, P.J., 2006. Microbial biogeography: putting microorganisms on the map. *Nature Reviews Microbiology*, *4*(2), pp.102–112.

Medlin, L.K. and Hasle, G.R., 1990. Some *Nitzschia* and related diatom species from fast ice samples in the Arctic and Antarctic. *Polar Biology*, *10*(6), pp.451–479.

McMinn, A., Bleakley, N., Steinburner, K., Roberts, D. and Trenerry, L., 2000. Effect of permanent sea ice cover and different nutrient regimes on the phytoplankton succession of fjords of the Vestfold Hills Oasis, eastern Antarctica. *Journal of Plankton Research*, *22*(2), pp.287–303.

Ohtsuka, T., Kudoh, S., Imura, S. and Ohtani, S., 2006. Diatoms composing benthic microbial mats in freshwater lakes of Skarvsnes ice-free area, East Antarctica. *Polar Bioscience, 20,* pp.113–130

Oksanen, J., Blanchet, G.F., Friendly,M., Kindt,R., Legendre,P., Mcglinn, D., Minchin, P.R., O'hara, R. B., Simpson, G.L., Solymos, P., Stevens, M.H.H., Szoecs, E. and Wagner, H., 2019. Vegan: Community Ecology Package. R package version 2.5–6. Available from: https://CRAN.R-project.org/package=vegan [Accessed 15 Jan 2019]

R Development Core Team. 2018. R: a language and environment for statistical computing. R Foundation for Statistical Computing. Available from: https://www.R-project.org/ [Accessed 20 March 2018]

Roberts, D. and McMinn, A., 1996. Relationships between surface sediment diatom assemblages and water chemistry gradients in saline lakes of the Vestfold Hills, Antarctica. *Antarctic Science*, *8*(4), pp.331–341.

Roberts, D. and McMinn, A., 1998. A weighted-averaging regression and calibration model for inferring lakewater salinity from fossil diatom assemblages in saline lakes of the Vestfold Hills: a new tool for interpreting Holocene lake histories in Antarctica. *Journal of Paleolimnology*, *19*(2), pp.99–113.

Roberts, D. and McMinn, A., 1999. Diatoms of the saline lakes of the Vestfold Hills, Antarctica. *Bibliotheca Diatomologica*, *44*, pp.1–82.

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

Sakaeva, A., Sokol, E.R., Kohler, T.J., Stanish, L.F., Spaulding, S.A., Howkins, A., Welch, K.A., Lyons, W.B., Barrett, J.E. and McKnight, D.M., 2016. Evidence for dispersal and habitat controls on pond diatom communities from the McMurdo Sound Region of Antarctica. *Polar Biology*, *39*(12), pp.2441–2456.

Seppelt, R.D., Broady, P.A., Pickard, J. and Adamson, D.A., 1988. Plants and landscape in the Vestfold Hills, Antarctica. *Hydrobiologia*, *165*(1), pp.185–196.

Šmilauer, P. & Lepš, J., 2014. *Multivariate Analysis of Ecological Data Using CANOCO 5.* 2nd Edition. Cambridge University Press, Cambridge. 362 pp.

Spaulding, S.A. and Stoermer, E.F., 1997. Taxonomy and distribution of the genus *Muelleria* Frenguelli. *Diatom research*, *12*(1), pp.95–113

Spaulding, S.A., Kociolek, J.P. and Wong, D., 1999. A taxonomic and systematic revision of the genus *Muelleria* (Bacillariophyta). *Phycologia*, *38*(4), pp.314–341.

Terauds, A., Chown, S.L., Morgan, F., J. Peat, H., Watts, D.J., Keys, H., Convey, P. and Bergstrom, D.M., 2012. Conservation biogeography of the Antarctic. *Diversity and Distributions*, *18*(7), pp.726–741.

Terauds, A. and Lee, J.R., 2016. Antarctic biogeography revisited: updating the Antarctic Conservation Biogeographic Regions. *Diversity and Distributions*, *22*(8), pp.836–840.

Ter Braak, C.J.F., 1996. Unimodal models to relate species to environment. DLO-Agricultural Mathematics group. Wageningen, the Netherlands, 266 pp.

Ter Braak, C.J.F. and Šmilauer, P., 2012. Canoco reference manual and user's guide: software for ordination (version 5.0), Microcomputer Power (Ithaca, NY, USA), 496 pp.

Tyler, P.A. 1996. Endemism in freshwater algae, with special reference to the Australian region. In: *Biogeography of freshwater algae* (Ed. J. Kristiansen). *Hydrobiologia* 336: 127–135. Springer, Dordrecht.

Van de Vijver, B., Frenot, Y. and Beyens, L., 2002. Freshwater diatoms from Ile de la Possession (Crozet Archipelago, Subantarctica). *Bibliotheca Diatomologica* 46, pp.1–412.

Van De Vijver, B. and Mataloni, G., 2008. New and interesting species in the genus *Luticola* D.G.Mann (Bacillariophyta) from Deception Island (South Shetland Islands). *Phycologia* 47(5), pp. 451–467.

Van de Vijver, B., Mataloni, G., Stanish, L. and Spaulding, S.A., 2010. New and interesting species of the genus *Muelleria* (Bacillariophyta) from the Antarctic region and South Africa. *Phycologia*, *49*(1), pp.22–41.

Van de Vijver, B., Zidarova, R., Sterken, M., Verleyen, E., de Haan, M., Vyverman, W., Hinz, F. and Sabbe, K., 2011. Revision of the genus *Navicula* ss (Bacillariophyceae) in inland waters of the Sub-Antarctic and Antarctic with the description of five new species. *Phycologia*, *50*(3), pp.281–297.

Van de Vijver, B., Tavernier, I., Kellogg, T.B., Gibson, J., Verleyen, E., Vyverman, W. and Sabbe, K., 2012. Revision of type materials of Antarctic diatom species (Bacillariophyta) described by West & West (1911), with the description of two new species. *Fottea*, *12*(2), pp.149–169.

Van de Vijver, B., Kopalová, K., Zidarova, R. and Levkov, Z., 2014. Revision of the genus *Halamphora* (Bacillariophyta) in the Antarctic Region. *Plant Ecology and Evolution*, *147*(3), pp.374–391.

Van de Vijver, B. and Kusber, WH., 2018. Validation of *Navicula adminensis* D.Roberts & McMinn ("*Navicula adminii*" D.Roberts & McMinn) (Naviculaceae, Bacillariophyceae). *Notulae algarum*, *65*, pp.1.

van der Gast, C.J., 2015. Microbial biogeography: the end of the ubiquitous dispersal hypothesis?. *Environmental Microbiology*, *17*(3), pp.544–546.

Verleyen, E., Vyverman, W., Sterken, M., Hodgson, D.A., De Wever, A., Juggins, S., Van de Vijver, B., Jones, V.J., Vanormelingen, P., Roberts, D. and Flower, R., 2009. The importance of dispersal related and local factors in shaping the taxonomic structure of diatom metacommunities. *Oikos*, *118*(8), pp.1239–1249.

Vyverman, W., Verleyen, E., Sabbe, K., Vanhoutte, K., Sterken, M., Hodgson, D.A., Mann, D.G., Juggins, S., Vijver, B.V.D., Jones, V. and Flower, R., 2007. Historical processes constrain patterns in global diatom diversity. *Ecology*, *88*(8), pp.1924–1931.

Vyverman, W., Verleyen, E., Wilmotte, A., Hodgson, D.A., Willems, A., Peeters, K., Van de Vijver, B., De Wever, A., Leliaert, F. and Sabbe, K., 2010. Evidence for widespread endemism among Antarctic micro-organisms. *Polar Science*, *4*(2), pp.103–113.

Wauchope, H.S., Shaw, J.D. and Terauds, A., 2019. A snapshot of biodiversity protection in Antarctica. *Nature communications*, *10*(1), pp.1–6.

Witkowski, A. Lange-Bertalot, H. and Metzeltin, D., 2000. *Diatom flora of Marine Coasts* I. *Iconographia Diatomologica.* 7. 925pp.

Zidarova, R., Levkov, Z. and Van de Vijver, B., 2014. Four new *Luticola* taxa (Bacillariophyta) from Maritime Antarctica. *Phytotaxa*, *170*(3), pp.155–168.

Zidarova R., Kopalová K. and Van de Vijver B. 2016: Diatoms from the Antarctic Region. I: Maritime Antarctica. *Iconographia Diatomologica*. 24. 509pp.

Zwartz, D., Bird, M., Stone, J. and Lambeck, K., 1998. Holocene sea-level change and ice-sheet history in the Vestfold Hills, East Antarctica. *Earth and Planetary Science Letters*, *155*(1–2), pp.131–145.

Chapter 4

Do water and nutrient availability influence the diatom communities found in mosses and lichens in the Windmill Islands, East Antarctica?

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DO WATER AND NUTRIENT AVAILABILITY INFLUENCE THE DIATOM COMMUNITIES FOUND IN MOSSES AND LICHENS IN THE WINDMILL ISLANDS, EAST ANTARCTICA?

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Abstract: Continental Antarctica is a cold polar desert containing sparse pockets of vegetation within ice-free areas. In the Windmill Islands, bryophyte vegetation is a common feature, but despite a well-known association between mosses and epiphytic diatoms (Bacillariophyceae), environmental factors controlling moss diatom community structure are poorly understood. In this study, the associations of epiphytic diatoms on two bryophyte (healthy and moribund) and two lichen (crustose and *Usnea*) vegetation types were investigated through a field manipulation which experimentally added nutrients and/or water based on projected availability due to climate change. Diatom communities were characterized, diversity indices calculated, and differences between treatments and vegetation types tested. We found that bryophyte and lichen vegetation types harbored significantly different epiphytic diatom communities, in terms of composition and calculated diversity indices. Only 8 of 49 diatom taxa occurred at or above 1% relative abundance, with *Usnea* lichens showing lower species richness than healthy bryophytes and crustose lichens. Interestingly, there was no effect of the nutrient and water treatments on diatom community structure. This suggests that while projected increases in nutrient and water availability may have a limited effect on diatom communities, changes in vegetation type and coverage will likely have large impacts on regional diatom distributions.

Key words: Bryophyte, climate change, environmental influence, Bacillariophyceae, algae, Antarctic Region

Introduction

Despite Antarctica's vast area, less than 1% of the continent is ice-free (Convey and Peck 2019). While ice free areas remain largely barren and free of vascular plants, mosses and lichens are common (Convey et al. 2014), as well as an increasingly studied "microflora" of micro-eukaryotes, bacteria and fungi (Zhang et al. 2019). Antarctic bryophytes (including mosses and liverworts) are limited in growth by extremes in wind, temperature, and photoperiod (Wasley et al. 2006a, b, Clarke et al. 2012, Robinson et al., 2018). Although there is a distinct lack of bioavailable (liquid) water and nutrients (Convey et al. 2014), Antarctica features about 100 bryophyte and 200 lichen species (Chown et al. 2015). Throughout East Antarctica, mosses have been extensively studied (Kurbatova and Ochyra 2012) across a number of localities including the Sôya Coast, as "moss pillars" arising from benthic cyanobacterial, or as a component in algal mats (Imura et al. 1999). Terrestrial Antarctic mosses have long been understood to provide suitable microclimates that harbor a diverse community, including arthropods (Nielsen and King 2015), green algae, and diatoms (Ohtani 1986).

Diatoms are ubiquitous across Antarctica, present within both marine habitats, as well as terrestrial and freshwater benthic habitats (Kellogg and Kellogg 2002). The non-marine Antarctic diatom flora is composed of a high number of endemic taxa specific to particular bioregions, reflecting their sensitivity to the physiochemical parameters of their habitats and likely dispersal limitation, in combination with geographic isolation (Sakaeva et al. 2016, Zidarova et al. 2016). Because of this, diatoms have been used to assess the ecological status of Antarctic lakes (Spaulding et al. 2010). Moss-associated diatoms have been well-characterized on the Sub-Antarctic islands, such as Heard Island (Van de Vijver et al. 2004), the Prince Edward Islands (Van de Vijver et al. 2008) and Ile de la Possession (Crozet Archipelago) (Van de Vijver et al. 2002). Further work has focused on Maritime Antarctic and the Antarctic Peninsula regions, such as Livingston Island and James Ross Island (Kopalová et al. 2014). However, despite the wealth of historical sources, biogeographical and ecological studies on the Antarctic Continent have examined diatoms and mosses separately (Opalinski 1972). In general, studies of benthic lake diatoms in East Antarctica comprise the majority of ecological works (Sabbe et al. 2003, Gibson et al. 2006, Sakaeva et al. 2016).

Microclimates within the matrix of soil and vegetation may be a driving factor in successful microbial colonization due in part to the availability of water in the presence of a less extreme environment (Beyer et al. 2000 and references therein). Kopalová et al. (2014) discussed the ecological differences amongst “wet” and “dry” moss taxa that harbor diatom communities within the Maritime Antarctic. Moss inhabiting diatom communities were dependent upon moss water content in the Sub-Antarctic islands (Van de Vijver et al. 2002, 2004, 2008) due in part to heterogenous climatic regimes throughout the region. Over recent decades, the Windmill Islands within East Antarctica have experienced a drying trend (Robinson et al. 2018). The expected impacts in East Antarctica are thought to be analogous to the resulting of the warming trends currently being observed throughout the Antarctic Peninsula. Specifically, increased water availability and associated habitat connectivity is anticipated through a reduction in ice and permafrost cover within coastal areas (Lee et al., 2017), which is likely to also coincide with increased nutrient liberation (Convey & Peck 2019). A warmer, wetter climate in the Windmill Islands may result in the regeneration and expansion of moss beds based on species specific differences and indirect effects of climate change (Wasley et al. 2012, Robinson et al. 2018)

Within close proximity to Casey Station, Wasley et al. (2006a) tested climate change responses spanning a bryophyte community transect using *in situ* water and nutrient additions based upon projected changes in nutrient and water availability. The test area originated at the edge of a meltwater lake, spanning from bryophyte-dominated to lichen-encrusted moss communities up the hill, and included four main vegetation types: 1) healthy bryophytes, 2) moribund bryophytes, 3) crustose lichens, and 4) lichens belonging to the genus *Usnea* Dillenius ex Adanson. Increased productivity was observed with the combined treatment of water and nutrients. However, when examined separately, nutrient additions appeared to illicit a stronger response than water. Additionally, both healthy bryophytes and *Usnea* lichens were shown to be positively impacted by nutrient additions (Wasley et al. 2006a). This suggests that Antarctic bryophyte communities are responsive to anticipated shifts in climate, which may in turn create carry-over effects to their associated epiphytes (Robinson et al. 2018), though these impacts have not been investigated.

In the current study, we characterize the diatom communities inhabiting the bryophyte and lichen samples from the experiment by Wasley et al. (2006a) to gain further insights into potential regional impacts from projected increases in water and nutrient availability. Our objectives were twofold. First, are diatom communities different for different bryophyte and lichen vegetation types, and secondly, how do these communities respond to experimental treatments of water and/or nutrients? Given the results of Wasley et al. (2006a), we expected to find more diverse diatom communities on those bryophyte and lichen vegetation types where nutrients and water were supplemented in comparison to control treatments.

Methods

Study area and sampling

The study site was located within Antarctic Specially Protected Area (ASPA) 135, about 1 km away from Casey Station on Bailey Peninsula, Windmill Islands (Wilkes Land), East Antarctica. The Windmill Islands are collectively one of the most extensively studied areas on the continent and are placed within Antarctic Conservation Biogeographic Region 7 (Terauds et al. 2012). The area is known for its well-developed lichen and bryophyte vegetation, due to a long history of nutrient and salinity inputs by numerous penguin colonies, creating strong gradients of both water and nutrient availability (Melick et al. 1994). At present, there are 14 actual breeding sites (Woehler et al. 1991), which strongly impact the surrounding flora due to increased nutrient inputs (Melick et al. 1994, Beyer et al. 2000).

The experimental site was located nearby an abandoned penguin rookery on the western edge of a meltwater lake originating from a snow slope, of northeasterly aspect, above Thala Valley (66°116.03’S, 110°132.53’E) located at the northern boundary of ASPA 135. This site featured a bryophyte vegetation gradient starting at the meltwater lake and spanning up the ridge, with an eastern aspect, away from the lake. Vegetation was categorized based on the percent coverage of four key components: healthy bryophytes, moribund bryophytes, crustose lichens, and lichens of the genus *Usnea* (Table 1).

Table 1. Characteristics of the bryophyte and lichen vegetation types within the experimental site, including “color coding” and descriptions of individual attributes.

Community Type	Description
Bryophyte	Healthy, "Green" brophytes are dominant at >90% cover
Moribund	Mixed Community. Approximately 50% cover of moribund bryophytes, occuring predominantly within upon ridges and 50% cover of healthy bryophytes, occuring predominantly in valleys
Crustose	Mixed Community. Dominance of Moribund bryophytes with 50% cover encrusted with both yellow and white lichens
Usnea	Mixed Community. Thin moribund bryophyte crust with dominant cover (>50%) of macrolichen *Usnea*

The order of these four vegetation types reflects their proximity to the meltwater lake, respectively, with healthy bryophytes at the edge of the lake, whereas the *Usnea* community was located closer to the ridge, furthest from the lake. The dominant bryophyte across the site was the Antarctic endemic *Schistidium antarctici* Card. (Wasley et al. 2006a), previously identified as *Grimmia antarctici* (Cardot) L.I. Savicz & Smirnova (Robinson et al. 2018).

Wasley et al. (2006a) performed a field manipulation experiment (altered nutrient and water regimes along the transect) to simulate predicted water and nutrient increases due to climate change, and examine the physiological responses generated within each community across treatments. In the present study, we retain the overall experimental design, and the sample coding scheme indicated in parentheses originates from Wasley et al. (2006a) (Figure 1). Briefly, thirty-two quadrats (25 x 25 cm) within each community were randomly assigned one of the following four treatments: (1) Control (no treatment) (C), (2) Water only (W), (3) Nutrient only (N) , or (4) Water + Nutrient (WN). From December to February of two consecutive summer seasons (1998–1999 and 1999–2000), the two water addition treatments

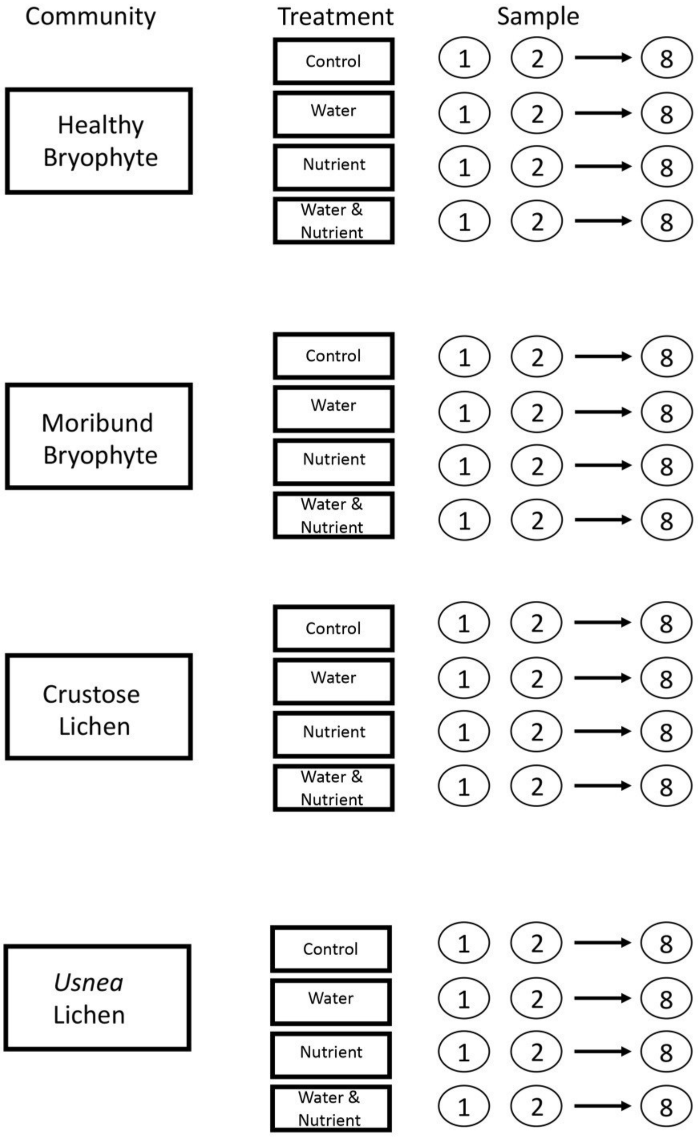

Figure 1. Experimental design displaying the four vegetation types (healthy bryophyte, moribund bryophyte, crustose lichen, and *Usnea* lichen) alongside randomly assigned treatments (Control, Water, Nutrients, and Water + Nutrients).

(Water and, Water + Nutrient) received applications of 500 mL of lake water approximately every two days. At the start of the treatment period (15 December 1999), 10 g of slow release fertilizer beads (Osmocote, Scotts Australia Pty. Ltd., Castle Hill, NSW, Australia) was applied to quadrats marked to receive nutrient additions (Nutrient and Water + Nutrient). A low phosphorous Osmocote variety was chosen, which composed of 18% nitrogen, 4.8% phosphorous and 9.1% potassium. For a more detailed description of experimental methods, see Wasley et al. (2006a)

Representative community samples were collected at the end of the treatment period (3-8 March 2000). A sample from each of the 16 treatment and community groups was collected, one sample from each replicate from each community and treatment type. Samples of approximately 4 cm^2 were collected from the center of each quadrat but for our diatom study one sample is equal to one quadrat. A total of 128 samples were originally collected (Table 2), but only 99 of these were available for our study due to low sample amounts and processing failures for several samples.

Table 2. List of samples used within the analysis. Diversity measures calculated for each sample include species richness, genera richness, Shannon diversity index, and Evenness.

Sample	Treatment	Community	SppRich	GenRich	ShanDiv	Even
1	Control	Healthy bryophyte	11	7	1.182	0.493
2	Control	Healthy bryophyte	10	5	1.602	0.696
3	Control	Healthy bryophyte	11	5	1.095	0.457
4	Control	Healthy bryophyte	6	4	0.807	0.450
5	Control	Healthy bryophyte	7	5	1.395	0.717
6	Control	Healthy bryophyte	10	5	1.110	0.482
7	Control	Healthy bryophyte	7	4	0.918	0.472
8	Control	Healthy bryophyte	6	5	0.628	0.351
9	Control	Moribund bryophyte	4	3	0.804	0.580
10	Control	Moribund bryophyte	13	7	1.877	0.732

Table 2. Continued

Sample	Treatment	Community	SppRich	GenRich	ShanDiv	Even
11	Control	Moribund bryophyte	8	4	1.394	0.670
12	Control	Moribund bryophyte	6	5	1.166	0.651
13	Control	Moribund bryophyte	8	5	1.451	0.698
14	Control	Moribund bryophyte	9	5	1.018	0.463
15	Control	Moribund bryophyte	9	3	1.210	0.551
16	Control	Crustose lichen	7	5	1.262	0.649
17	Control	Crustose lichen	7	5	1.267	0.651
18	Control	Crustose lichen	7	4	0.728	0.374
19	Control	*Usnea* lichen	9	6	0.882	0.401
20	Control	*Usnea* lichen	7	4	0.765	0.393
21	Control	*Usnea* lichen	5	4	0.468	0.291
22	Control	*Usnea* lichen	8	6	0.675	0.324
23	Control	*Usnea* lichen	6	5	0.665	0.371
24	Control	*Usnea* lichen	8	6	0.887	0.427
25	Control	*Usnea* lichen	6	5	0.839	0.468
26	Control	*Usnea* lichen	8	5	0.943	0.453
27	Water	Healthy bryophyte	8	4	1.317	0.634
28	Water	Healthy bryophyte	8	6	0.942	0.453
29	Water	Healthy bryophyte	6	4	0.724	0.404
30	Water	Healthy bryophyte	7	4	1.149	0.590
31	Water	Healthy bryophyte	7	4	0.745	0.383
32	Water	Healthy bryophyte	11	7	0.705	0.294
33	Water	Healthy bryophyte	9	5	1.547	0.704
34	Water	Healthy bryophyte	9	7	1.044	0.475
35	Water	Moribund bryophyte	11	5	1.018	0.424
36	Water	Moribund bryophyte	5	4	0.590	0.367
37	Water	Moribund bryophyte	7	3	1.286	0.661
38	Water	Moribund bryophyte	10	5	1.685	0.732
39	Water	Moribund bryophyte	7	4	1.707	0.877

Table 2. Continued

Sample	Treatment	Community	SppRich	GenRich	ShanDiv	Even
40	Water	Moribund bryophyte	9	6	1.188	0.541
41	Water	Crustose lichen	9	5	1.347	0.613
42	Water	Crustose lichen	8	4	1.159	0.557
43	Water	Crustose lichen	10	5	1.492	0.648
44	Water	*Usnea lichen*	6	4	0.948	0.529
45	Water	*Usnea lichen*	4	3	0.676	0.488
46	Water	*Usnea lichen*	7	5	0.670	0.344
47	Water	*Usnea lichen*	11	8	1.669	0.696
48	Nutrient	Healthy bryophyte	8	4	0.949	0.456
49	Nutrient	Healthy bryophyte	6	4	0.972	0.543
50	Nutrient	Healthy bryophyte	10	6	1.044	0.453
51	Nutrient	Healthy bryophyte	12	8	1.069	0.430
52	Nutrient	Healthy bryophyte	8	5	0.871	0.419
53	Nutrient	Healthy bryophyte	8	5	1.176	0.566
54	Nutrient	Healthy bryophyte	8	4	1.204	0.579
55	Nutrient	Healthy bryophyte	10	4	0.987	0.429
56	Nutrient	Moribund bryophyte	7	4	1.404	0.721
57	Nutrient	Moribund bryophyte	7	6	0.549	0.282
58	Nutrient	Moribund bryophyte	7	4	0.950	0.488
59	Nutrient	Moribund bryophyte	7	4	1.528	0.785
60	Nutrient	Moribund bryophyte	6	3	1.290	0.720
61	Nutrient	Moribund bryophyte	6	4	0.807	0.450
62	Nutrient	Moribund bryophyte	8	4	1.368	0.658
63	Nutrient	Crustose lichen	8	4	1.432	0.689
64	Nutrient	Crustose lichen	8	5	1.021	0.491
65	Nutrient	Crustose lichen	9	5	0.997	0.454
66	Nutrient	Crustose lichen	8	5	1.594	0.767
67	Nutrient	Crustose lichen	7	4	0.989	0.508
68	Nutrient	Crustose lichen	13	7	1.702	0.664

Table 2. Continued

Sample	Treatment	Community	SppRich	GenRich	ShanDiv	Even
69	Nutrient	*Usnea* lichen	5	4	0.656	0.408
70	Nutrient	*Usnea* lichen	7	5	0.956	0.491
71	Nutrient	*Usnea* lichen	6	5	1.002	0.559
72	Nutrient	*Usnea* lichen	8	6	0.782	0.376
73	Nutrient	*Usnea* lichen	5	4	0.469	0.291
74	Nutrient	*Usnea* lichen	8	5	1.075	0.517
75	Nutrient	*Usnea* lichen	7	4	0.639	0.328
76	Nutrient	*Usnea* lichen	6	5	0.427	0.238
77	Water+Nutrient	Healthy bryophyte	10	5	0.981	0.426
78	Water+Nutrient	Healthy bryophyte	9	6	1.344	0.611
79	Water+Nutrient	Healthy bryophyte	9	5	1.445	0.658
80	Water+Nutrient	Healthy bryophyte	7	4	1.104	0.567
81	Water+Nutrient	Healthy bryophyte	6	4	0.512	0.286
82	Water+Nutrient	Healthy bryophyte	8	4	1.220	0.587
83	Water+Nutrient	Healthy bryophyte	8	5	1.109	0.533
84	Water+Nutrient	Moribund bryophyte	7	4	1.531	0.787
85	Water+Nutrient	Moribund bryophyte	11	6	1.550	0.647
86	Water+Nutrient	Moribund bryophyte	7	4	1.508	0.775
87	Water+Nutrient	Moribund bryophyte	8	4	1.482	0.713
88	Water+Nutrient	Moribund bryophyte	8	4	1.169	0.562
89	Water+Nutrient	Crustose lichen	10	5	1.493	0.648
90	Water+Nutrient	Crustose lichen	10	5	1.645	0.714
91	Water+Nutrient	Crustose lichen	7	4	1.311	0.674
92	Water+Nutrient	Crustose lichen	7	4	1.157	0.594
93	Water+Nutrient	*Usnea* lichen	11	9	1.304	0.544
94	Water+Nutrient	*Usnea* lichen	7	5	0.716	0.368
95	Water+Nutrient	*Usnea* lichen	7	6	0.593	0.305
96	Water+Nutrient	*Usnea* lichen	5	4	0.419	0.260
97	Water+Nutrient	*Usnea* lichen	6	5	0.771	0.430

Table 2. Continued

Sample	Treatment	Community	SppRich	GenRich	ShanDiv	Even
98	Water+Nutrient	*Usnea* lichen	10	7	1.091	0.474
99	Water+Nutrient	*Usnea* lichen	7	5	0.545	0.280

Sample preparation and analyses

Samples were prepared for light microscopy (LM) observation following the method described in van der Werff (1955). Subsamples of dried bryophytes or lichens were transferred into 50 mL beakers and soaked for 10 – 14 days in 37% (v/v) H_2O_2. Once organic matter was oxidized, the sample was further boiled for about 1 h, or until total volume was reduced to <10 mL. The liquid was left to cool for 1 h before the addition of $KMnO_4$ to remove undigested moss material. This resultant liquid was then "cleaned" with approximately 2–5 mL of HCl to complete the reaction. Following digestion and centrifugation (three times for 10 minutes at 3,500 *g*), cleaned diatom valves were mounted on glass microscope slides using Naphrax for further LM observation.

Light Microscopy was performed on an Olympus BX43 equipped with a Differential Interference Contrast (Nomarski) optic at 1000x magnification with oil immersion. Images were taken using an Olympus PD27 Color camera with CellSens Entry 1.15 software. Diatom valves were counted (Table S1) in full fields of view along random transects, of up to 400 valves (Max/Min: 437/36). Only two samples were unable to be counted to greater than or equal to 400 valves: Sample 84 (63 valves) and Sample 9 (36 valves). Alongside species and genus richness, Shannon's diversity index and Evenness values for each sample were determined.

Taxonomic affiliations and biogeographic data have been compiled based mainly on Sabbe et al. (2003), Van de Vijver et al. (2002, 2012), Kohler et al. (2015) and Zidarova et al. (2016). In the event of ambiguous or uncertain taxa, images were taken and corresponding measurements of valve length, valve width at mid-valve, and stria density per 10 ∝m. When

Table S1. Diatom relative abundance data from each sample within the study.

	Dia_gal	Hum_aus	Pin_bor	Psa_pap	Psa_sta	Psa_ros	Pla_ren	Lut_xxx	Lcf_kat	Lut_aus	Lut_mut	Lut_dol	Lut_ele	Lut_per	Lut_psu	Lut_sp2	Lut_sp3
Sample 1	0.667	0.017	0.087	0.082	0.002	0.000	0.005	0.005	0.000	0.000	0.005	0.000	0.000	0.000	0.000	0.000	0.000
Sample 2	0.254	0.307	0.284	0.055	0.008	0.000	0.010	0.015	0.000	0.000	0.053	0.000	0.005	0.000	0.000	0.000	0.000
Sample 3	0.716	0.064	0.068	0.088	0.017	0.002	0.000	0.012	0.002	0.012	0.000	0.000	0.000	0.015	0.000	0.000	0.000
Sample 4	0.782	0.077	0.087	0.037	0.000	0.000	0.000	0.007	0.000	0.000	0.010	0.000	0.000	0.000	0.000	0.000	0.000
Sample 5	0.392	0.355	0.136	0.056	0.007	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.034	0.000	0.000	0.000	0.000
Sample 6	0.624	0.042	0.238	0.064	0.007	0.000	0.000	0.002	0.000	0.000	0.005	0.000	0.002	0.000	0.000	0.000	0.000
Sample 7	0.740	0.064	0.126	0.043	0.007	0.000	0.000	0.012	0.000	0.000	0.000	0.000	0.000	0.007	0.000	0.000	0.000
Sample 8	0.844	0.059	0.034	0.056	0.000	0.000	0.000	0.000	0.000	0.000	0.005	0.000	0.000	0.000	0.000	0.000	0.000
Sample 9	0.750	0.000	0.111	0.028	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sample 10	0.359	0.098	0.235	0.034	0.000	0.000	0.000	0.093	0.000	0.061	0.024	0.000	0.029	0.000	0.000	0.000	0.000
Sample 11	0.062	0.002	0.045	0.010	0.000	0.000	0.000	0.524	0.000	0.136	0.196	0.000	0.025	0.000	0.000	0.000	0.000
Sample 12	0.632	0.127	0.061	0.099	0.000	0.000	0.000	0.000	0.000	0.000	0.078	0.000	0.000	0.000	0.000	0.000	0.000
Sample 13	0.438	0.078	0.321	0.019	0.000	0.000	0.000	0.068	0.000	0.034	0.034	0.000	0.000	0.000	0.000	0.000	0.000
Sample 14	0.741	0.073	0.086	0.020	0.010	0.000	0.000	0.030	0.000	0.008	0.000	0.000	0.005	0.000	0.000	0.000	0.000
Sample 15	0.152	0.000	0.009	0.004	0.000	0.000	0.000	0.637	0.000	0.056	0.070	0.000	0.063	0.004	0.000	0.004	0.000
Sample 16	0.248	0.302	0.405	0.010	0.000	0.000	0.000	0.025	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.005
Sample 17	0.390	0.078	0.429	0.012	0.000	0.000	0.000	0.020	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sample 18	0.044	0.000	0.113	0.002	0.000	0.000	0.000	0.801	0.000	0.032	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sample 19	0.716	0.209	0.022	0.025	0.002	0.000	0.000	0.010	0.000	0.007	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sample 20	0.765	0.166	0.033	0.026	0.002	0.002	0.000	0.005	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sample 21	0.885	0.076	0.015	0.020	0.000	0.000	0.000	0.005	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sample 22	0.832	0.084	0.015	0.050	0.000	0.002	0.000	0.000	0.000	0.000	0.010	0.000	0.000	0.000	0.000	0.000	0.000
Sample 23	0.792	0.161	0.002	0.032	0.000	0.000	0.000	0.007	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sample 24	0.676	0.259	0.003	0.030	0.008	0.000	0.000	0.008	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sample 25	0.707	0.222	0.039	0.025	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sample 26	0.718	0.163	0.057	0.007	0.000	0.000	0.000	0.010	0.000	0.000	0.005	0.000	0.000	0.000	0.000	0.000	0.000
Sample 27	0.520	0.261	0.095	0.075	0.010	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sample 28	0.719	0.078	0.041	0.144	0.009	0.000	0.000	0.000	0.000	0.000	0.005	0.000	0.000	0.000	0.000	0.000	0.000
Sample 29	0.798	0.075	0.025	0.098	0.003	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sample 30	0.654	0.070	0.142	0.085	0.007	0.000	0.000	0.020	0.000	0.000	0.000	0.000	0.000	0.022	0.000	0.000	0.000
Sample 31	0.801	0.065	0.012	0.099	0.005	0.000	0.000	0.005	0.000	0.000	0.012	0.000	0.000	0.000	0.000	0.000	0.000
Sample 32	0.843	0.067	0.014	0.036	0.000	0.000	0.000	0.005	0.002	0.000	0.010	0.000	0.000	0.012	0.000	0.000	0.000
Sample 33	0.380	0.203	0.270	0.059	0.000	0.000	0.000	0.037	0.000	0.000	0.020	0.000	0.000	0.000	0.000	0.000	0.005
Sample 34	0.644	0.046	0.022	0.013	0.000	0.000	0.005	0.005	0.000	0.000	0.011	0.000	0.000	0.000	0.000	0.000	0.000
Sample 35	0.749	0.090	0.020	0.035	0.000	0.000	0.000	0.037	0.002	0.002	0.045	0.010	0.000	0.000	0.000	0.000	0.000
Sample 36	0.858	0.038	0.028	0.063	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000

Table S1. Continued

	Lut_sp4	Lut_sp5	Ccf_fas	Coc_sp1	Gen_xxx	Fra_xxx	Fop_sp1	Fop_sp2	Ncf_cre	Nav_sp1	Nit_sp1	Nit_sp2	Nit_sp3	Pla_sp1	Pla_sp2	Pla_sp3
Sample 1	0.015	0.000	0.000	0.000	0.005	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sample 2	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sample 3	0.000	0.000	0.000	0.000	0.000	0.000	0.002	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sample 4	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sample 5	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sample 6	0.010	0.000	0.000	0.000	0.005	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sample 7	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sample 8	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sample 9	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sample 10	0.005	0.000	0.000	0.000	0.049	0.000	0.000	0.000	0.000	0.000	0.000	0.005	0.005	0.000	0.000	0.002
Sample 11	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sample 12	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sample 13	0.000	0.000	0.000	0.000	0.007	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sample 14	0.000	0.000	0.000	0.000	0.028	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sample 15	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sample 16	0.000	0.000	0.005	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sample 17	0.000	0.000	0.000	0.000	0.005	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sample 18	0.005	0.000	0.002	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sample 19	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sample 20	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sample 21	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sample 22	0.000	0.000	0.000	0.000	0.005	0.000	0.000	0.002	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sample 23	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sample 24	0.000	0.000	0.000	0.000	0.015	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sample 25	0.000	0.000	0.005	0.000	0.000	0.000	0.000	0.002	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sample 26	0.000	0.000	0.002	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sample 27	0.010	0.005	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sample 28	0.000	0.000	0.000	0.000	0.002	0.002	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sample 29	0.003	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sample 30	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sample 31	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sample 32	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.005	0.000	0.000	0.000	0.005	0.000
Sample 33	0.000	0.022	0.000	0.000	0.005	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sample 34	0.000	0.000	0.000	0.000	0.005	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sample 35	0.005	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.005	0.000	0.000	0.000	0.000	0.000	0.000
Sample 36	0.015	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000

Table S1. Continued

	Pla_sp4	Sta_ine	Acn_sp1	Ach_tay	Gom_sp1	Hum_inc	Hcf_inc	Dcf_gal	Str_sp1	Nan_shi	Cnt_xxx	Sta_sp1	Pse_sp1	Cha_cym	Fop_xxx	Smt_xxx
Sample 1	0.000	0.109	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sample 2	0.000	0.000	0.000	0.000	0.000	0.010	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sample 3	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sample 4	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sample 5	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.019	0.000	0.000	0.000	0.000	0.000	0.000
Sample 6	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sample 7	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sample 8	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.002	0.000	0.000	0.000	0.000	0.000
Sample 9	0.000	0.111	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sample 10	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sample 11	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sample 12	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.002	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sample 13	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sample 14	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sample 15	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sample 16	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sample 17	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.066	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sample 18	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sample 19	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.002	0.000	0.000	0.005	0.000	0.000
Sample 20	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sample 21	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sample 22	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sample 23	0.005	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sample 24	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.003	0.000	0.000	0.000
Sample 25	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sample 26	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.037	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sample 27	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.025	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sample 28	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sample 29	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sample 30	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sample 31	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sample 32	0.000	0.000	0.000	0.002	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sample 33	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sample 34	0.000	0.000	0.248	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sample 35	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sample 36	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000

Table S1. Continued

	Dia_gal	Hum_aus	Pin_bor	Psa_pap	Psa_sta	Psa_ros	Pla_ren	Lut_xxx	Lcf_kat	Lut_aus	Lut_mut	Lut_dol	Lut_ele	Lut_per	Lut_psu	Lut_sp2	Lut_sp3
Sample 37	0.057	0.005	0.037	0.000	0.000	0.000	0.000	0.595	0.000	0.122	0.144	0.000	0.040	0.000	0.000	0.000	0.000
Sample 38	0.432	0.041	0.155	0.058	0.005	0.000	0.000	0.152	0.000	0.029	0.111	0.000	0.005	0.000	0.000	0.000	0.000
Sample 39	0.286	0.031	0.111	0.026	0.000	0.000	0.000	0.267	0.000	0.149	0.130	0.000	0.000	0.000	0.000	0.000	0.000
Sample 40	0.656	0.061	0.141	0.024	0.000	0.000	0.000	0.020	0.000	0.000	0.078	0.000	0.007	0.000	0.000	0.000	0.000
Sample 41	0.581	0.063	0.061	0.051	0.015	0.000	0.000	0.191	0.000	0.024	0.012	0.000	0.000	0.000	0.000	0.000	0.000
Sample 42	0.559	0.005	0.288	0.005	0.000	0.000	0.000	0.092	0.000	0.000	0.010	0.000	0.017	0.000	0.000	0.000	0.000
Sample 43	0.537	0.032	0.030	0.025	0.000	0.000	0.000	0.200	0.000	0.039	0.069	0.000	0.000	0.000	0.000	0.000	0.000
Sample 44	0.686	0.190	0.032	0.080	0.010	0.000	0.000	0.002	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sample 45	0.760	0.198	0.000	0.037	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sample 46	0.817	0.123	0.015	0.027	0.000	0.000	0.000	0.010	0.000	0.000	0.002	0.000	0.000	0.000	0.000	0.000	0.000
Sample 47	0.454	0.080	0.117	0.027	0.000	0.000	0.000	0.190	0.000	0.034	0.061	0.000	0.000	0.000	0.000	0.000	0.000
Sample 48	0.758	0.053	0.048	0.061	0.010	0.005	0.000	0.005	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sample 49	0.636	0.267	0.039	0.044	0.000	0.000	0.000	0.000	0.000	0.000	0.005	0.000	0.000	0.000	0.000	0.000	0.009
Sample 50	0.696	0.147	0.026	0.090	0.012	0.005	0.000	0.005	0.000	0.000	0.007	0.000	0.000	0.000	0.000	0.000	0.000
Sample 51	0.698	0.054	0.161	0.037	0.010	0.000	0.000	0.000	0.000	0.002	0.012	0.000	0.000	0.005	0.000	0.000	0.000
Sample 52	0.738	0.154	0.005	0.022	0.002	0.000	0.000	0.002	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sample 53	0.603	0.214	0.033	0.108	0.000	0.000	0.000	0.014	0.000	0.000	0.000	0.000	0.000	0.005	0.000	0.000	0.000
Sample 54	0.650	0.125	0.078	0.064	0.002	0.000	0.000	0.042	0.000	0.000	0.034	0.000	0.000	0.000	0.000	0.000	0.000
Sample 55	0.744	0.098	0.022	0.053	0.057	0.000	0.000	0.007	0.000	0.000	0.005	0.000	0.005	0.000	0.000	0.000	0.000
Sample 56	0.402	0.057	0.348	0.012	0.000	0.000	0.000	0.087	0.000	0.000	0.090	0.000	0.000	0.000	0.000	0.000	0.005
Sample 57	0.875	0.054	0.025	0.034	0.000	0.000	0.000	0.005	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sample 58	0.750	0.083	0.043	0.038	0.000	0.000	0.000	0.015	0.000	0.000	0.005	0.000	0.000	0.000	0.000	0.000	0.000
Sample 59	0.143	0.002	0.322	0.002	0.000	0.000	0.000	0.290	0.000	0.081	0.160	0.000	0.000	0.000	0.000	0.000	0.000
Sample 60	0.042	0.020	0.256	0.000	0.000	0.000	0.000	0.527	0.000	0.062	0.094	0.000	0.000	0.000	0.000	0.000	0.000
Sample 61	0.724	0.212	0.005	0.039	0.000	0.000	0.000	0.010	0.000	0.000	0.010	0.000	0.000	0.000	0.000	0.000	0.000
Sample 62	0.088	0.000	0.093	0.005	0.000	0.000	0.000	0.598	0.000	0.055	0.103	0.000	0.020	0.000	0.000	0.000	0.000
Sample 63	0.571	0.073	0.135	0.025	0.000	0.000	0.000	0.080	0.000	0.000	0.071	0.000	0.000	0.000	0.000	0.000	0.000
Sample 64	0.711	0.129	0.076	0.018	0.000	0.000	0.000	0.018	0.000	0.005	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sample 65	0.737	0.115	0.015	0.054	0.000	0.000	0.000	0.034	0.000	0.010	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sample 66	0.229	0.037	0.359	0.010	0.000	0.000	0.000	0.234	0.000	0.046	0.076	0.000	0.000	0.000	0.000	0.000	0.000
Sample 67	0.629	0.034	0.274	0.005	0.000	0.000	0.000	0.046	0.000	0.000	0.002	0.000	0.010	0.000	0.000	0.000	0.000
Sample 68	0.409	0.057	0.152	0.025	0.005	0.000	0.000	0.244	0.000	0.015	0.035	0.000	0.000	0.000	0.000	0.000	0.005
Sample 69	0.739	0.244	0.005	0.007	0.000	0.000	0.000	0.005	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sample 70	0.713	0.146	0.083	0.027	0.000	0.000	0.000	0.002	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sample 71	0.609	0.296	0.037	0.027	0.000	0.000	0.000	0.025	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sample 72	0.798	0.066	0.090	0.019	0.000	0.000	0.000	0.008	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sample 73	0.878	0.092	0.005	0.015	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000

Table S1. Continued

	Lut_sp4	Lut_sp5	Ccf_fas	Coc_sp1	Gen_xxx	Fra_xxx	Fop_sp1	Fop_sp2	Ncf_cre	Nav_sp1	Nit_sp1	Nit_sp2	Nit_sp3	Pla_sp1	Pla_sp2	Pla_sp3
Sample 37	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sample 38	0.000	0.000	0.000	0.000	0.012	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sample 39	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sample 40	0.000	0.000	0.000	0.007	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sample 41	0.000	0.000	0.000	0.002	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sample 42	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sample 43	0.005	0.000	0.000	0.000	0.005	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sample 44	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sample 45	0.005	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sample 46	0.000	0.000	0.000	0.000	0.005	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sample 47	0.000	0.000	0.002	0.000	0.010	0.000	0.000	0.000	0.002	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sample 48	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sample 49	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sample 50	0.000	0.000	0.000	0.000	0.010	0.000	0.000	0.002	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sample 51	0.000	0.000	0.002	0.000	0.010	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.005	0.000
Sample 52	0.000	0.000	0.000	0.000	0.007	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sample 53	0.000	0.000	0.000	0.000	0.014	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sample 54	0.005	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sample 55	0.005	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sample 56	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sample 57	0.000	0.000	0.000	0.000	0.002	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.005	0.000	0.000
Sample 58	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sample 59	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sample 60	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sample 61	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sample 62	0.000	0.000	0.000	0.000	0.040	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sample 63	0.014	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sample 64	0.000	0.000	0.003	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sample 65	0.007	0.000	0.000	0.000	0.000	0.000	0.000	0.002	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sample 66	0.000	0.000	0.000	0.000	0.010	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sample 67	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sample 68	0.000	0.000	0.010	0.000	0.000	0.000	0.005	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sample 69	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sample 70	0.000	0.000	0.000	0.000	0.024	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sample 71	0.000	0.000	0.005	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sample 72	0.000	0.000	0.003	0.000	0.005	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sample 73	0.000	0.000	0.000	0.000	0.010	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000

Table S1. Continued

	Pla_sp4	Sta_ine	Acn_sp1	Ach_tay	Gom_sp1	Hum_inc	Hcf_inc	Dcf_gal	Str_sp1	Nan_shi	Cnt_xxx	Sta_sp1	Pse_sp1	Cha_cym	Fop_xxx	Smt_xxx
Sample 37	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sample 38	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sample 39	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sample 40	0.000	0.000	0.000	0.000	0.005	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sample 41	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sample 42	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.024	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sample 43	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.059	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sample 44	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sample 45	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sample 46	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sample 47	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.022	0.000	0.000	0.000	0.000	0.000
Sample 48	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.061	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sample 49	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sample 50	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sample 51	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.002
Sample 52	0.000	0.000	0.000	0.000	0.000	0.000	0.068	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sample 53	0.000	0.000	0.000	0.000	0.000	0.009	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sample 54	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sample 55	0.000	0.000	0.000	0.000	0.000	0.005	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sample 56	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sample 57	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sample 58	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.068	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sample 59	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sample 60	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sample 61	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sample 62	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sample 63	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.032	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sample 64	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.039	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sample 65	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.025	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sample 66	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sample 67	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sample 68	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.027	0.000	0.000	0.010	0.000	0.000	0.000	0.000	0.000
Sample 69	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sample 70	0.000	0.000	0.000	0.000	0.000	0.005	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sample 71	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sample 72	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.011	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sample 73	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000

Table S1. Continued

	Dia_gal	Hum_aus	Pin_bor	Psa_pap	Psa_sta	Psa_ros	Pla_ren	Lut_xxx	Lcf_kat	Lut_aus	Lut_mut	Lut_dol	Lut_ele	Lut_per	Lut_psu	Lut_sp2	Lut_sp3
Sample 74	0.684	0.154	0.029	0.071	0.022	0.000	0.000	0.000	0.000	0.000	0.005	0.000	0.000	0.000	0.000	0.000	0.000
Sample 75	0.843	0.091	0.017	0.022	0.000	0.000	0.000	0.010	0.000	0.000	0.002	0.000	0.000	0.000	0.000	0.000	0.000
Sample 76	0.908	0.042	0.022	0.017	0.000	0.000	0.000	0.007	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sample 77	0.662	0.014	0.258	0.019	0.005	0.000	0.000	0.009	0.000	0.000	0.007	0.000	0.000	0.000	0.000	0.000	0.000
Sample 78	0.517	0.256	0.127	0.022	0.000	0.000	0.000	0.027	0.000	0.000	0.015	0.000	0.000	0.000	0.000	0.000	0.000
Sample 79	0.522	0.102	0.172	0.047	0.007	0.000	0.000	0.020	0.000	0.010	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sample 80	0.562	0.301	0.085	0.032	0.000	0.000	0.000	0.005	0.000	0.000	0.005	0.000	0.000	0.000	0.000	0.000	0.000
Sample 81	0.878	0.071	0.027	0.015	0.000	0.000	0.000	0.005	0.000	0.000	0.005	0.000	0.000	0.000	0.000	0.000	0.000
Sample 82	0.434	0.127	0.388	0.015	0.000	0.000	0.000	0.017	0.010	0.000	0.005	0.000	0.000	0.005	0.000	0.000	0.000
Sample 83	0.643	0.141	0.144	0.010	0.000	0.000	0.000	0.002	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sample 84	0.476	0.079	0.175	0.000	0.000	0.000	0.000	0.000	0.000	0.063	0.032	0.000	0.000	0.000	0.000	0.000	0.000
Sample 85	0.349	0.112	0.347	0.005	0.000	0.005	0.000	0.090	0.000	0.015	0.067	0.000	0.000	0.000	0.000	0.000	0.000
Sample 86	0.198	0.022	0.067	0.015	0.000	0.000	0.000	0.337	0.000	0.040	0.322	0.000	0.000	0.000	0.000	0.000	0.000
Sample 87	0.210	0.047	0.017	0.020	0.000	0.000	0.000	0.317	0.000	0.005	0.354	0.000	0.000	0.000	0.000	0.000	0.000
Sample 88	0.648	0.120	0.029	0.012	0.005	0.000	0.000	0.137	0.000	0.000	0.022	0.000	0.027	0.000	0.000	0.000	0.000
Sample 89	0.459	0.085	0.067	0.020	0.002	0.000	0.000	0.269	0.000	0.000	0.075	0.005	0.000	0.000	0.000	0.000	0.000
Sample 90	0.356	0.117	0.258	0.036	0.005	0.000	0.000	0.169	0.000	0.000	0.036	0.000	0.000	0.000	0.000	0.000	0.005
Sample 91	0.060	0.017	0.362	0.000	0.000	0.000	0.000	0.457	0.000	0.045	0.035	0.000	0.000	0.000	0.000	0.000	0.000
Sample 92	0.251	0.057	0.011	0.000	0.000	0.000	0.000	0.600	0.000	0.000	0.034	0.000	0.023	0.000	0.000	0.000	0.000
Sample 93	0.602	0.124	0.162	0.022	0.000	0.000	0.000	0.015	0.000	0.000	0.000	0.000	0.000	0.000	0.002	0.000	0.000
Sample 94	0.826	0.034	0.081	0.029	0.000	0.000	0.000	0.007	0.000	0.000	0.000	0.000	0.007	0.000	0.000	0.000	0.000
Sample 95	0.855	0.078	0.032	0.007	0.000	0.000	0.000	0.002	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sample 96	0.888	0.095	0.005	0.008	0.000	0.000	0.000	0.000	0.000	0.000	0.005	0.000	0.000	0.000	0.000	0.000	0.000
Sample 97	0.784	0.118	0.060	0.024	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sample 98	0.696	0.149	0.047	0.045	0.000	0.000	0.000	0.025	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sample 99	0.875	0.034	0.060	0.017	0.000	0.000	0.000	0.007	0.000	0.005	0.000	0.000	0.000	0.000	0.000	0.000	0.000

Table S1. Continued

	Lut_sp4	Lut_sp5	Ccf_fas	Coc_sp1	Gen_xxx	Fra_xxx	Fop_sp1	Fop_sp2	Ncf_cre	Nav_sp1	Nit_sp1	Nit_sp2	Nit_sp3	Pla_sp1	Pla_sp2	Pla_sp3
Sample 74	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sample 75	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sample 76	0.000	0.000	0.000	0.000	0.002	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sample 77	0.005	0.005	0.000	0.000	0.017	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sample 78	0.000	0.000	0.005	0.000	0.027	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sample 79	0.000	0.000	0.000	0.000	0.000	0.000	0.002	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sample 80	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sample 81	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sample 82	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sample 83	0.000	0.000	0.000	0.000	0.002	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sample 84	0.000	0.000	0.000	0.000	0.032	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sample 85	0.000	0.005	0.002	0.000	0.000	0.000	0.000	0.002	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sample 86	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sample 87	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sample 88	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sample 89	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.002	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sample 90	0.000	0.000	0.000	0.000	0.005	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sample 91	0.000	0.000	0.000	0.000	0.025	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sample 92	0.000	0.000	0.000	0.000	0.023	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sample 93	0.000	0.000	0.032	0.000	0.020	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sample 94	0.000	0.000	0.000	0.000	0.015	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sample 95	0.000	0.000	0.002	0.000	0.022	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sample 96	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sample 97	0.005	0.000	0.000	0.000	0.010	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sample 98	0.005	0.000	0.002	0.000	0.007	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sample 99	0.000	0.000	0.002	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000

Table S1. Continued

	Pla_sp4	Sta_ine	Acn_sp1	Ach_tay	Gom_sp1	Hum_inc	Hcf_inc	Dcf_gal	Str_sp1	Nan_shi	Cnt_xxx	Sta_sp1	Pse_sp1	Cha_cym	Fop_xxx	Smt_xxx
Sample 74	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.032	0.000	0.000	0.002	0.000	0.000	0.000	0.000	0.000
Sample 75	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.015	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sample 76	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sample 77	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sample 78	0.000	0.000	0.000	0.000	0.000	0.000	0.005	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sample 79	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.117	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sample 80	0.000	0.000	0.000	0.000	0.000	0.010	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sample 81	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sample 82	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sample 83	0.000	0.000	0.000	0.000	0.000	0.012	0.045	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sample 84	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.143	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sample 85	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sample 86	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sample 87	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.030	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sample 88	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sample 89	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.015	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sample 90	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.014	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sample 91	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sample 92	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sample 93	0.000	0.000	0.000	0.015	0.000	0.000	0.000	0.000	0.000	0.000	0.002	0.000	0.000	0.000	0.002	0.000
Sample 94	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sample 95	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sample 96	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sample 97	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Sample 98	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.020	0.000	0.000	0.000	0.005	0.000	0.000	0.000	0.000
Sample 99	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000

the identity of a taxon could not be confirmed based on the existing literature, the designations “cf.” or “sp.” were indicated alongside a proposed generic and/or species affiliation. In the study, a large number of *Luticola* D.G.Mann specimens were encountered as complete valves within girdle view, making them impossible to definitively attribute to a particular known taxon. These specimens were instead attributed to an “unidentified” taxon belonging to *Luticola* despite only being identified to the genus level. As such, this taxon was present within the initial diatom counts and determining of diatom relative abundances and is retained throughout all subsequent analyses.

Statistical analyses

Count data were first transformed to relative abundances by dividing individual counts by the total number of valves counted for the corresponding sample. From these, diversity indices including species richness, Evenness, and Shannon’s diversity ($\log_{10}$ – based) were calculated. A series of two-factor analysis of variance (ANOVA) tests were performed to examine if the treatments (Control, Water, Nutrients, and Water + Nutrients), or vegetation type (healthy bryophytes, moribund bryophytes, crustose lichens, and lichens of the genus *Usnea*) significantly influenced diversity metrics. Lastly, the effect of interaction between treatment and vegetation type was tested. Significant results were followed by applying Tukey’s Honest Significant Differences (HSD) to directly compare means between categories.

Four genera were dominant within the dataset. As such, these were extracted to test the effect of treatment and vegetation type on the abundance of individual genera using ANOVA and Tukey’s HSD as outlined for diversity indices above. The genera dataset was formed using the generic affiliation of those taxa which occurred at >1% relative abundance within the study. The dataset is comprised of *Luticola* D.G.Mann (12 taxa), *Humidophila* Lowe, Kociolek, Johansen, Van de Vijver, Lange-Bertalot & Kopalová (5 taxa)*, Psammothidium* Buhtkiyarova & Round (3 taxa) and *Pinnularia* Ehrenberg (1 taxon).

Initial exploration of community data began with the creation of dot plot diagrams and continued with the creation of ordinations. Diatom relative abundance data were Hellinger transformed (Legendre and Gallagher 2001), and redundancy analyses (RDA) constrained the dataset separately by treatment and for each individual vegetation type to quantify their role in explaining community structure using the *vegan* package, version 2.5–6 (Oksanen et al. 2019) in R. Rare taxa were filtered from the dataset, excluding those taxa that occurred at less than 1% relative abundance throughout the study. To test whether the diatom community structure differed significantly between the aforementioned vegetation types and treatments, permutational analysis of variance (PERMANOVA, Anderson 2001) was performed, with significance designated at α = 0.05. Visualizations and statistical analyses were performed using the R console, version 3.5.0 (R Core Team 2018).

Results

Diatom flora

Overall, 49 taxa belonging to 20 genera were observed. Table 3 presents all diatom taxa, as species, forms, and varieties encountered within the study. The genera *Luticola* (12 taxa) and *Humidophila* (5 taxa) represent the most diverse genera. The five most abundant taxa, representing approximately 92% of all valves counted within the analysis, are: *Humidophila gallica* (W.Smith) Lowe, Kociolek, Q.You, Q.Wang & Stepanek (59%), *Pinnularia borealis* Ehrenberg (~11%), *Humidophila australis* (Van de Vijver & Sabbe) R.L.Lowe, Kociolek, J.R.Johansen, Van de Vijver, Lange-Bertalot & Kopalová (~11%), *Luticola* (sensu D.G.Mann) (9%), and *Psammothidium papilio* (D.E.Kellogg, M.Stuiver, T.B.Kellogg & G.H.Denton) Kopalová & Van de Vijver (3%). At least one of these five most abundant taxa occurred in

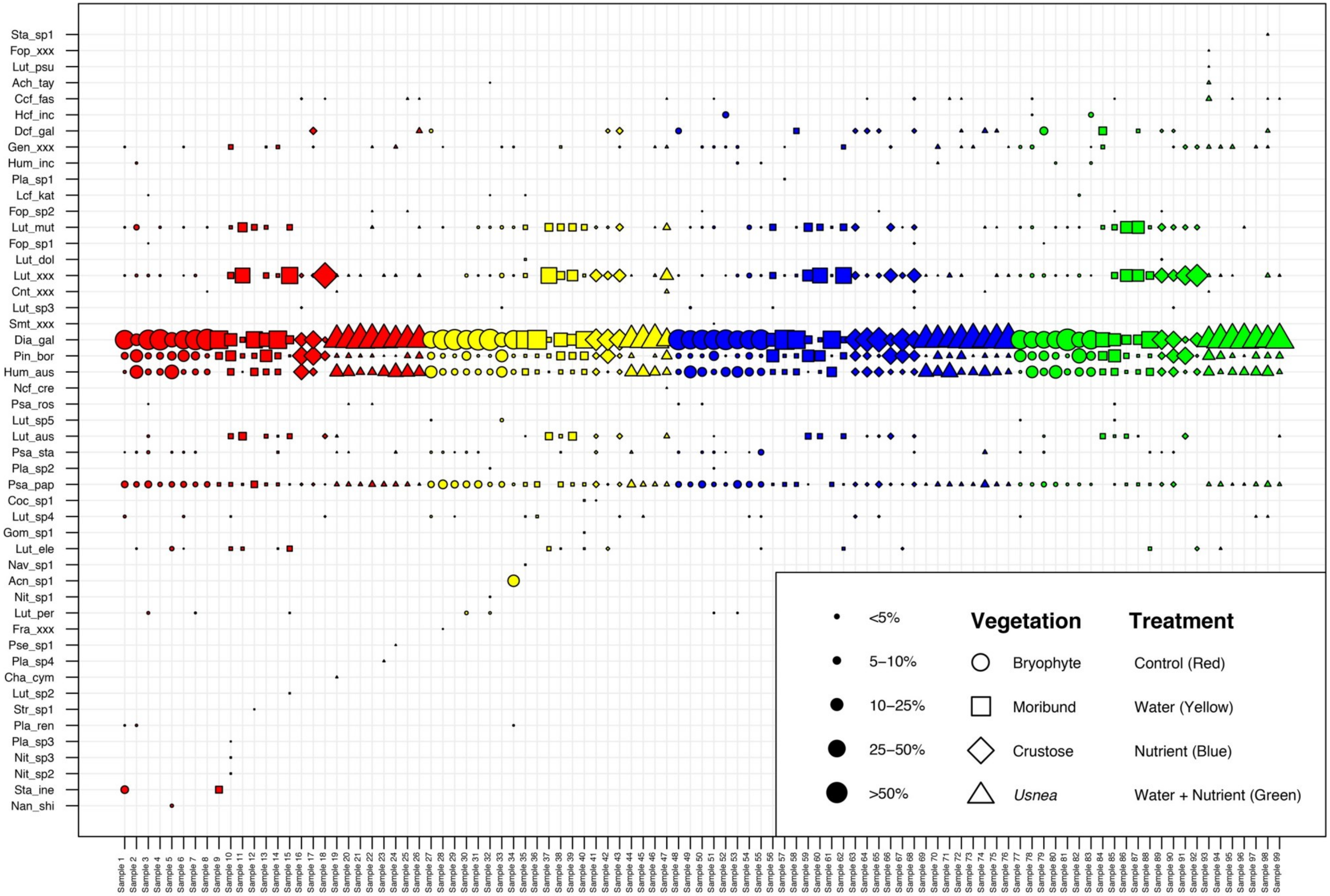

Figure. 2. Dot plot diagram of all diatom taxa across all samples within the study. Treatments are color coded within the plot, Control (Red), Water (Yellow), Nutrients (Blue) and Water + Nutrients (Green). Vegetation type is coded by shape: "Circle" (healthy bryophyte), "Square" (moribund bryophyte), "Diamond" (crustose lichen), and "Triangle" (*Usnea* lichen).

each sample (Figure 2). Only eight taxa occurred with a relative abundance >1% in the study as a whole (Figure 3).

Table 3. Diatom taxa and authorities, their code within the analysis and distribution data of taxa observed within the study.

Taxon	Code	Distribution
Humidophila gallica (W.Smith) Lowe, Kociolek, Q.You, Q.Wang & Stepanek	Dia_Gal	Cosmopolitan
Humidophila australis (Van de Vijver & Sabbe) R.L.Lowe, Kociolek, J.R.Johansen, Van de Vijver, Lange-Bertalot & Kopalová	Hum_Aus	MA/CA
Humidophila inconspicua (Kopalová & Van de Vijver) R.L.Lowe, Kociolek, J.R.Johansen, Van de Vijver, Lange-Bertalot & Kopalová	Hum_Inc	MA
Humidophila cf. *inconspicua* (Kopalová & Van de Vijver) R.L. Lowe, Kociolek, J.R.Johansen, Van de Vijver, Lange-Bertalot & Kopalová	Hcf_Inc	—
Humidophila cf. *gallica* (W.Smith) Lowe, Kociolek, Q.You, Q.Wang & Stepanek	Dcf_Gal	—
Pinnularia borealis Ehrenberg	Pin_Bor	Cosmopolitan
Psammothidium papilio (D.E. Kellogg, M. Stuiver, T.B. Kellogg & G.H. Denton) Kopalová & Van de Vijver	Psa_Pap	MA/CA
Psammothidium stauroneioides (Manguin) Buhktiyarova	Psa_Sta	SA/CA
Psammothidium rostrogermainii Vam de Vijver, Kopalová & Zidarova	Psa_Ros	MA/CA
Planothidum renei (Lange-Bertalot & Schmidt) Van de Vijver	Pla_Ren	Southern Hemisphere
Planothidium Round & L.Bukhtiyarova sp. 1	Pla_Sp1	—
Planothidium Round & L.Bukhtiyarova sp. 2	Pla_Sp2	—
Planothidium Round & L.Bukhtiyarova sp. 3	Pla_Sp3	—
Planothidium Round & L.Bukhtiyarova sp. 4	Pla_Sp4	—
Luticola muticopsis (Van Heurck) D.G. Mann	Lut_Mut	Southern Hemisphere
Luticola austroatlantica Van de Vijver, Kopalová, Spaulding & Esposito	Lut_Aus	MA/CA
Luticola dolia Spaulding & Esposito	Lut_Dol	CA
Luticola elegans (West & West) Kohler & Kopalová	Lut_Ele	CA
Luticola permuticopsis Kopalová & Van de Vijver	Lut_Per	MA/CA
Luticola pseudomurrayi Van de Vijver & Tavernier	Lut_Psu	CA
Luticola cf. *katkae* Van de Vijver & Zidarova	Lcf_Kat	—
Luticola D.G. Mann	Lut_Xxx	—
Luticola D.G. Mann sp. 2	Lut_Sp2	—
Luticola D.G. Mann sp. 3	Lut_Sp3	—
Luticola D.G. Mann sp. 4	Lut_Sp4	—
Luticola D.G. Mann sp. 5	Lut_Sp5	—
Cocconeis cf. *fasciolata* (Ehrenberg) N.E.Brown	Ccf_Fas	—
Cocconeis Ehrenberg	Coc_Sp1	—
Fragilaria Lyngbye	Fra_Xxx	—
Fragilariopsis Hustedt sp. 1	Fop_Sp1	—
Fragilariopsis Hustedt sp. 2	Fop_Sp2	—
Fragilariopsis Hustedt sp. 3	Fop_Xxx	—
Navicula cf. *cremeri* Van de Vijver & Zidarova	Ncf_Cre	—
Navicula Bory sp. 1	Nav_Sp1	—
Nitzschia Hassall sp. 1	Nit_Sp1	—
Nitzschia Hassall sp. 2	Nit_Sp2	—
Nitzschia Hassall sp. 3	Nit_Sp3	—
Stauroneis Ehrenberg	Sta_Sp1	—
Stauroforma inermis Flower, Jones & Round	Sta_Ine	MA/CA
Achnanthes Bory sp. 1	Acn_Sp1	—
Achnanthes taylorensis D.E.Kellogg, Stuiver, T.B.Kellogg & G.H.Denton	Ach_Tay	CA
Gomphonema Ehrenberg	Gom_Sp1	—

Table 3. Continued

Taxon	**Code**	**Distribution**
Staurosirella D.M.Wiliams & Round sp. 1	Str_Sp1	—
Nanofrustulum shiloi (Lee, Reimer & McEnery) Round, Hallsteinsen & Paache	Nan_Shi	Marine
Pseudostaurosira D.M.Williams & Round sp. 1	Pse_Sp1	—
Chamaepinnularia cymatopleura (West & G.S.West) Cavacini	Cha_Cym	CA
Centric unidentified	Cnt_Xxx	—
Genus uncertain 1	Gen_Xxx	—
Genus uncertain 2	Smt_Xxx	—

Diversity metrics

Boxplots displaying Species Richness, Shannon's Diversity, and Evenness, grouped by vegetation type and separated by treatment (Figure 4), show species richness ranged between 4 – 13 taxa per sample. An average of eight taxa (median = 8) was observed across the samples. Shannon's diversity ranged between 0.5 to 2.0 for all samples, however the majority possessed a value of approximately 1. Evenness scores for the majority of samples were between approximately 0.5 to 0.7, with the upper extreme value of nearly 0.9 only seldom observed.

The results of a two-way ANOVA testing the effect of vegetation type on species richness ($p=0.0149$), Shannon's diversity ($p<<0.01$), and Evenness ($p<<0.01$) were all significant, whereas neither treatment nor the combined treatment*vegetation type effects were significant (Table 4). Tukey's HSD post-hoc comparisons of species richness by community

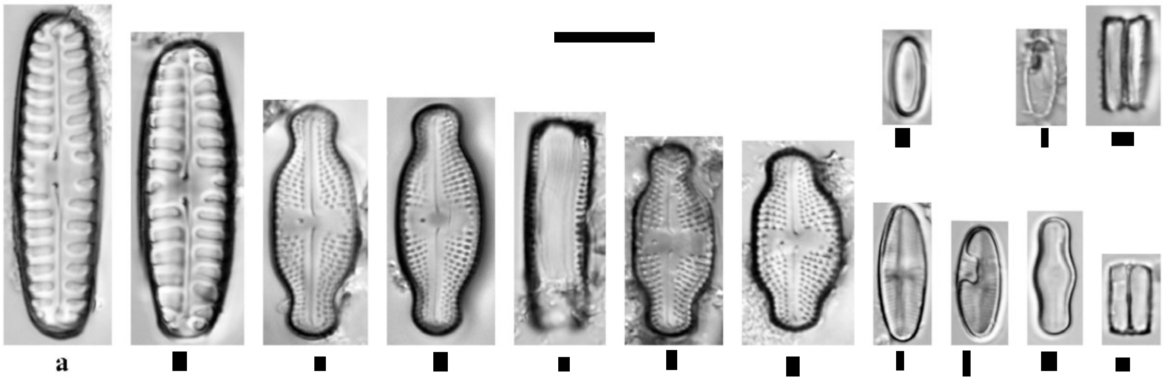

Figure 3. Common diatom species associated with bryophyte and lichen vegetation types. All taxa shown occurred at greater than or equal to 1% relative abundance across samples. a, b. *Pinnularia borealis*. c, d. *Luticola austroatlantica*. e. *Luticola* in girdle view. f, g. *Luticola. muticopsis*. h. *Humidophila* cf. *gallica*. i, j *Psammothidium papilio*. l, m. *Humidophila gallica*. k, n. *Humidophila. australis*. Central 10 µm scale bar applies to all images.

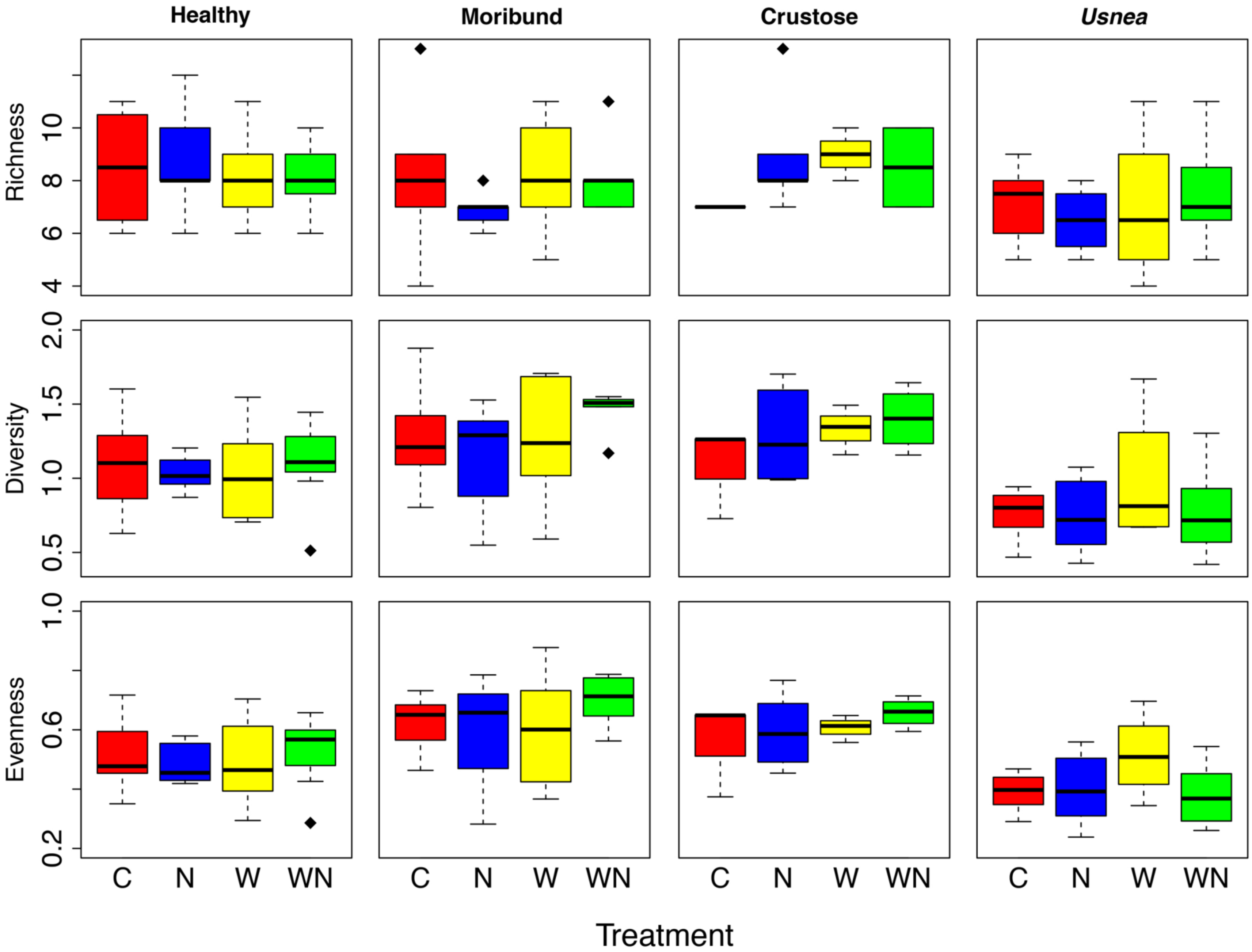

Figure 4. Box plots of species richness, Shannon's diversity index and Evenness arranged by vegetation type and treatment. Treatments are color coded, with abbreviations, within the plot, Control (Red)-"C", Water (Yellow)-"W", Nutrients (Blue)-"N", and Water + Nutrients (Green)-"WN". Vegetation types follow the designation: "Healthy" (healthy bryophyte), "Moribund" (moribund bryophyte), "Usnea" (*Usnea* lichen), and "Crustose" (crustose lichen).

Table 4. The results of ANOVA, PERMANOVA, and RDA models. Significant results are in bold.

Statistical Test	Variable	Transformation	Test	DF (model, error)	*F* Ratio	P Value	Post Hoc Comparison	diff	P
ANOVA	Species Richness	Log 10	Whole Model	15, 83	1.15E+00	3.31E-01	Crustone - *Usnea*	8.44E-02	3.81E-02
			Treatment	3	2.25E-01	8.79E-01	*Usnea* - Healthy	-8.02E-02	1.34E-02
			Community	**3**	**3.70E+00**	**1.49E-02**			
			Treatment x Community	9	5.91E-01	8.00E-01			
ANOVA	Shannon Diversity	None	Whole Model	15, 83	3.34E+00	2.16E-04	Crustone - *Usnea*	4.90E-01	3.30E-06
			Treatment	3	7.79E-01	5.08E-01	*Usnea* - Healthy	-2.64E-01	4.34E-03
			Community	**3**	**1.40E+01**	**1.77E-07**	*Usnea* - Moribund	-4.64E-01	6.00E-07
			Treatment x Community	9	6.29E-01	7.68E-01			
ANOVA	Evenness	None	Whole Model	15, 83	3.70E+00	6.13E-05	Moribund - Healthy	1.18E-01	2.20E-03
			Treatment	3	5.59E-01	6.43E-01	Crustose - Healthy	1.02E-01	3.19E-02
			Community	**3**	**1.58E+01**	**3.20E-08**	Crustone - *Usnea*	1.96E-01	6.80E-06
			Treatment x Community	9	6.96E-01	7.10E-01	*Usnea* - Healthy	-9.30E-02	1.93E-02
ANOVA	*Luticola*	Square Root	Whole Model	15, 83	5.77E+00	6.11E-08	Moribund - Healthy	3.02E-01	3.00E-07
			Treatment	3	9.51E-01	4.20E-01	Crustose - Healthy	2.41E-01	4.77E-04
			Community	**3**	**2.64E+01**	**4.30E-12**	Crustone - *Usnea*	2.46E-01	4.89E-04
			Treatment x Community	9	5.39E-01	8.42E-01	*Usnea* - Moribund	-3.08E-01	4.00E-07
ANOVA	*Pinnularia*	Square Root	Whole Model	15, 83	2.72E+00	1.96E-03	Crustose - Healthy	8.34E-02	4.08E-02
			Treatment	3	1.86E+00	1.42E-01	Crustone - *Usnea*	1.49E-01	5.00E-05
			Community	**3**	9.15E+00	2.68E-05	*Usnea* - Moribund	-8.30E-02	1.92E-02
			Treatment x Community	9	1.05E+00	4.06E-01			
ANOVA	*Psammothidium*	Square Root	Whole Model	15, 83	4.80E+00	1.41E-06	Moribund - Healthy	-3.71E-02	1.00E-05
			Treatment	**3**	**6.02E+00**	**9.17E-04**	Crustose - Healthy	-4.19E-02	1.31E-05
			Community	**3**	**1.47E+01**	**9.53E-08**	*Usnea* - Healthy	-3.23E-02	6.92E-05
			Treatment x Community	9	9.07E-01	5.23E-01	(Water+Nutrient) - Water	-3.42E-02	1.55E-03
ANOVA	*Humidophila*	Square Root	Whole Model	15, 83	4.27E+00	8.44E-06	Moribund - Healthy	-2.78E-01	6.70E-06
			Treatment	3	5.65E-01	6.40E-01	Crustose - Healthy	-2.72E-01	1.42E-04
			Community	**3**	**1.86E+01**	**2.53E-09**	Crustone - *Usnea*	-3.84E-01	1.00E-07
			Treatment x Community	9	8.24E-01	5.96E-01			

Table 4. Continued

Statistical Test	Variable	Comparisons	Test	DF (model, error)	F Model	P Value
PERMANOVA	Full Diatom Dataset	Treatment *Community	Treatment	3	7.50E-01	6.11E-01
			Community	**3**	**1.41E+01**	**1.00E-04**
			Treatment*Community	9	8.84E-01	6.42E-01
PERMANOVA	Full Diatom Dataset	Water*Nutrient	Water	1	3.98E-01	7.26E-01
			Nutrient	1	3.22E-01	7.85E-01
			Water*Nutrient	1	8.87E-01	3.95E-01
PERMANOVA	Genera Dataset	Water*Nutrient	Water	1	2.61E-01	7.24E-01
			Nutrient	1	2.68E-01	7.17E-01
			Water*Nutrient	1	2.40E-01	7.45E-01
PERMANOVA	Genera Dataset	Treatment *Community	Treatment	3	3.86E-01	8.41E-01
			Community	**3**	**1.82E+01**	**1.00E-04**
			Treatment*Community	9	5.49E-01	8.92E-01

RDA	RDA Axis 1 Eigenvalue	RDA Axis 2 Eigenvalue	RDA Axis 3 Eigenvalue	Total Variance
Healthy	0.109	0.027	0.010	0.068
Moribund	0.027	0.011	0.002	0.231
Crustose	0.195	0.074	0.005	0.141
Usnea	0.112	0.038	0.000	0.030

type demonstrated *Usnea* was less species-rich than the healthy bryophytes (p=0.013) and the crustose lichens were more species rich than *Usnea* (p=0.038). Furthermore, *Usnea* vegetation had lower Shannon diversity than healthy (p<0.01) and moribund (p<<0.01) bryophytes. Crustose lichens had significantly greater Shannon's diversity than *Usnea* (p<<0.01). *Post hoc* analysis of Evenness between vegetation types showed that both moribund bryophytes (p<0.01) and crustose lichens (p=0.03) were greater than healthy bryophytes. Moribund bryophyte diatom community Evenness was also greater than in *Usnea* (p<<0.001). Lastly, *Usnea* Evenness values were lower than in healthy bryophytes (p=0.02).

Genus-level analyses

Relative abundances of genera *Luticola, Pinnularia,* and *Humidophila* were significantly different between vegetation types, though there were no significant differences among treatments when examined with two-way ANOVA. Only the genus *Psammothidium* showed significantly different relative abundances between vegetation types and among treatments.

Moribund (p<<0.01), *Usnea* (p<<0.01), and crustose (p<<0.01) vegetation types showed lower relative abundances of *Psammothidium* when compared with healthy bryophytes. *Post hoc* analysis of treatment categories showed that the Water + Nutrient treatment had lower relative abundances of *Psammothidium* than the Water-only treatment (p<<0.01).

Moribund (Tukey's HSD, p<<0.01) and crustose (p<<0.01) vegetation types had greater relative abundances of *Luticola* than healthy bryophytes. Relative abundances of *Luticola* were also greater in crustose lichens than in *Usnea* (p<<0.01), but lower in *Usnea* than in moribund bryophytes (p<<0.01).

Larger relative abundances of *Pinnularia* were observed upon crustose lichens than in both healthy bryophyte ($p=0.04$) and *Usnea* ($p<<0.01$) vegetation. *Pinnularia* relative abundances were lower on *Usnea* than moribund bryophyte vegetation ($p=0.02$).

Lastly, *Humidophila* showed lower relative abundances on moribund bryophytes than for healthy bryophytes ($p<<0.01$) and *Usnea* ($p<<0.01$) vegetation, while relative abundances on moribund bryophytes were lower than healthy bryophytes ($p<<0.01$).

Community analyses

Separate redundancy analyses were performed for each vegetation type, where diatom relative abundance data were constrained against treatments (Figure 5). *Pinnularia borealis* (Pin_bor) showed a high affinity for healthy and crustose vegetation types, whereas *Luticola* (as the "unidentified" taxon, Lut_Xxx) was similarly associated with *Usnea* vegetation types. No apparent "groupings" of samples by treatment were present within the RDA analyses. Total variance explained for each RDA was between 3% for *Usnea* and 23% for moribund vegetation types. Eigenvalues for the first three constrained axes are displayed within Table 4.

Permutational analysis of variance (PERMANOVA) examining the effect of the vegetation type upon diatom communities yielded a significant result ($p=<0.01$, $R^2=0.31$), although treatment ($p=0.61$) and the combined effect of treatment * vegetation type ($p=0.64$) was not significant (Table 4). This same trend was seen when four most abundant diatom genera were compared against vegetation type*treatment, yield a significant result ($p<0.01$, $R^2=0.38$). There were no significant results for treatments of water, nutrients nor their combined effects (Water + Nutrients), when diatom relative abundances of the four most abundant genera were examined.

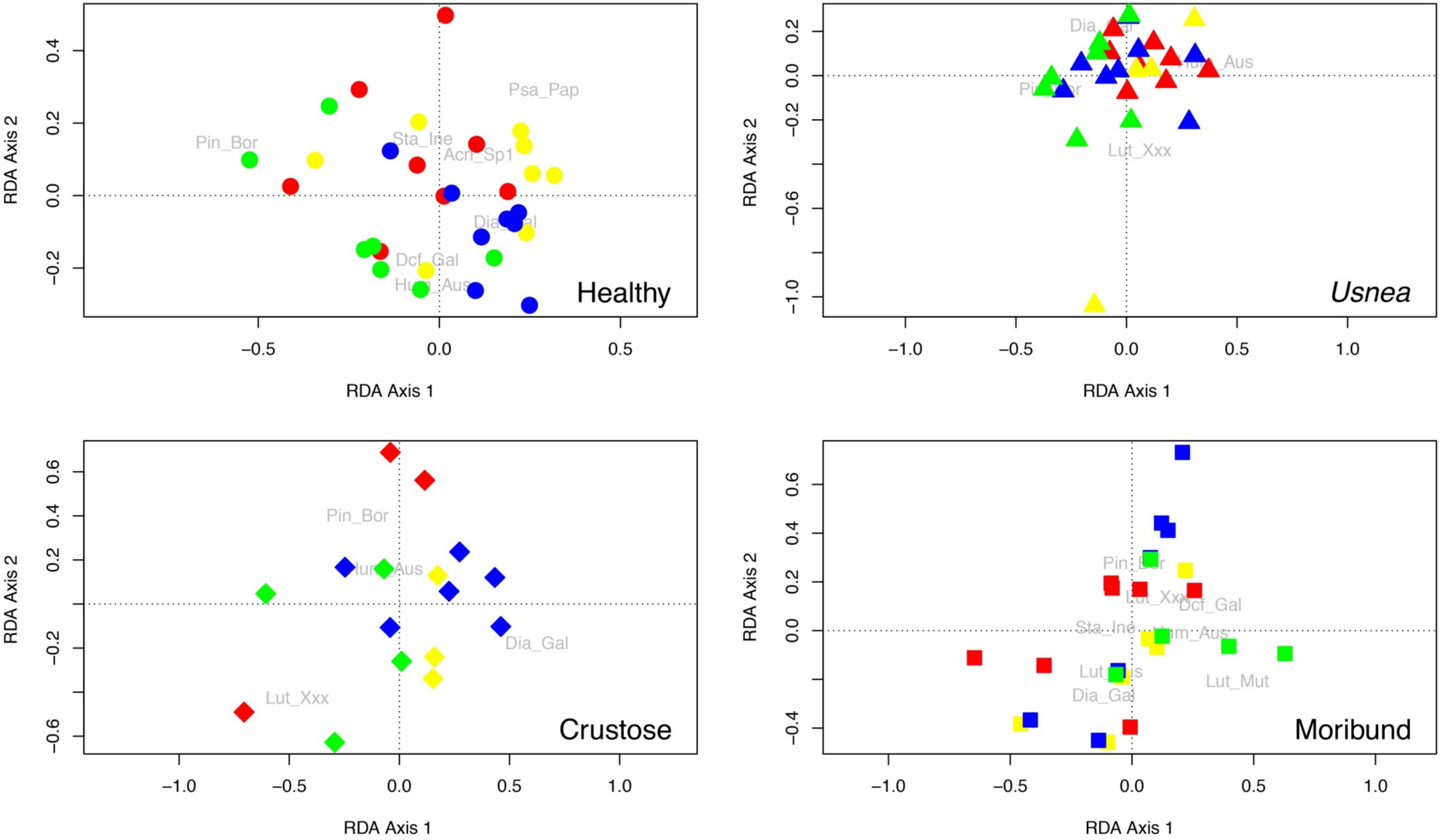

Figure 5. Results of RDA grouped by vegetation type, displaying diatom taxa aligned against treatment. Individual vegetation types are labeled within the corner of each RDA. Vegetation type is coded by shape: “Circle” (healthy bryophyte), “Square” (moribund bryophyte), “Diamond” (crustose lichen), and “Triangle” (*Usnea* lichen). Treatments are color coded within each plot, Control (Red), Water (Yellow), Nutrients (Blue), and Water + Nutrients (Green).

Discussion

In this experiment, four treatments (Control, Water, Nutrients and Water + Nutrients) were applied to four terrestrial vegetation types (healthy and moribund bryophytes as well as crustose and *Usnea* lichens) in order to gauge their impact on epiphytic diatom communities. We found that only the genus *Psammothidium* demonstrated a response between treatments. Beyond this exception, no significant result for diatom diversity indices and community structure could be found when investigating the impacts of treatment on vegetation types. However, vegetation type was a highly influential factor for both diversity metrics and community structure, and potentially point to micro-habitat preferences among diatom species and genera. As field manipulations studying Antarctic flora are exceedingly rare, these results are important as they provide experimental support that habitat loss, or gain, via bryophyte and lichen vegetation contraction/expansion due to climate change will impact the associated diatom community.

Diatom host preferences and treatment effects

Our findings that diatom community composition is largely determined by the underlying vegetation type has implications for potential habitat loss due to climate change. Three bryophyte species (*Schistidium antarctici*, *Ceratodon purpureus* (Hedwig) Bridel and *Bryum pseudotriquetrum* (Hedwig) P.G.Gäertner, B.Meyer & Scherbius) were examined to assess stresses associated with desiccation and submergence, both of which are common in Antarctic bryophyte communities. Of these, the endemic *S. antarctici*, was shown to be less tolerant to desiccation stress while being highly tolerant of submergence (Wasley et al. 2006b). Within the current study, *S. antarctici* is the major component of the healthy bryophyte vegetation type and the dominant bryophyte across the remainder of the experimental gradient. Within close proximity to the current study site, the dominant bryophyte *S. antarctici* occurred at over 90%

relative abundance within the bryophyte communities and was present within the "transitional" (equivalent to the moribund community) and crustose lichen communities at approximately 40% and 20% relative abundance, respectively (Wasley et al. 2012). Robinson et al. (2018) detailed a drying trend within recent years in the Windmill islands and a concomitant reduction in the abundance of *S. antarctici*, whereas the abundance of the more desiccation tolerant (and submergence intolerant) cosmopolitan moss species *C. purpureus* and *B. pseudotriquetrum* increased. Within this adjacent study site, (ASPA 135 melt puddle) the proportion of moribund moss also increased. Given the observed differences in relative abundances of the four genera among different vegetation types, an increase in moribund vegetation may preferentially favor *Luticola*, whereas healthy bryophyte vegetation (stands comprised predominantly of *S. antarctici*) may demonstrate higher abundances of *Humidophila* and *Psammothidium.*

The "turf morphology", or the degree of complexity and folding within vegetation, of *S. antarctici*, *C. purpureus* and *B. pseudotriquetrum* has been previously suggested to be an avenue of water retention, and thereby preventing vegetation desiccation (Wasley et al. 2006b). As both temperature and water levels were shown to vary within the fine scale microclimate of mixed bryophyte vegetation types of *Ceratodon* Brisson and *Bryum* Hedwig (Lewis Smith 1999), turf morphology may play a role in the selective pressures on diatoms, especially if *S. antarctici* is in decline. This could potentially influence dispersion/colonization between bryophyte communities at large. However, our results suggest that *P. borealis* and *Luticola* (most likely as *L. muticopsis*) may be better able to inhabit a broad range of conditions, such as variable nutrient availability, site topology and bryophyte and lichen vegetation types, as these widely distributed taxa demonstrate a larger range of environmental preferences.

Luticola, Pinnularia and *Humidophila* did not show significant interactions between treatments. However, all four genera showed significant differences in relative abundance upon the healthy bryophyte vegetation. All four genera contain significant differences in relative abundances when comparing the crustose lichen community to the healthy bryophyte community. For example, in the crustose lichen community, *Luticola* and *Pinnularia* showed greater relative abundances, contrasting the lower relative abundances of *Psammothidium* and *Humidophila*. Similarly, these trends are reflected in species Evenness as well.

Biogeographic and taxonomic notes

The current study provides some of the first observations of diatoms associated with bryophyte and lichen vegetation from the Windmill Islands. Previous studies throughout the Windmill Islands have examined benthic diatoms within marine bays (Cunningham & McMinn 2004) and lake and pond sediments (Roberts et al. 2001). The current study contrasts these surveys in both ecological setting and observed flora. In the present work, the predominant taxa belong to the genera *Luticola, Psammothidium, Pinnularia,* and *Humidophila*. However, though Roberts et al. (2001) most likely observed *L. muticopsis* within lake sediments (there described as the complex *Luticola mutica* (Kützing) D.G.Mann/*muticopsis* (Van Heurck) D.G.Mann) this record must be examined further given the recent revision of *Luticola* within Continental Antarctica (Kohler et al. 2015). The marine diatom genus *Fragilariopsis* Hustedt, and freshwater *Stauroforma inermis* Flower, V.J.Jones & Round while represented by single valves in the current study were observed in much larger proportions by Roberts et al. (2001).

The terrestrial diatom species complex of *Pinnularia borealis,* is capable of surviving extremes in habitat (Hejduková et al. 2019, Pinseel et al. 2019) and the only member of the genus reported within the study. The largest proportion of *Luticola* is represented by an unidentified grouping of specimens present as complete valves in girdle view. Given the low number of species of *Luticola* reported overall, and that the second most reported member of the genus within the study is *Luticola muticopsis*, we believe the *Luticola* specimens in girdle view most likely can be attributed to *L. muticopsis.* A limno-terrestrial species, *L. muticopsis* is distributed widely across the Southern Hemisphere, within the entirety of the Antarctic Region as well as into southern South America (Zidarova et al. 2016). *Humidophila* is represented by the endemic *H. australis* and the cosmopolitan *H. gallica*. *Humidophila* is common within the Maritime Antarctic (Kopalová et al. 2014) and Continental Antarctic (Sabbe et al. 2003).

The dominant *Psammothidium* taxon was *P. papilio,* with only minor occurrences of *P. stauroneioides* (Manguin) Buhktiyarova and *P. rostrogermainii* Van de Vijver, Kopalová & Zidarova. All three species are endemic to the Antarctic region, often associated with mosses and rarely, with the exception of *P. papilio*, within the lake benthic environment (Zidarova et al. 2016). However, *P. papilio* was quite common in streams within the McMurdo Dry Valleys (Spaulding et al. 2020). Together, *P. papilio* and *P. rostrogermainii* are common constituents of the Continental and Maritime Antarctic diatom flora, whereas *P. stauroneioides* is only distributed on the Continent and the Sub-Antarctic Islands of the southern Indian Ocean (Van de Vijver et al. 2002, Gibson et al. 2006).

The diatom community structure within the present study differs when compared to moss diatom communities within other East Antarctic localities, but also both the Maritime and Sub-Antarctic biogeographical regions. The McMurdo Sound Long Term Ecological Research (LTER) Project has maintained a database of diatom counts from throughout the McMurdo Dry Valleys (MDV). Here, across two lake basins within Taylor Valley, the predominant moss-inhabiting genera include *Hantzschia* Grunow and *Nitzschia* Hassall. Specifically, a majority of the sites are dominated by *Hantzschia amphioxys* (Ehrenberg) Grunow, known to be a species complex (Souffreau et al. 2013), and *Nitzschia australocommutata* Hamsher, Kopalová, Kociolek, Zidarova & Van de Vijver where these taxa may be present at approximately 30% and 40%, respectively **(**Spaulding et al. 2020**).** However, similar to the present study, sites within the MDV still contain overall species richness values of 10 – 20 species per site.

A number of diatom taxa are shared between the MDV and other East Antarctic localities. Examples include endemics such as *Chamaepinnularia cymatopleura* (West & G.S.West) Cavacini (Van de Vijver et al. 2012) and members of *Luticola* (Kohler et al. 2015). Comparing our diatom communities with those from the Maritime Antarctic Region (MA), Livingston and James Ross Island demonstrated greater species richness with 123 and 57 moss diatom species, respectively (Kopalová et al. 2014). Although the MA and AC share common genera, they are more speciose in the former. For example, *Humidophila* (reported as *Diadesmis* Kützing), *Muelleria* (Frenguelli) Frenguelli, *Navicula* Bory, and *Nitzschia* all contained 7 species each, whereas the dominant genera *Pinnularia, Luticola* and *Psammothidium* contained 16, 13, and 9 species, respectively. Upon James Ross Island, *Luticola, Diadesmis* and *Pinnularia* featured 11, 6, and 5 species respectively, with *Pinnularia borealis, Hantzschia amphioxys* and *Nitzschia perminuta* Grunow appearing at 24.6%, 10.7% and 8.9% relative abundance across sites (Kopalová et al. 2014).

Conclusions

Within this study, field manipulations of nutrient and water were added to four vegetation types within the projected range expected due to climate change. Our initial hypothesis that nutrient and water additions would influence diatom communities was not supported. Instead, vegetation type best explained differences in diatom community composition. Although water and nutrient additions did not structure the diatom community composition, their influence upon the bryophyte and lichen community structures has more indirect impacts through diatom habitat loss or gains through the expansion and/or contraction of different vegetation types. These results inform larger trends within microbial and macroflora diversity within Antarctica as microbial manipulative experiments within Antarctica are quite sparse. The possible effects of climate change upon the microbial biota of Antarctica are not well understood, and more specifically, these impacts are not expected to elicit the same responses across microbial phyla. As such, this study represents an important dataset for the inclusion of microbial biodiversity into management and preservation.

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Author Contributions

JW, MJW and SAR performed field work and collected samples. KK subsampled the collections. JB processed moss and lichen samples within the laboratory, prepared and counted slides. JB, KK, BVDV, TJK contributed equally to identify diatom taxa, statistical analyses and data interpretation. The manuscript was written with significant input and editing from all authors.

References

Anderson, M.J. 2001. A new method for non- parametric multivariate analysis of variance. *Austral ecology, 26*(1), pp. 32–46.

Beyer, L., Bölter, M. and Seppelt, R.D., 2000. Nutrient and thermal regime, microbial biomass, and vegetation of Antarctic soils in the Windmill Islands region of East Antarctica (Wilkes Land). *Arctic, Antarctic, and Alpine Research*, *32*(1), pp.30–39.

Chown, S.L., Clarke, A., Fraser, C.I., Cary, S.C., Moon, K.L. and McGeoch, M.A., 2015. The changing form of Antarctic biodiversity. *Nature*, *522*(7557), pp.431–438.

Clarke, L.J., Robinson, S.A., Hua, Q., Ayre, D.J. and Fink, D., 2012. Radiocarbon bomb spike reveals biological effects of Antarctic climate change. *Global Change Biology*, *18*(1), pp.301–310.

Convey, P. and Peck, L.S., 2019. Antarctic environmental change and biological responses. *Science Advances*, *5*(11), p.eaaz0888.

Convey, P., Chown, S. L., Clarke, A., Barnes, D. K. A., Bokhorst, S., Cummings, V., Ducklow, H. W., Frati, F., Green, T. G. A., Gordon, S., Griffiths, H. J., Howard-Williams, C., Huiskes, A. H. L., Laybourn-Parry, J., Lyons, W. B., mcminn, A., Morley, S. A., Peck, L. S., Quesada, A., Robinson, S. A., Schiaparelli, S. & Wall, D. H. 2014. The spatial structure of Antarctic biodiversity. *Ecological monographs, 84(2),* pp.203–244.

Cunningham, L. and McMinn, A., 2004. The influence of natural environmental factors on benthic diatom communities from the Windmill Islands, Antarctica. *Phycologia*, *43*(6), pp.744–755.

Hejduková, E., Pinseel, E., Vanormelingen, P., Nedbalová, L., Elster, J., Vyverman, W. and Sabbe, K., 2019. Tolerance of pennate diatoms (Bacillariophyceae) to experimental freezing: comparison of polar and temperate strains. *Phycologia*, *58*(4), pp.382–392.

Imura, S., Bando, T., Saito, S., Seto, K. and Kanda, H., 1999. Benthic moss pillars in Antarctic lakes. *Polar Biology*, *22*(2), pp.137–140.

Kellogg, T.B. and Kellogg, D.E. (2002) Non-marine and littoral diatoms from Antarctic and subantarctic regions. Distribution and updated taxonomy. *Diatom monographs* 1, A.R.G Gantner Verlag K.G., 795 pp.

Kohler, T.J., Kopalová, K., Van De Vijver, B. and Kociolek, J.P., 2015. The genus *Luticola* D.G.Mann (Bacillariophyta) from the McMurdo Sound Region, Antarctica, with the description of four new species. *Phytotaxa, 208*(2), pp.103–134.

Kopalová, K., Ochyra, R., Nedbalová, L. and Van de Vijver, B., 2014. Moss-inhabiting diatoms from two contrasting Maritime Antarctic islands. *Plant Ecology and Evolution*, *147*(1), pp.67–84.

Kurbatova, L.E. and Ochyra, R., 2012. Two noteworthy additions to the moss flora of the Schirmacher Oasis in continental Antarctica. *Cryptogamie, Bryologie*, *33*(2), pp.159–167.

Lee, J.R., Raymond, B., Bracegirdle, T.J., Chadès, I., Fuller, R.A., Shaw, J.D. and Terauds, A., 2017. Climate change drives expansion of Antarctic ice-free habitat. *Nature*, *547*(7661), pp.49–54.

Legendre, P. and Gallagher, E.D., 2001. Ecologically meaningful transformations for ordination of species data. *Oecologia*, *129*(2), pp.271–280.

Lewis Smith, R.I., 1999. Biological and environmental characteristics of three cosmopolitan mosses dominant in continental Antarctica. *Journal of Vegetation Science*, *10*(2), pp.231–242.

Melick, D.R., Hovenden, M.J. and Seppelt, R.D., 1994. Phytogeography of bryophyte and lichen vegetation in the Windmill Islands, Wilkes Land, Continental Antarctica. *Vegetatio*, *111*(1), pp.71–87.

Nielsen, U.N. and King, C.K., 2015. Abundance and diversity of soil invertebrates in the Windmill Islands region, East Antarctica. *Polar Biology*, *38*(9), pp.1391–1400.

Ohtani, S., 1986. Epiphytic algae on mosses in the vicinity of Syowa Station, Antarctica. *Memoirs of National Institute of Polar Research Special Issue*, *44*, pp.209–19.

Oksanen, J., Blanchet, G.F., Friendly,M., Kindt,R., Legendre,P., Mcglinn, D., Minchin, P.R., O'hara, R. B., Simpson, G.L., Solymos, P., Stevens, M.H.H., Szoecs, E. and Wagner, H., 2019. Vegan: Community Ecology Package. R package version 2.5–6. Available from: https://CRAN.R-project.org/package=vegan [Accessed 15 Jan 2019]

Opalinski, K.W. 1972. Flora and Fauna in Freshwater Bodies of the Thala Hills Oasis (Enderby Land, Eastern Antarctica). *Polish Archives of Hydrobiology*, *19*(4), pp.383–398

Pinseel, E., Kulichová, J., Scharfen, V., Urbánková, P., Van de Vijver, B. and Vyverman, W., 2019. Extensive cryptic diversity in the terrestrial diatom *Pinnularia borealis* (Bacillariophyceae). *Protist*, *170*(2), pp.121–140.

R Development Core Team. 2018. R: a language and environment for statistical computing. R Foundation for Statistical Computing. Available from: https://www.R-project.org/ [Accessed 20 March 2018]

Robinson, S.A., King, D.H., Bramley-Alves, J., Waterman, M.J., Ashcroft, M.B., Wasley, J., Turnbull, J.D., Miller, R.E., Ryan-Colton, E., Benny, T. and Mullany, K., 2018. Rapid change in East Antarctic terrestrial vegetation in response to regional drying. *Nature Climate Change*, *8*(10), pp.879–884.

Roberts, D., McMinn, A., Johnston, N., Gore, D.B., Melles, M. and Cremer, H., 2001. An analysis of the limnology and sedimentary diatom flora of fourteen lakes and ponds from the Windmill Islands, East Antarctica. *Antarctic Science*, *13*(4), p.410–419.

Sabbe, K., Verleyen, E., Hodgson, D.A., Vanhoutte, K. and Vyverman, W., 2003. Benthic diatom flora of freshwater and saline lakes in the Larsemann Hills and Rauer Islands, East Antarctica. *Antarctic Science*, *15*(2), p.227.

Sakaeva, A., Sokol, E.R., Kohler, T.J., Stanish, L.F., Spaulding, S.A., Howkins, A., Welch, K.A., Lyons, W.B., Barrett, J.E. and McKnight, D.M., 2016. Evidence for dispersal and habitat controls on pond diatom communities from the McMurdo Sound Region of Antarctica. *Polar Biology*, *39*(12), pp.2441–2456.

Souffreau, C., Vanormelingen, P., Van de Vijver, B., Isheva, T., Verleyen, E., Sabbe, K. and Vyverman, W., 2013b. Molecular evidence for distinct Antarctic lineages in the cosmopolitan terrestrial diatoms *Pinnularia borealis* and *Hantzschia amphioxys. Protist, 164*(1), pp.101–115

Spaulding, S.A., Van de Vijver, B., Hodgson, D.A., McKnight, D.M., Verleyen, E. and Stanish, L., 2010. Diatoms as indicators of environmental change in Antarctic and subantarctic freshwaters. In: *The diatoms: applications for the environmental and earth sciences*, pp.267–283.

Spaulding, S., Esposito, R., Lubinski, D., Horn, S., Cox, M., mcknight, D., Alger, A., Hall, B., Mayernick, M., Whittaker, T., & Yang, C. Antarctic Freshwater Diatoms web site, mcmurdo Dry Valleys LTER, visited 22 Jan 2020 at http://huey.colorado.edu/diatoms/ Terauds, A., Chown, S.L., Morgan, F., J. Peat, H., Watts, D.J., Keys, H., Convey, P. and Bergstrom, D.M., 2012. Conservation biogeography of the Antarctic. *Diversity and distributions*, *18*(7), pp.726–741.

Van de Vijver, B., Frenot, Y. and Beyens, L., 2002. Freshwater diatoms from Ile de la Possession (Crozet Archipelago, Subantarctica). *Bibliotheca Diatomologica* 46, pp.1–412.

Van de Vijver, B., Beyens, L., Vincke, S. and Gremmen, N.J., 2004. Moss-inhabiting diatom communities from Heard Island, sub-Antarctic. *Polar biology*, *27*(9), pp.532–543.

Van de Vijver, B., Gremmen, N. and Smith, V., 2008. Diatom communities from the sub-Antarctic Prince Edward Islands: diversity and distribution patterns. *Polar biology*, *31*(7), pp.795–808.

Van de Vijver, B., Tavernier, I., Kellogg, T.B., Gibson, J., Verleyen, E., Vyverman, W. and Sabbe, K., 2012. Revision of type materials of Antarctic diatom species (Bacillariophyta) described by West & West (1911), with the description of two new species. *Fottea*, *12*(2), pp.149–169.

Van der Werff, A. 1955. A new method for cleaning and concentrating diatoms and other organisms. *Verhandlungen der Internationalen Vereinigung für theoretische und angewandte Limnologie*, *12*, pp.276–277.

Wasley, J., Robinson, S.A., Lovelock, C.E. and Popp, M., 2006a. Climate change manipulations show Antarctic flora is more strongly affected by elevated nutrients than water. *Global Change Biology*, *12*(9), pp.1800–1812.

Wasley, J., Robinson, S.A., Lovelock, C.E. and Popp, M., 2006b. Some like it wet—biological characteristics underpinning tolerance of extreme water stress events in Antarctic bryophytes. *Functional plant biology*, *33*(5), pp.443–455.

Wasley, J., Robinson, S.A., Turnbull, J.D., King, D.H., Wanek, W. and Popp, M., 2012. Bryophyte species composition over moisture gradients in the Windmill Islands, East Antarctica: development of a baseline for monitoring climate change impacts. *Biodiversity*, *13*(3–4), pp.257–264.

Woehler, E.J., Slip, D.J., Robertson, L.M., Fullagar, P.J. and Burton, H.R., 1991. The distribution, abundance and status of adélie penguins *Pygoscelis adeliae* at the windmill islands, wilkes land, antarctica. *Marine Ornithology*, *19*, 1–18.

Zhang, E., Thibaut, L.M., Terauds, A., Wong, S., van Dorst, J., Tanaka, M.M. and Ferrari, B.C., 2019. Extreme niche partitioning promotes a remarkably high diversity of soil microbiomes across eastern Antarctica. *bioRxiv*, p.559666.

Zidarova R., Kopalová K. and Van de Vijver B., 2016: Diatoms from the Antarctic Region. I: Maritime Antarctica. *Iconographia Diatomologica*. 24. 509pp.

Chapter 5

Discussion

Conclusions of the dissertation.

The true extent of the diatom flora of Continental Antarctica's diatom diversity is still being uncovered. "Species force-fitting" of inconsistent, broadly-defined boundaries through the application of European and American floras now results in historical records that must be treated with caution and updated. Because of this, the ecological characteristics of benthic and terrestrial diatom communities within Continental Antarctica are poorly understood. Placed more widely, this gap in knowledge has led to the exclusion, or improper usage, of diatom community metadata within largescale biogeographic studies that focus on the distribution of Antarctic biodiversity.

This dissertation synthesized current and historic literature and samples in order to construct an updated, working diatom flora of selected localities within East Antarctica. This updated flora was then applied to examine diatom community structuring within lakes (Chapter three) and terrestrial (Chapter four) ecosystems. In this regard, the dissertation provides an up-to-date accounting of the benthic Vestfold Hills and terrestrial Windmill Islands diatom taxa. The revised taxonomic description of *Sabbea adminensis* (D.Roberts & McMinn) Van de Vijver, Bishop & Kopalová (Chapter two), originally described from the Vestfold Hills, but cross referenced with samples from the Bunger Hills and the McMurdo Sound Region, effectively compiles ecological and taxonomic datapoints from three separate localities across Continental Antarctica. The revised flora of the Vestfold Hills yielded an increased understanding of the diatom diversity of Continental Antarctica, as well as the salinity tolerances of revised, endemic taxa (Chapter three). The ecological interpretation of the 30 examined lakes did not change from Roberts and McMinn (1999) but remained structured chiefly by salinity. Lastly, the epiphytic diatom flora of Windmill Islands mosses and lichens was dominated by six species, accounting for 92% of all taxa present (Chapter four). Despite experimental nutrient and water additions, the diatom communities were structured according to underlying moss or lichen vegetation type, but not according to the applied treatments.

The Continental Antarctic diatom flora

Overall, the Continental Antarctic diatom flora displays a mixture of mostly endemic and some cosmopolitan taxa. The Vestfold Hills (Figure 1) diatom flora shows moderate to high similarity with other East Antarctic localities, such as the Larsemann Hills and Rauer Islands (Sabbe et al. 2003), the Amery Oasis (Cremer et al. 2004), Windmill Islands (marine flora; Cremer et al. 2003), the Skarvsnes ice-free areas, approximately 60 km from Syowa station (Ohtsuka et al. 2006), the Bunger Hills (Gibson et al. 2006), and the McMurdo Sound Region (Esposito et al. 2008, Van de Vijver et al. 2012). However, differences do exist amongst East Antarctic localities. More specifically, only single valves have been attributed to *Eunotia* Ehrenberg within the Vestfold Hills, though these taxa were quite small to be certain (Appendix 1). Single valves were also seen within the Amery Oasis, within Terrasovoje Lake, but these taxa were much larger in valve length (Cremer et al. 2004). However, it is important to note the records of Cremer et al. (2003, 2004) should be carefully re-verified due to possible contamination of sediments during preparation. *Muelleria* (Frenguelli) Frenguelli has not yet been observed within the Vestfold Hills, despite widely occurring within other East Antarctic localities, with the exception of Skarvsnes (Ohtsuka et al. 2006). Although not the focus of the dissertation, the Vestfold Hills displayed a large influence of marine taxa, sharing a number of widely distributed taxa identified also within the marine bays of the Windmill Islands, notably a number of *Fragilariopsis* Hustedt and *Cocconeis* Ehrenberg species (Cremer et al. 2003). This was the case also with *Amphora antarctica* Hustedt also identified from King George Island (Al-Handal and Wulff 2008a,b).

Figure 1. A map of Continental Antarctica showing important biological localities throughout East Antarctica.

Taxonomic references cited within Roberts and McMinn (1999) were in large part based upon continental European diatom floras. A number of *Navicula* Bory taxa discussed within the original study were not observed within the re-analysis when consulting the taxonomic references discussed within Roberts and McMinn (1999) against valve shape characteristics of these taxa, and measures such as valve length, valve width and striae density. As such, many of these unclear taxa, bearing quite similar structure to small, marine *Navicula* taxa, are thought to be of marine origin. For these 22 taxa, we have formed an artificial grouping

"MRN" to denote what we believe are marine, or otherwise strongly halophilic taxa (Appendix 1). Unfortunately, SEM analysis for these taxa was not possible given that the original materials from Roberts and McMinn (1999), save for one set of LM slides, have been lost or destroyed (Andrew McMinn, Pers. Comm.). Despite attempts to recover specific taxa out of the scores of assumed *Navicula* marine taxa, without SEM, this remains impossible to be done correctly (Reed Scherer, Pers. Comm.).

Although some *Navicula* taxa were not observed, other taxa within the original Roberts and McMinn (1999) study have since undergone significant revision, resulting in a number of taxa being "split" from the singular taxon. The most striking example of this is the taxon group discussed within Roberts and McMinn (1999) as the *Navicula mutica* Kützing*/muticopsis* Van Heurck group. Roberts and McMinn (1999) cite difficulties in identifying a number of taxa that at that point were discussed as possible sub-species, varieties or forms. Since then, and reflected within the current work, a number of these infraspecific taxa have been raised to the species level. Works such as Kohler et al. (2015a), Van de Vijver et al. (2012), revised a number of *Navicula* or *Luticola* D.G.Mann taxa and elevated them to *Luticola* taxa. In total, within the Vestfold Hills, 9 taxa are attributed to *Luticola* as a species, variety or form.

The updated flora from the Vestfold Hills confirms the presence of a number of endemic diatom taxa that were hitherto undescribed within the Vestfold Hills due to incorrect nomenclature, omission and recent updates, as the original work was performed over two decades ago. It must be noted the difficulty in attributing taxa across a number of localities. Where publications present LM and SEM micrographs, comparisons are made easier than such publications where only species are listed without accompanying micrographs and morphological valve descriptions. Such is the case for the non-marine flora of the Windmill Islands where studies (Roberts et al. 2001, 2004), that utilized the same training set, as mentioned before, for the Vestfold Hills. In total, 19 of the 58 taxa identified to species level are believed to be marine taxa while the remaining 39 are believed to be freshwater taxa.

This revised benthic diatom flora of the Vestfold Hills was then used to investigate the epiphytic diatom community within the Windmill Islands. Overall, the flora of moss-associated diatoms of the Windmill Islands consists mainly of members of *Humidophila* (Lange-Bertalot & Werum) R.L.Lowe, Kociolek, J.R.Johansen, Van de Vijver, Lange-Bertalot & Kopalová*, Luticola, Psammothidium* L.Buhtkiyarova & Round*,* and *Pinnularia* Ehrenberg*.* Work in the greater (Sub)-Antarctic Region has highlighted genera often associated with mosses, such as *Eunotia* (Van de Vijver et al. 2014, *Hantzschia* Grunow (Bulínová et al. 2018), *Humidophila* (Kopalová et al. 2015), *Pinnularia* and *Luticola* (Zidarova et al. 2012, 2016). Upon Continental Antarctica, Esposito et al. (2008) detailed "aerophilic" genera within the McMurdo Dry Valleys such namely *Luticola, Diadesmis* Kützing (which have been transferred to *Humidophila*)*, Hantzschia, Muelleria* and *Psammothidium* (Kohler et al. 2015b). Kohler et al. (2015a), again focused within the McMurdo Sound Region, confirmed the moss-associated *L. dolia* Spaulding & Esposito and *L. laeta* Spaulding & Esposito first described in Esposito et al. (2008), and described yet another moss-associated taxon, *L. macknightiae* T.J.Kohler & Kopalová. Indeed, *Luticola* demonstrates a strong degree of endemism to the Antarctic Realm, across the limno-terrestrial habitat including mosses (Kociolek et al. 2017). Overall, despite the Windmill Island moss diatom flora sharing similar genera from both the Maritime and Sub-Antarctic Regions, the Windmill Islands appear to possess a subset of those taxa present within McMurdo Dry Valleys. Overall, the Windmill Islands moss and lichen associated flora are dominated by a few "representative" taxa (approx. 92% of observed valves) from each genus: *L. muticopsis* (Van Heurck) D.G.Mann*, P. borealis* Ehrenberg*, Psammothidium papilio* (D.E.Kellogg, M.Stuiver, T.B.Kellogg & G.H.Denton) Kopalová & Van de Vijver*, H. gallica*

(W.Smith) R.L.Lowe, Kociolek, Q.You, Q.Wang & Stepanek and *H. australis* (Van de Vijver & Sabbe) R.L.Lowe, Kociolek, J.R.Johansen, Van de Vijver, Lange-Bertalot & Kopalová.

The ecology of the Continental Antarctic diatom flora

Within the Vestfold Hills, we confirmed the initial results discussed by Roberts and McMinn (1999) that diatom community structure is determined chiefly by salinity, then alkalinity. Increased taxonomic resolution within the current study did not appear to alter the interpretation of the limnological variables structuring diatom communities. Results showed the primary axis corresponded with salinity and correlated ions (Cl^-, Na^+, etc), whereas the second axis was correlated with both alkalinity and silicate. However, due to the increased taxonomic resolution, we can more accurately compare species responses to environmental variables not only within the Vestfold Hills, but to other East Antarctic localities. Oftentimes, species demonstrated more restrictive environmental tolerances than originally thought. For example, two species of *Halamphora* (Cleve) Mereschkowsky were originally lumped together into a single *Amphora* Ehrenberg ex. Kützing taxon within Roberts and McMinn (1999) and displayed a wide tolerance across fresh and hyposaline lakes. We have shown that these two taxa in fact prefer fresh and hyposaline lakes, respectively. Within the Skarvsnes ice-free area, *Halamphora* (there as *Amphora* sp.) was also shown to favor fresh, low conductivity lakes (Ohtsuka et al. 2006), as it has been demonstrated within the Vestfold Hills.

Within the Windmill Islands experiment, the community structure of terrestrial epiphytic diatoms on two bryophyte vegetation types (healthy and moribund) and two lichen vegetation types (crustose and those belonging to the genus *Usnea* Dillenius ex. Adanson) was determined by the aforementioned underlying vegetation type. Diatom community structure was influenced neither by the addition of nutrients, nor water, nor by the combined effect of both added together. The vegetation stands within the Windmill Islands are well characterized and extensively studied insofar as their growth is monitored and component species are known. Recent range expansions of cosmopolitan moss species and contractions of the endemic *Schistidium antarctici* Cardot, which was the dominant bryophyte within the experimental transect, have been documented (Wasley et al. 2006, Robinson et al. 2018). Our results showed that the most abundant diatom taxa within the study, collectively 92% of all counted valves, showed significant differences in relative abundances upon the different vegetation types, but also the healthy bryophyte vegetation type, dominated by the *S. antarctici*. Our results suggest that moss and lichen vegetation range expansion and contraction is expected to have concomitant impacts on the structuring of the associated epiphytic diatom communities.

Future work and considerations

Despite recent progress within microbial ecology, there are many questions that remain within the field as they pertain to diatoms. In their review of the spatial ecology of freshwater benthic diatoms, Soininen and Teittinen (2019) discuss the state of diatom biogeographical research methodologies, including limited evidence for diatoms exhibiting species-area relationships and the efficacy of a metacommunity framework within diatoms. However, with regard to Antarctic biogeography, they also point out that the majority of biogeographical lake and stream benthic diatom studies are still dominated by North American and European publications (Soininen and Teittinen 2019). As work continues within the Antarctic Realm, the investigation of spatial patterns structuring diatom communities must be investigated further. Recent studies have suggested a number of interacting mechanisms, including local abiotic factors, spatial scale and dispersal play a role in determining microbial community structure in Antarctica (Chong et al. 2015, Hughes et al. 2015, Sokol et al. 2013). Specific attention to diatoms has been sparse. With regard to benthic lake diatoms, evidence of dispersal limitation was found within the McMurdo Sound Region (Sakaeva et al. 2016). Given the strong winds present on Continental Antarctica, aeolian transport is likely one mechanism for diatom dispersal (Šabacka et al. 2012, Diaz et al. 2018).

Spatial analyses within terrestrial diatom communities offer abundant avenues of research to determine those processes structuring terrestrial diatoms. Andersen et al. (2011) cites the work of Broady (1989) in their assertion that within some areas, diatoms are noticeably absent. Within Broady (1989), the terrestrial mosses, lichens and microflora of Edward VII Peninsula, Marie Byrd Land, West Antarctica were explored, with a noted absence of diatoms. Specifically, Broady (1989) notes the absences of *P. borealis, Hantzschia amphioxys* (Ehrenberg) Grunow and *L. muticopsis* (there listed as *Navicula muticopsis* Van Heurck) on particular types of vegetation. To date, the diatom communities present within West Antarctica, especially terrestrial communities, are largely unexplored and poorly understood.

Applications for conservation and preservation

These revised taxonomic and ecological data have potential to be used within applied research, such as ongoing Antarctic conservation management efforts. These data may aid in capturing the current state of Antarctic microbial diversity before a number of projected impacts become more widespread. As it is expected that anthropogenic and climate changes impacts, among others, are expected to act in tandem as has been seen throughout the wider Antarctica Realm, these data are especially prescient.

Anthropogenic impacts to the Antarctic Realm manifest themselves in an increasing number of ways. Humans disproportionately impact ice-free areas within Antarctica with over 80% of the structures located on these areas. Specifically, the physical structures represent a small fraction of the total human “footprint”, as these structures have an area around them of potential damage, wastes, and contamination (Hawes et al. 1999, Brooks et al. 2019). Many of the impacts we expect to see within Continental Antarctica have already been observed within the Maritime and Sub-Antarctic Regions, for example, with inadvertent introductions of invasive plants and invertebrates (Chown et al. 2012, Huiskes et al. 2014, Malfasi et al. 2020). While the Maritime and Sub-Antarctic Regions are currently milder and, arguably, more conducive to biological invasion, the forecasted changes to Continental Antarctica resulting in increased ice-free areas are projected to aid in the establishment of non-native species around research bases in particular (Duffy and Lee 2019).

The Antarctic Treaty System (ATS), as described within Tin and Hemmings (2011) originates with the 1959 Antarctic Treaty and its subsequent legal instruments. Since that time, additions to the treaty have been adopted with the latest enacted in 1998, known as the Protocol on Environmental Protection to the Antarctic Treaty but more commonly as the Madrid Protocol. This action was responsible for the network of Antarctic Specially Protected Areas (ASPAs) and Antarctic Specially Managed Areas (ASMAs). The former provides the basis of protection on the grounds of environmental, scientific, historic, aesthetic or wilderness reasons, while the latter is concerned with minimizing environmental impacts so that a site may be utilized currently or in the future (Senatore and Zarankin 2012). Despite these actions, there is criticism that these protected areas in Antarctic offer insufficient protections and should be expanded. Globally, designation of protected areas has increased while concurrently remaining stagnant within Antarctica (Coetzee et al. 2017). Overwhelmingly, protected areas are designated with the purpose of preserving or protecting macroscopic organisms. But as recent reviews have shown, the microbial diversity of Antarctic is slowly being uncovered and their exact protections remain ambiguous (Convey and Peck 2019).

Approximately one-third of algal species occur within areas currently designated as Antarctic Specially Protected Areas (ASPA) (Wauchope et al. 2019). Extending this, of the 55 terrestrial ASPAs, only 16 ASPAs have expressed "protected values" for algae, while cyanobacteria and snow algae being restricted to 7 and 3 cases, respectively (Hughes et al.

2015). Indeed, a number of confounding factors suggest that the possibility to investigate Antarctica as an intact, pristine environment is fading. Biological contamination and invasions, from both external and intra-continental region origins are just now beginning to be studied, without a framework to account for and quantify their impacts (McGeoch et al. 2015, Hughes et al. 2016). Antarctic climate extremes have been recorded near Casey Station, with a recorded temperature in excess of 20°C within the 2019/2020 summer (Robinson et al. 2020). Mining is prohibited in Antarctica, though amendments may be made to the mining clauses within the Antarctic Protocol, thus opening Antarctica for mineral extraction (McLean and Rock 2016). Given the lack of clarity within the proposed date of expiration, or renewal, of the Antarctic Treaty in 2048, primary scientific works adopt a greater significance on what will ultimately become a markedly changed Continent in the face of evolving global economic development (Ferrada 2018).

Final Conclusions

As a whole, this dissertation has explored the non-marine Continental Antarctic diatom flora within two biologically and historically relevant areas, the Vestfold Hills and the Windmill Islands. The data contained within this work has contributed to the understanding of the processes that structure benthic lake and terrestrial epiphytic diatom communities. These data may now be confidently applied to study larger trends within Antarctic biodiversity, not limited to microbial biodiversity and biogeographical trends.

References

Al-Handal, A.Y. and Wulff, A., 2008a. Marine benthic diatoms from Potter Cove, King George Island, Antarctica. *Botanica Marina*, *51*(1), pp.51–68.

Al-Handal, A.Y. and Wulff, A., 2008b. Marine epiphytic diatoms from the shallow sublittoral zone in Potter Cove, King George Island, Antarctica. *Botanica Marina*, *51*(5), pp. 411–435.

Andersen, D.T., Sumner, D.Y., Hawes, I., Webster- Brown, J. and McKay, C.P., 2011. Discovery of large conical stromatolites in Lake Untersee, Antarctica. *Geobiology, 9*(3), pp.280–293

Broady, P.A., 1989. Survey of algae and other terrestrial biota at Edward VII Peninsula, Marie Byrd Land. *Antarctic Science*, *1*(3), pp.215–224.

Brooks, S.T., Jabour, J., Van Den Hoff, J. and Bergstrom, D.M., 2019. Our footprint on Antarctica competes with nature for rare ice-free land. *Nature Sustainability*, *2*(3), pp.185–190.

Bulínová, M., Kochman-Kędziora, N., Kopalová, K. and Van De Vijver, B., 2018. Three new *Hantzschia* species (Bacillariophyta) from the Maritime Antarctic Region. *Phytotaxa, 371*(3), pp.168–184

Chong, C.W., Pearce, D.A. and Convey, P., 2015. Emerging spatial patterns in Antarctic prokaryotes. *Frontiers in Microbiology*, *6* (1058), pp.1–14

Chown, S.L., Huiskes, A.H., Gremmen, N.J., Lee, J.E., Terauds, A., Crosbie, K., Frenot, Y., Hughes, K.A., Imura, S., Kiefer, K. and Lebouvier, M., 2012. Continent-wide risk assessment for the establishment of nonindigenous species in Antarctica. *Proceedings of the National Academy of Sciences*, *109*(13), pp.4938–4943.

Coetzee, B.W., Convey, P. and Chown, S.L., 2017. Expanding the protected area network in Antarctica is urgent and readily achievable. *Conservation Letters, 10*(6), pp.670–680.

Convey, P. and Peck, L.S., 2019. Antarctic environmental change and biological responses. *Science Advances*, *5*(11), p.eaaz0888.

Cremer, H., Roberts, D., McMinn, A., Gore, D. and Melles, M., 2003. The Holocene diatom flora of marine bays in the Windmill Islands, East Antarctica. *Botanica Marina*, *46*(1), pp.82–106.

Cremer, H., Gore, D., Hultzsch, N., Melles, M. and Wagner, B., 2004. The diatom flora and limnology of lakes in the Amery Oasis, East Antarctica. *Polar Biology*, *27*(9),pp.513–531.

Diaz, M.A., Adams, B.J., Welch, K.A., Welch, S.A., Opiyo, S.O., Khan, A.L., McKnight, D.M., Cary, S.C. and Lyons, W.B., 2018. Aeolian material transport and its role in landscape connectivity in the McMurdo Dry Valleys, Antarctica. *Journal of Geophysical Research: Earth Surface*, *123*(12), pp.3323–3337

Duffy, G.A. and Lee, J.R., 2019. Ice-free area expansion compounds the non-native species threat to Antarctic terrestrial biodiversity. *Biological conservation*, *232*, pp.253–257.

Esposito, R.M.M., Spaulding, S.A., Mcknight, D.M., Van De Vijver, B., Kopalová K., Lubinski, D., Hall, B. and Whittaker, T., 2008. Inland diatoms from the McMurdo Dry Valleys and James Ross Island, Antarctica. *Botany 86*, pp.1378–1392.

Ferrada, L.V., 2018. Five factors that will decide the future of Antarctica. *The Polar Journal*, *8*(1), pp. 84–109.

Gibson, J.A., Roberts, D. and Van de Vijver, B., 2006. Salinity control of the distribution of diatoms in lakes of the Bunger Hills, East Antarctica. *Polar Biology*, *29*(8), pp.694–704.

Hawes, I., Smith, R. and Sutherland, D., 1999. Development of microbial mats on contaminated soils from the former site of Vanda Station, Antarctica. *New Zealand Sciences, 24,* pp.*53–68.*

Hughes, K.A., Pertierra, L.R., Molina-Montenegro, M.A. and Convey, P., 2015. Biological invasions in terrestrial Antarctica: what is the current status and can we respond?. *Biodiversity and Conservation*, *24*(5), pp.1031–1055.

Hughes, K.A., Ireland, L.C., Convey, P. and Fleming, A.H., 2016. Assessing the effectiveness of specially protected areas for conservation of Antarctica's botanical diversity. *Conservation Biology*, *30*(1), pp.113–120.

Huiskes, A.H., Gremmen, N.J., Bergstrom, D.M., Frenot, Y., Hughes, K.A., Imura, S., Kiefer, K., Lebouvier, M., Lee, J.E., Tsujimoto, M. and Ware, C., 2014. Aliens in Antarctica: assessing transfer of plant propagules by human visitors to reduce invasion risk. *Biological Conservation*, *171*, pp.278–284.

Kociolek, J.P., Kopalová, K., Hamsher, S.E., Kohler, T.J., Van de Vijver, B., Convey, P. and McKnight, D.M., 2017. Freshwater diatom biogeography and the genus *Luticola*: an extreme case of endemism in Antarctica. *Polar Biology*, *40*(6), pp.1185–1196.

Kohler, T.J., Kopalová, K., Van De Vijver, B. and Kociolek, J.P., 2015a. The genus *Luticola* D.G.Mann (Bacillariophyta) from the McMurdo Sound Region, Antarctica, with the description of four new species. *Phytotaxa, 208*(2), pp.103–134.

Kohler, T.J., Chatfield, E., Gooseff, M.N., Barrett, J.E. and McKnight, D.M., 2015b. Recovery of Antarctic stream epilithon from simulated scouring events. *Antarctic Science*, *27*(4), pp.341–354.

Kopalová, K., Kociolek, J.P., Lowe, R.L., Zidarova, R. and Van de Vijver, B. 2015. Five new species of the genus *Humidophila* (Bacillariophyta) from the Maritime Antarctic Region. *Diatom Research*, *30*(2), pp.117–131.

Malfasi, F., Convey, P., Zaccara, S. and Cannone, N., 2020. Establishment and eradication of an alien plant species in Antarctica: *Poa annua* at Signy Island. *Biodiversity and Conservation*, *29*(1), pp.173–186.

McGeoch, M.A., Shaw, J.D., Terauds, A., Lee, J.E. and Chown, S.L., 2015. Monitoring biological invasion across the broader Antarctic: a baseline and indicator framework. *Global Environmental Change, 32,* pp.108–125.

McLean, L. and Rock, J., 2016. The importance of Antarctica: assessing the values ascribed to Antarctica by its researchers to aid effective climate change communication. *The Polar Journal*, *6*(2), pp.291–306.

Ohtsuka, T., Kudoh, S., Imura, S. and Ohtani, S., 2006. Diatoms composing benthic microbial mats in freshwater lakes of Skarvsnes ice-free area, East Antarctica. *Polar Bioscience, 20,* pp.113–130

Roberts, D. and McMinn, A., 1999. Diatoms of the saline lakes of the Vestfold Hills, Antarctica. *Bibliotheca Diatomologica*, *44*, pp.1–82.

Roberts, D., McMinn, A., Johnston, N., Gore, D.B., Melles, M. and Cremer, H., 2001. An analysis of the limnology and sedimentary diatom flora of fourteen lakes and ponds from the Windmill Islands, East Antarctica. *Antarctic Science*, *13*(4), pp.410–419.

Roberts, D., McMinn, A., Cremer, H., Gore, D.B. and Melles, M., 2004. The Holocene evolution and palaeosalinity history of Beall Lake, Windmill Islands (East Antarctica) using an expanded diatom-based weighted averaging model. *Palaeogeography, Palaeoclimatology, Palaeoecology*, *208*(1–2), pp.121–140.

Robinson, S.A., King, D.H., Bramley-Alves, J., Waterman, M.J., Ashcroft, M.B., Wasley, J., Turnbull, J.D., Miller, R.E., Ryan-Colton, E., Benny, T. and Mullany, K., 2018. Rapid change in East Antarctic terrestrial vegetation in response to regional drying. *Nature Climate Change*, *8*(10), pp.879–884.

Robinson, S.A., Klekociuk, A.R., King, D.H., Pizarro Rojas, M., Zúñiga, G.E. and Bergstrom, D.M., 2020. The 2019/2020 summer of Antarctic heatwaves. *Global Change Biology, 26*(2), pp.3178–3180.

Šabacká, M., Priscu, J.C., Basagic, H.J., Fountain, A.G., Wall, D.H., Virginia, R.A. and Greenwood, M.C., 2012. Aeolian flux of biotic and abiotic material in Taylor Valley, Antarctica. *Geomorphology*, *155*, pp.102–111.

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

Sakaeva, A., Sokol, E.R., Kohler, T.J., Stanish, L.F., Spaulding, S.A., Howkins, A., Welch, K.A., Lyons, W.B., Barrett, J.E. and McKnight, D.M., 2016. Evidence for dispersal and habitat controls on pond diatom communities from the McMurdo Sound Region of Antarctica. *Polar Biology*, *39*(12), pp.2441–2456.

Senatore, M.X. and Zarankin, A., 2012. Tourism and the invisible historic sites in Antarctica. In: ICOMOS 17th General Assembly, 2011–11–27 / 2011–12–02. pp.599–608.

Soininen, J. and Teittinen, A., 2019. Fifteen important questions in the spatial ecology of diatoms. *Freshwater Biology*, *64*(11), pp.2071–2083.

Sokol, E.R., Herbold, C.W., Lee, C.K., Cary, S.C. and Barrett, J.E., 2013. Local and regional influences over soil microbial metacommunities in the Transantarctic Mountains. *Ecosphere 4*(11), pp.1-24.

Tin, T. and Hemmings, A., 2011. Challenges in protecting the wilderness of Antarctica. In: *Science and stewardship to protect and sustain wilderness values: Ninth World Wilderness Congress symposium. US Department of Agriculture, Proceedings RMRS 64,* 64, pp.147–152.

Van de Vijver, B., Tavernier, I., Kellogg, T.B., Gibson J., Verleyen, E., Vyverman, W. and Sabbe, K., 2012. Revision of type materials of Antarctic diatom species (Bacillariophyta) described by West & West (1911), with the description of two new species. *Fottea, 12*(2), pp.149–169.

Van de Vijver, B., de Haan, M. and Lange-Bertalot, H., 2014. Revision of the genus *Eunotia* (Bacillariophyta) in the Antarctic Region. *Plant Ecology and Evolution*, *147*(2), pp.256–284.

Wasley, J., Robinson, S.A., Lovelock, C.E. and Popp, M., 2006. Climate change manipulations show Antarctic flora is more strongly affected by elevated nutrients than water. *Global Change Biology*, *12*(9), pp.1800–1812.

Wauchope, H.S., Shaw, J.D. and Terauds, A., 2019. A snapshot of biodiversity protection in Antarctica. *Nature communications*, *10*(1), pp.1–6.

Zidarova, R., Kopalová, K. and Van de Vijver, B., 2012. The genus *Pinnularia* (Bacillariophyta) excluding the section Distantes on Livingston Island (South Shetland Islands) with the description of twelve new taxa. *Phytotaxa*, *44*(1), pp.11–37.

Zidarova R., Kopalová K. and Van de Vijver B. 2016: Diatoms from the Antarctic Region. I: Maritime Antarctica. *Iconographia Diatomologica*. 24. 509pp.

Appendix 1

Table 1. Taxa list for the Vestfold Hills and Windmill Islands

Image Plates 1–13

Table 1. Taxa list for the Vestfold Hills and Windmill Islands.

Taxon	Plate Location	Figure	Distribution	Notes
Achnanthes taylorensis D.E.Kellogg, Stuiver, T.B.Kellogg & G.H.Denton	Plate 4	Figs. 5–6	Vestfold Hills & Windmill Islands	–
Achnanthidium Kützing sp1	Plate 3	Fig. 11	Windmill Islands	As *Achnanthes* Bory sp1 in Windmill Islands
Astartiella A.Witkowski, Lange-Bertalot & Metzeltin sp1	Chapter 3	Figs 55–56	Vestfold Hills	–
Astartiella cf. sp1	Plate 12	Fig. 22	Vestfold Hills	–
Amphora antarctica Hustedt	Chapter 3	Fig. 52	Vestfold Hills	–
Amphora Ehrenberg ex Kützing sp1	Plate 5	Fig. 7	Vestfold Hills	–
Amphora Ehrenberg ex Kützing sp2	Plate 5	Fig. 6	Vestfold Hills	–
Amphora Ehrenberg ex Kützing sp3	Plate 5	Fig. 8	Vestfold Hills	–
Berkeleya Greville sp1	Plate 5	Fig. 4	Vestfold Hills	–
Catenula Mereschkowsky sp1	Chapter 3	Figs 57–58	Vestfold Hills	–
Catenula Mereschkowsky sp2	Plate 12	Fig. 23	Vestfold Hills	–
Catenula Mereschkowsky sp3	Plate 12	Fig. 18	Vestfold Hills	–
Centric sp1	Plate 6	Fig. 7	Vestfold Hills	–
Centric sp2	Plate 6	Fig. 3	Vestfold Hills	–
Centric sp3	Plate 6	Fig. 6	Vestfold Hills	–
Centric sp4	Plate 6	Fig. 5	Vestfold Hills	–
Centric sp5	Plate 6	Fig. 1–2	Vestfold Hills	–
Centric sp6	Plate 6	Fig. 4	Vestfold Hills	–
Centric unidentified	Plate 6	Figs 9–10	Windmill Islands	–
Thalassiosira antarctica Comber	Plate 6	Fig. 8	Vestfold Hills	–
Cocconeis costata Gregory	Plate 1	Figs 8–9	Vestfold Hills	–
Cocconeis cf. *fasciolata* (Ehrenberg) N.E.Brown	Plate 2	Fig. 3	Windmill Islands	–
Cocconeis pinnata Gregory	Plate 2	Fig. 2	Vestfold Hills	–
Cocconeis Ehrenberg sp1	Plate 2	Figs 4–5	Vestfold Hills	–
Cocconeis Ehrenberg sp2	Plate 2	Fig. 6	Windmill Islands	As *Cocconeis* Ehrenberg sp1 in the Windmill Islands
Chaetoceros Ehrenberg vegetative cells	Chapter 3	Fig. 62	Vestfold Hills	–

Table 1. Continued

Taxon	Plate Location	Figure	Distribution	Notes
Chaetoceros Ehrenberg resting spores	Chapter 3	Figs 63–66	Vestfold Hills	–
Chamaepinnularia Lange-Bertalot & Krammer sp1	Plate 10	Fig. 27	Vestfold Hills	–
Chamaepinnularia cymatopleura (W. et G.S.West) Cavacini	Chapter 3	Figs 40–41	Vestfold Hills & Windmill Islands	–
Craspedostauros laevissimum (W. et G.S.West) Sabbe	Chapter 3	Figs 50–51	Vestfold Hills	–
Craticula cf. *submolesta* (Hustedt) Lange-Bertalot var 1	Plate 7	Fig. 19	Vestfold Hills	–
Craticula cf. *submolesta* (Hustedt) Lange-Bertalot var 2	Plate 7	Fig. 18	Vestfold Hills	–
Craticula antarctica Van de Vijver & Sabbe	Chapter 3	Figs 28–29	Vestfold Hills	–
Craticula cf. *antarctica* Van de Vijver & Sabbe	Plate 7	Fig. 20	Vestfold Hills	–
Diploneis splendida Cleve	Plate 1	Fig. 4	Vestfold Hills	–
Eucampia antarctica (Castracane) Mangin	Plate 2	Fig. 9	Vestfold Hills	–
Entomoneis Ehrenberg sp1	Plate 2	Fig. 1	Vestfold Hills	–
Eunotia Ehrenberg sp1	Plate 12	Figs 19–20	Vestfold Hills	–
Eunotia Ehrenberg sp2	Plate 12	Fig. 24	Vestfold Hills	–
Eunotia Ehrenberg sp3	Plate 12	Fig. 21	Vestfold Hills	–
Fragilaria Lyngbye unidentifiable valve	Plate 7	Fig. 23	Windmill Islands	–
Fragilariopsis curta (Van Heurck) Hustedt	Chapter 3	Figs 44–45	Vestfold Hills & Windmill Islands	As *Fragilariopsis* Hustedt sp1 in the Windmill Islands
Fragilariopsis cylindrus (Grunow ex Cleve) Helmcke & Krieger	Chapter 3	Figs 46–47	Vestfold Hills	As *Fragilariopsis* Hustedt sp2 in the Windmill Islands
Fragilariopsis peragalloi (Hasle) Cremer	Plate 10	Fig. 31	Vestfold Hills	–
Fragilariopsis rhombica (O'Meara) Hustedt	Plate 10	Fig. 29	Vestfold Hills	–
Fragilariopsis sublinearis (Van Heurck) Heiden & Kolbe	Plate 10	Fig. 32	Vestfold Hills	As *Fragilariopsis* Hustedt sp3 in the Windmill Islands
Fragilariopsis vanheurckii (Peragallo) Hustedt	Plate 10	Fig. 28	Vestfold Hills	–
Fragilariopsis Hustedt sp1	Plate 10	Fig. 30	Vestfold Hills	–

Table 1. Continued

Taxon	**Plate Location**	**Figure**	**Distribution**	**Notes**
Gomphonemopsis littoralis (Hendey) Medlin	Plate 10	Figs. 18–19	Vestfold Hills	–
Gomphonemopsis cf. *littoralis* (Hendey) Medlin	Plate 10	Fig. 20	Vestfold Hills	–
Gomphonema Ehrenberg sp1	Plate 10	Fig. 16	Vestfold Hills	–
Gomphonema Ehrenberg sp2	Plate 10	Fig. 14	Vestfold Hills	–
Gomphonema Ehrenberg sp3	Plate 10	Fig. 15	Vestfold Hills	–
Gomphonema Ehrenberg sp4	Plate 10	Fig. 17	Vestfold Hills	–
Gomphonema Ehrenberg sp5	Plate 10	Fig. 24	Vestfold Hills	–
Gomphonema Ehrenberg sp6	Plate 10	Fig. 21	Windmill Islands	As *Gomphonema* Ehrenberg sp1 in the Windmill Islands
Halamphora vyvermaniana Van de Vijver, Kopalová, Zidarova & Levkov	Chapter 3	Figs 16–17	Vestfold Hills	–
Halamphora lateantarctica Van de Vijver, Kopalová, Zidarova & Levkov	Chapter 3	Figs 18–19	Vestfold Hills	–
Halamphora (Cleve) Levkov sp1	Plate 5	Fig. 9	Vestfold Hills	–
Halamphora (Cleve) Levkov sp2	Plate 5	Fig. 10	Vestfold Hills	–
Halamphora (Cleve) Levkov sp3	Plate 5	Fig. 11	Vestfold Hills	–
Halamphora (Cleve) Levkov sp4	Plate 5	Fig. 12	Vestfold Hills	–
Halamphora (Cleve) Levkov sp5	Plate 5	Fig. 13	Vestfold Hills	–
Halamphora (Cleve) unidentifiable valve	Unshown	Unshown	Vestfold Hills	As *Halamphora* (Cleve) Levkov sp6 in Chapter 3
Hantzschia Grunow sp1	Plate 4	Figs. 7–9	Vestfold Hills	As *Hantzschia* cf. *amphioxys* (Ehrenberg) Grunow in Chapter 3. A species complex, see Souffreau et al. 2013
Humidophila australis (Van de Vijver & Sabbe) R.L.Lowe, Kociolek, J.R.Johansen, Van de Vijver, Lange-Bertalot & Kopalová	Chapter 4	Figs 3k, 3n	Vestfold Hills & Windmill Islands	–
Humidophila gallica (W.Smith) Lowe, Kociolek, Q.You, Q.Wang & Stepanek	Chapter 4	Fig. 3l–3m	Windmill Islands	–
Humidophila cf. *gallica* (W.Smith) Lowe, Kociolek, Q.You, Q.Wang & Stepanek	Chapter 4	Fig. 3h	Windmill Islands	–

Table 1. Continued

Taxon	Plate Location	Figure	Distribution	Notes
Humidophila inconspicua (Kopalová & Van de Vijver) R.L.Lowe, Kociolek, J.R.Johansen, Van de Vijver, Lange-Bertalot & Kopalová	Plate 3	Figs 13–14	Windmill Islands	–
Humidophila cf. *inconspicua* (Kopalová & Van de Vijver) R.L. Lowe, Kociolek, J.R.Johansen, Van de Vijver, Lange-Bertalot & Kopalová	Plate 3	Fig. 15	Windmill Islands	–
Luticola austroatlantica Van de Vijver, Kopalová, Spaulding & Esposito	Chapters 3, 4	Fig. 4, Figs 3c–3d	Vestfold Hills & Windmill Islands	–
Luticola dolia Spaulding & Esposito	Plate 13	Fig. 3	Windmill Islands	–
Luticola elegans (West & West) Kohler & Kopalová	Plate 13	Fig. 1	Windmill Islands	–
Luticola murrayi (West & West) D.G.Mann	Plate 13	Fig. 7	Vestfold Hills	–
Luticola muticopsis (Van Heurck) D.G.Mann	Chapters 3, 4	Figs 5–6, Figs 3f–3g	Vestfold Hills & Windmill Islands	–
Luticola cf. *muticopsis* (Van Heurck) D.G.Mann	Plate 13	Fig. 17	Vestfold Hills	–
Luticola olegsakharovii Levkov & Van de Vijver	Plate 13	Figs 9–10	Vestfold Hills	–
Luticola permuticopsis Kopalová & Van de Vijver	Plate 13	Figs 15–16	Windmill Islands	–
Luticola pseudomurrayi Van de Viver & Tavernier	Chapter 3	Figs 2–3	Vestfold Hills & Windmill Islands	–
Luticola cf. *katkae* Van de Vijver & Zidarova	Plate 13	Fig. 5	Windmill Islands	–
Luicola cf. *gaussii* (Heiden) D.G.Mann	Plate 13	Fig. 8	Vestfold Hills	–
Luticola cf. *transantarctica* Kohler & Kopalová	Plate 13	Fig. 6	Vestfold Hills	–
Luticola D.G.Mann sp1	Plate 13	Fig. 11	Vestfold Hills	–
Luticola D.G.Mann sp2	Plate 13	Fig. 2	Windmill Islands	–
Luticola D.G.Mann sp3	Plate 13	Figs 13–14	Windmill Islands	–
Luticola D.G.Mann sp4	Plate 13	Fig. 12	Windmill Islands	–
Luticola D.G.Mann sp5	Plate 13	Fig. 4	Windmill Islands	–
Luticola in girdle view	Chapter 4	Fig. 3e	Windmill Islands	–

Table 1. Continued

Taxon	Plate Location	Figure	Distribution	Notes
Luticola D.G.Mann unidentifiable valve	Unshown	Unshown	Vestfold Hills	–
Microfissurata Lange-Bertalot, Cantonati & Van de Vijver sp1	Chapter 3	Fig. 61	Vestfold Hills	–
Microfissurata Lange-Bertalot, Cantonati & Van de Vijver sp2	Plate 10	Fig. 13	Vestfold Hills	–
Nanofrustulum shiloi (Lee, Reimer & McEnery) Round, Hallsteinsen & Paache	Plate 10	Figs 10–11	Vestfold Hills & Windmill Islands	–
Navicula collersonii Roberts & McMinn	Chapter 3	Figs 42–43	Vestfold Hills	–
Navicula cf. *criophila* (Castracane) Van Heurck	Plate 1	Fig. 5	Vestfold Hills	–
Navicula directa (W.Smith) Ralfs	Chapter 3	Fig. 54	Vestfold Hills	–
Navicula ectoris Van de Vijver	Chapter 3	Figs 14–15	Vestfold Hills	GRP; Chapter 3
Navicula cf. *ectoris* Van de Vijver 1	Chapter 3	Figs 9–10	Vestfold Hills	GRP; Chapter 3
Navicula cf. *ectoris* Van de Vijver 2	Plate 7	Fig. 6	Vestfold Hills	GRP; Chapter 3
Navicula gregaria Donkin	Chapter 3	Figs 11–12	Vestfold Hills	GRP; Chapter 3
Navicula cf. *gregaria* Donkin	Plate 7	Figs 3–4	Vestfold Hills	GRP; Chapter 3
Navicula cf. *perminuta* Grunow	Plate 7	Fig. 8	Vestfold Hills	–
Navicula phyllepta Kützing	Chapter 3	Fig. 13	Vestfold Hills	GRP; Chapter 3
Navicula cf. *phyllepta* Kützing	Plate 12	Fig. 10	Vestfold Hills	GRP; Chapter 3
Navicula phylleptosoma Lange-Bertalot	Plate 7	Fig. 5	Vestfold Hills	GRP; Chapter 3
Navicula cf. *phylleptosoma* Lange-Bertalot	Plate 7	Figs 1–2	Vestfold Hills	GRP; Chapter 3
Navicula glacei Van Heurck	Chapter 3	Figs 30–31	Vestfold Hills	MRN; Chapter 3
Navicula Bory sp1	Chapter 3	Figs 22–23	Vestfold Hills	MRN; Chapter 3
Navicula Bory sp2	Chapter 3	Figs 24–25	Vestfold Hills	MRN; Chapter 3
Navicula Bory sp3	Chapter 3	Figs 26–27	Vestfold Hills	MRN; Chapter 3
Navicula Bory sp4	Plate 12	Fig. 16	Vestfold Hills	MRN; Chapter 3
Navicula Bory sp5	Plate 12	Fig. 15	Vestfold Hills	MRN; Chapter 3
Navicula Bory sp6	Plate 12	Fig. 11	Vestfold Hills	MRN; Chapter 3
Navicula Bory sp7	Plate 12	Fig. 9	Vestfold Hills	MRN; Chapter 3
Navicula Bory sp8	Plate 12	Fig. 17	Vestfold Hills	MRN; Chapter 3
Navicula Bory sp9	Plate 12	Fig. 14	Vestfold Hills	MRN; Chapter 3

Table 1. Continued

Taxon	**Plate Location**	**Figure**	**Distribution**	**Notes**
Navicula Bory sp10	Plate 12	Figs 12–13	Vestfold Hills	MRN; Chapter 3
Navicula Bory sp11	Plate 7	Fig. 11	Vestfold Hills	MRN; Chapter 3
Navicula Bory sp12	Plate 7	Fig. 10	Vestfold Hills	MRN; Chapter 3
Navicula Bory sp13	Plate 12	Figs 1–2	Vestfold Hills	MRN; Chapter 3
Navicula Bory sp14	Plate 12	Fig. 8	Vestfold Hills	MRN; Chapter 3
Navicula Bory sp15	Plate 12	Fig. 7	Vestfold Hills	MRN; Chapter 3
Navicula Bory sp16	Plate 7	Fig. 7	Vestfold Hills	MRN; Chapter 3
Navicula Bory sp17	Plate 7	Figs 12–13	Vestfold Hills	MRN; Chapter 3
Navicula cf. *salinarum* Grunow	Chapter 3	Figs 7–8	Vestfold Hills	GRP; Chapter 3
Navicula shackletonii W.West & G.S.West	Plate 7	Figs 14–15	Vestfold Hills	–
Navicula Bory sp18	Plate 7	Fig. 16	Vestfold Hills	MRN; Chapter 3
Navicula Bory sp19	Plate 12	Fig. 4	Vestfold Hills	MRN; Chapter 3
Navicula Bory sp20	Plate 12	Figs 5–6	Vestfold Hills	MRN; Chapter 3
Navicula Bory sp21	Plate 12	Fig. 3	Vestfold Hills	MRN; Chapter 3
Navicula cf. *cremeri* Van de Vijver & Zidarova	Plate 7	Fig. 21	Windmill Islands	–
Navicula Bory sp22	Plate 7	Fig. 17	Windmill Islands	*Navicula* Bory sp1 in the Windmill Islands
Navicula Bory Unidentifiable Valve	Unshown	Unshown	Vestfold Hills	–
Nitzschia Hassall Unidentifiable Valve	Unshown	Unshown	Vestfold Hills	–
Nitzschia gracilis Hantzsch	Plate 11	Fig. 6	Vestfold Hills	–
Nitzschia cf. *gracilis* Hantzsch	Plate 11	Fig. 5	Vestfold Hills	–
Nitzschia australocommutata Hamsher, Kopalová, Kociolek, Zidarova & Van de Vijver	Plate 11	Fig. 20	Vestfold Hills	–
Nitzschia lecointei Van Heurck	Chapter 3	Fig. 53	Vestfold Hills	–
Nitzschia cf. *lecointei* Van Heurck	Plate 11	Figs 17–18	Vestfold Hills	–
Nitzschia cf. *westiorum* Kellogg et Kellogg	Plate 11	Fig. 19	Vestfold Hills	–
Nitzschia Hassall sp1	Chapter 3	Figs 59–60	Vestfold Hills	–
Nitzschia Hassall sp2	Plate 11	Figs 21–22	Vestfold Hills	–
Nitzschia Hassall sp3	Plate 11	Fig. 3	Vestfold Hills	–

Table 1. Continued

Taxon	**Plate Location**	**Figure**	**Distribution**	**Notes**
Nitzschia Hassall sp4	Plate 11	Fig. 4	Vestfold Hills	–
Nitzschia Hassall sp5	Plate 11	Fig. 16	Vestfold Hills	–
Nitzschia Hassall sp6	Plate 11	Fig. 15	Vestfold Hills	–
Nitzschia Hassall sp7	Plate 11	Fig. 2	Vestfold Hills	–
Nitzschia Hassall sp8	Plate 11	Fig. 1	Vestfold Hills	–
Nitzschia Hassall sp9	Plate 11	Figs 11–12	Vestfold Hills	–
Nitzschia Hassall sp10	Plate 11	Fig. 14	Vestfold Hills	–
Nitzschia Hassall sp11	Plate 11	Fig. 7	Vestfold Hills	–
Nitzschia Hassall sp12	Plate 7	Fig. 26	Windmill Islands	As *Nitzschia* Hassall sp1 in the Windmill Islands
Nitzschia Hassall sp13	Plate 7	Fig. 25	Windmill Islands	As *Nitzschia* Hassall sp2 in the Windmill Islands
Nitzschia Hassall sp14	Plate 7	Fig. 24	Windmill Islands	As *Nitzschia* Hassall sp3 in the Windmill Islands
Nitzschia cf. *medioconstricta* Hustedt	Plate 11	Fig. 10, 13	Vestfold Hills	–
Pinnularia australomicrostauron Zidarova, Kopalová & Van de Vijver morphotype 1	Plate 9	Figs 1–2	Vestfold Hills	_
Pinnularia australomicrostauron Zidarova, Kopalová & Van de Vijver morphotype 2	Plate 8	Figs 1–2	Vestfold Hills	_
Pinnularia australomicrostauron Zidarova, Kopalová & Van de Vijver morphotype 3	Plate 9	Figs 3–4	Vestfold Hills	_
Pinnularia australomicrostauron Zidarova, Kopalová & Van de Vijver morphotype 4	Plate 8	Figs 3–4	Vestfold Hills	_
Pinnularia australomicrostauron Zidarova, Kopalová & Van de Vijver morphotype 5	Plate 8	Fig. 5	Vestfold Hills	_
Pinnularia australomicrostauron Zidarova, Kopalová & Van de Vijver morphotype 6	Plate 9	Fig. 5	Vestfold Hills	_
Pinnularia borealis Ehrenberg	Chapter 4	Fig. 3a–3b	Windmills Islands	Species complex; See Pinseel et al. 2019, 2020
Pinnularia australoglobiceps Zidarova, Kopalová & Van de Vijver	Plate 1	Fig. 1	Vestfold Hills	* Further invetigation needing to examine possible conspecificty with a number of taxa with Antarctic records. Discussed in Zidarova et al. 2012
Pinnularia cf. *lundii* Hustedt	Plate 2	Figs 7–8	Vestfold Hills	*

Table 1. Continued

Taxon	**Plate Location**	**Figure**	**Distribution**	**Notes**
Pinnularia cf. *quadratarea* var. *bicuneata* Heiden	Plate 1	Figs 2–3	Vestfold Hills	–
Pinnularia cf. *viridis* (Nitzsch) Ehrenberg	Plate 5	Fig. 3	Vestfold Hills	–
Pinnularia Ehrenberg sp1	Plate 7	Fig. 9	Vestfold Hills	–
Pinnularia Ehrenberg sp2	Plate 7	Fig. 22	Vestfold Hills	–
Pinnularia Ehrenberg sp3	Plate 4	Fig. 3	Vestfold Hills	–
Pinnularia Ehrenberg sp4	Plate 5	Fig. 5	Vestfold Hills	–
Planothidium renei (Lange-Bertalot & Schmidt) Van de Vijver	Plate 3	Fig. 30	Windmill Islands	–
Planothidium cf. *renei* (Lange-Bertalot & Schmidt) Van de Vijver	Plate 3	Figs 31–32	Vestfold Hills	–
Planothidium quadripunctatum (Oppenheim) Sabbe	Plate 3	Figs 26–27	Vestfold Hills	–
Planothidium cf. *marginostriatum* Van de Vijver & Beyens	Plate 3	Fig. 25	Vestfold Hills	–
Planothidium dubium (Grunow) Round & Bukhtiyarova	Plate 3	Fig. 24	Vestfold Hills	–
Planothidium wetzelectorianum Kopalova, Zidarova & Van de Vijver	Plate 3	Figs 28–29	Vestfold Hills	–
Planothidium Round & L.Bukhtiyarova sp1	Plate 3	Fig. 40	Vestfold Hills	–
Planothidium Round & L.Bukhtiyarova sp2	Plate 3	Fig. 39	Vestfold Hills	–
Planothidium Round & L.Bukhtiyarova sp3	Plate 3	Fig. 37	Vestfold Hills	–
Planothidium Round & L.Bukhtiyarova sp4	Plate 3	Fig. 21	Vestfold Hills	–
Planothidium Round & L.Bukhtiyarova sp5	Plate 3	Fig. 34	Vestfold Hills	–
Planothidium Round & L.Bukhtiyarova sp6	Plate 3	Fig. 22	Vestfold Hills	–
Planothidium Round & L.Bukhtiyarova sp7	Plate 3	Fig. 33	Vestfold Hills	–
Planothidium Round & L.Bukhtiyarova sp8	Plate 3	Fig. 41	Vestfold Hills	–
Planothidium Round & L.Bukhtiyarova sp9	Plate 3	Fig. 38	Vestfold Hills	–
Planothidium Round & L.Bukhtiyarova sp10	Plate 3	Fig. 23	Vestfold Hills	–
Planothidium Round & L.Bukhtiyarova sp11	Plate 3	Figs 35–36	Vestfold Hills	–
Planothidium Round & L.Bukhtiyarova sp12	Plate 3	Fig. 19	Windmill Islands	–
Planothidium Round & L.Bukhtiyarova sp13	Plate 3	Fig. 20	Windmill Islands	–

Table 1. Continued

Taxon	Plate Location	Figure	Distribution	Notes
Planothidium Round & L.Bukhtiyarova sp14	Plate 3	Fig. 18	Windmill Islands	–
Planothidium Round & L.Bukhtiyarova sp15	Plate 3	Fig. 16	Windmill Islands	–
Psammothidium abundans (Manguin) Bukhtiyarova & Round	Chapter 3	Figs 34–35	Vestfold Hills	–
Psammothidium cf. *abundans* (Manguin) Bukhtiyarova & Round	Plate 3	Figs 7–8	Vestfold Hills	–
Psammothidium confusoneglectum Kopalová, Zidarova & Van de Vijver	Plate 3	Fig. 9	Vestfold Hills	–
Psammothidium papilio (D.E. Kellogg, M. Stuiver, T.B. Kellogg & G.H. Denton) Kopalová & Van de Vijver	Chapters 3, 4	Figs 32–33, Figs 3i–3j	Vestfold Hills & Windmill Islands	–
Psammothidium rostrogermainii Vam de Vijver, Kopalová & Zidarova	Plate 3	Fig. 17	Windmill Islands	–
Psammothidium superpapilio Kopalová, Zidarova & Van de Vijver	Plate 3	Figs 2–3	Vestfold Hills	–
Psammothidium subatomoides (Hustedt) Bukhtiyarova & Round	Plate 3	Fig. 10	Vestfold Hills	–
Psammothidium stauroneioides (Manguin) Buhktiyarova	Chapter 3	Figs 36–37	Vestfold Hills & Windmill Islands	–
Psammothidium incognitum (Krasske) Van de Vijer	Plate 3	Figs 4–6	Vestfold Hills	–
Pseudostaurosira D.M.Williams & Round sp1	Plate 10	Figs 7–9	Vestfold Hills & Windmill Islands	–
Sabbea adminensis (D.Roberts & McMinn) Van de Vijver, Bishop & Kopalová	Chapter 3	Figs 38–39	Vestfold Hills	–
Sellaphora seminulum (Grunow) D.G.Mann	Plate 10	Figs 1–3	Vestfold Hills	–
Sellaphora Mereschowsky sp1	Plate 10	Figs. 4–6	Vestfold Hills	–
Sellaphora Mereschowsky girdle view	Unshown	Unshown	Vestfold Hills	–
Stauroneis Ehrenberg sp1	Plate 4	Fig. 4	Vestfold Hills	–
Stauroneis Ehrenberg sp2	Plate 3	Fig. 1	Windmill Islands	As *Stauroneis* sp1 in the Windmill Islands, but this placement is uncertain
Stauroneis latistauros Van de Vijver & Lange-Bertalot	Chapter 3	Figs 20–21	Vestfold Hills	–
Stauroforma inermis Flower, Jones & Round	Plate 10	Figs 25–26	Vestfold Hills & Windmill Islands	Need for revision discussed in Zidarova et al. 2016

Table 1. Continued

Taxon	Plate Location	Figure	Distribution	Notes
Synedra Ehrenberg sp1	Plate 11	Fig. 8	Vestfold Hills	–
Nitzschia Hassall girdle view	unshown	unshown	Vestfold Hills	–
Synedra Ehrenberg sp2	Plate 11	Fig. 9	Vestfold Hills	–
Staurosira Ehrenberg sp1	Plate 10	Fig. 12	Vestfold Hills	–
Staurosirella D.M.Wiliams & Round sp1	Plate 3	Fig. 12	Windmill Islands	–
Thalassionema Grunow ex Mereschkowsky sp1	Plate 2	Fig. 10	Vestfold Hills	–
Tryblionella marginulata (Grunow) Mann	Plate 1	Figs 6–7	Vestfold Hills	–
Elongated Pennate Frustule *incertae sedis*	Plate 4	Figs 1–2	Vestfold Hills	–
Pennate Frustule *incertae sedis 2*	Plate 5	Fig. 1	Vestfold Hills	–
incertae sedis Ellipsoid Pennate diatom	Plate 10	Figs 22–23	Vestfold Hills	–
incertae sedis Pennate diatom < 5µm	Plate 12	Figs 25–26	Vestfold Hills	–
Genus uncertain 1 unidentifiable valve	Unshown	Unshown	Windmill Islands	–
Genus uncertain 2	Plate 5	Fig. 2	Windmill Islands	–

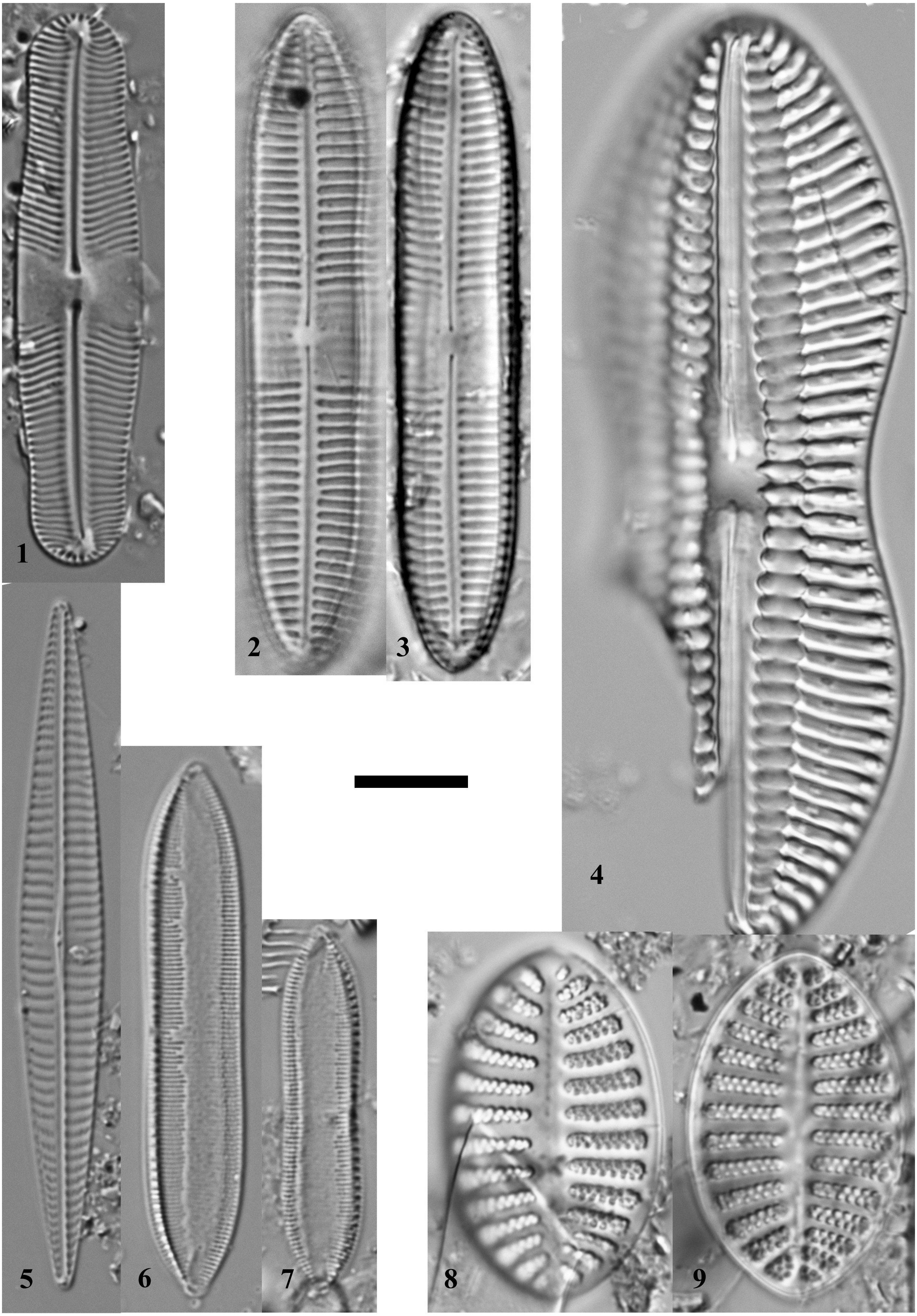


Plate 1. Fig. 1 *Pinnularia australoglobiceps*, Figs 2-3 *Pinnularia* cf. *quadratarea* var. *bicuneata*, Fig. 4 *Diploneis splendida*, Fig. 5 *Navicula* cf. *criophila*, Figs 6-7 *Tryblionella marginulata*, Figs 8-9 *Cocconeis costata*. 10µm scale bar applies to all images.

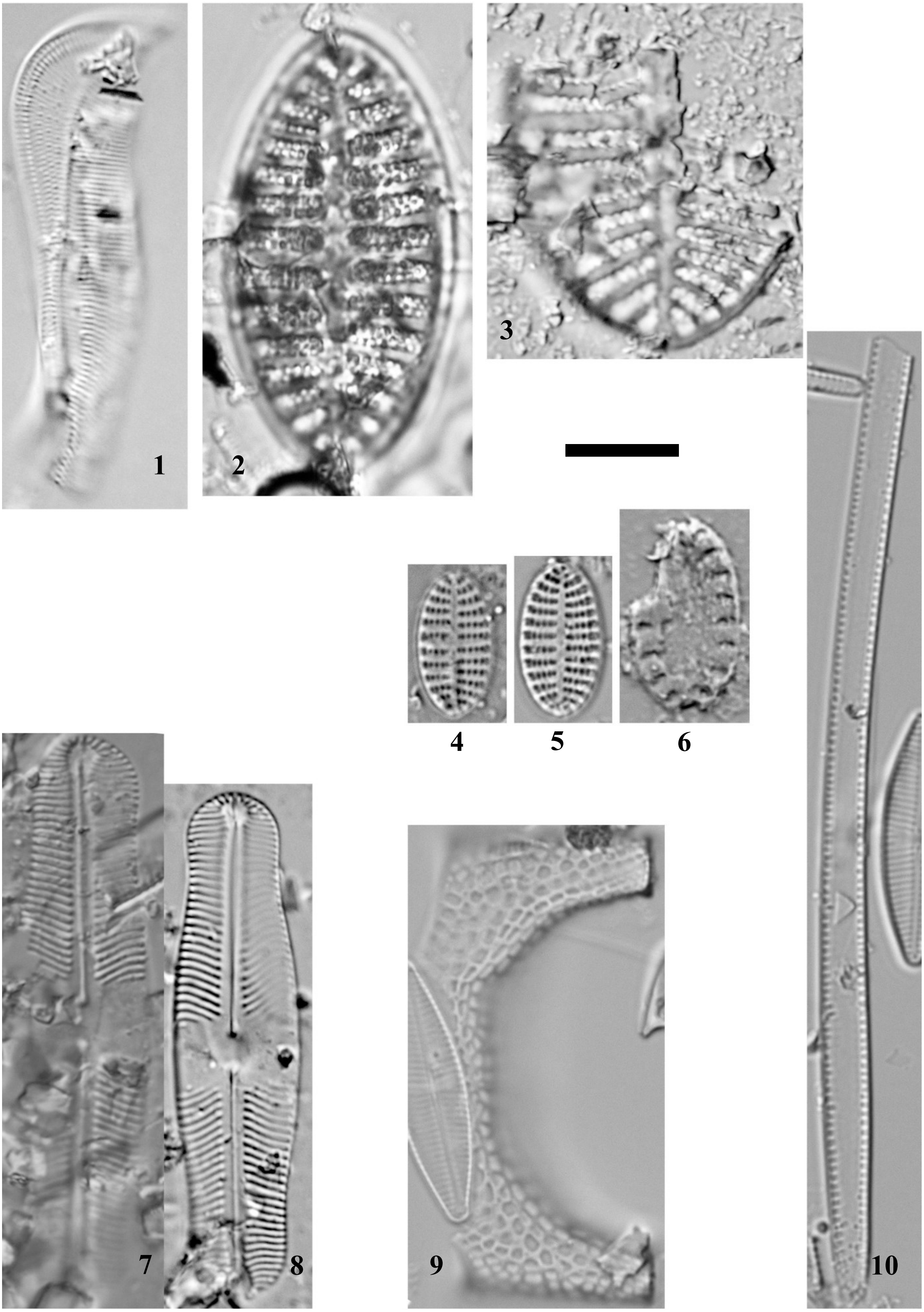


Plate 2. Fig. 1 *Entomoneis* sp1, Fig. 2 *Cocconeis pinnata*, Fig. 3 *Cocconeis* cf. *fasciolata*, Figs 4-5 *Cocconeis* sp1, Fig. 6 *Cocconeis* sp2, Figs 7-8 *Pinnularia* cf. *lundii*, Fig. 9 *Eucampia antarctica*, Fig. 10 *Thalassionema* sp1. 10µm scale barapplies to all images.

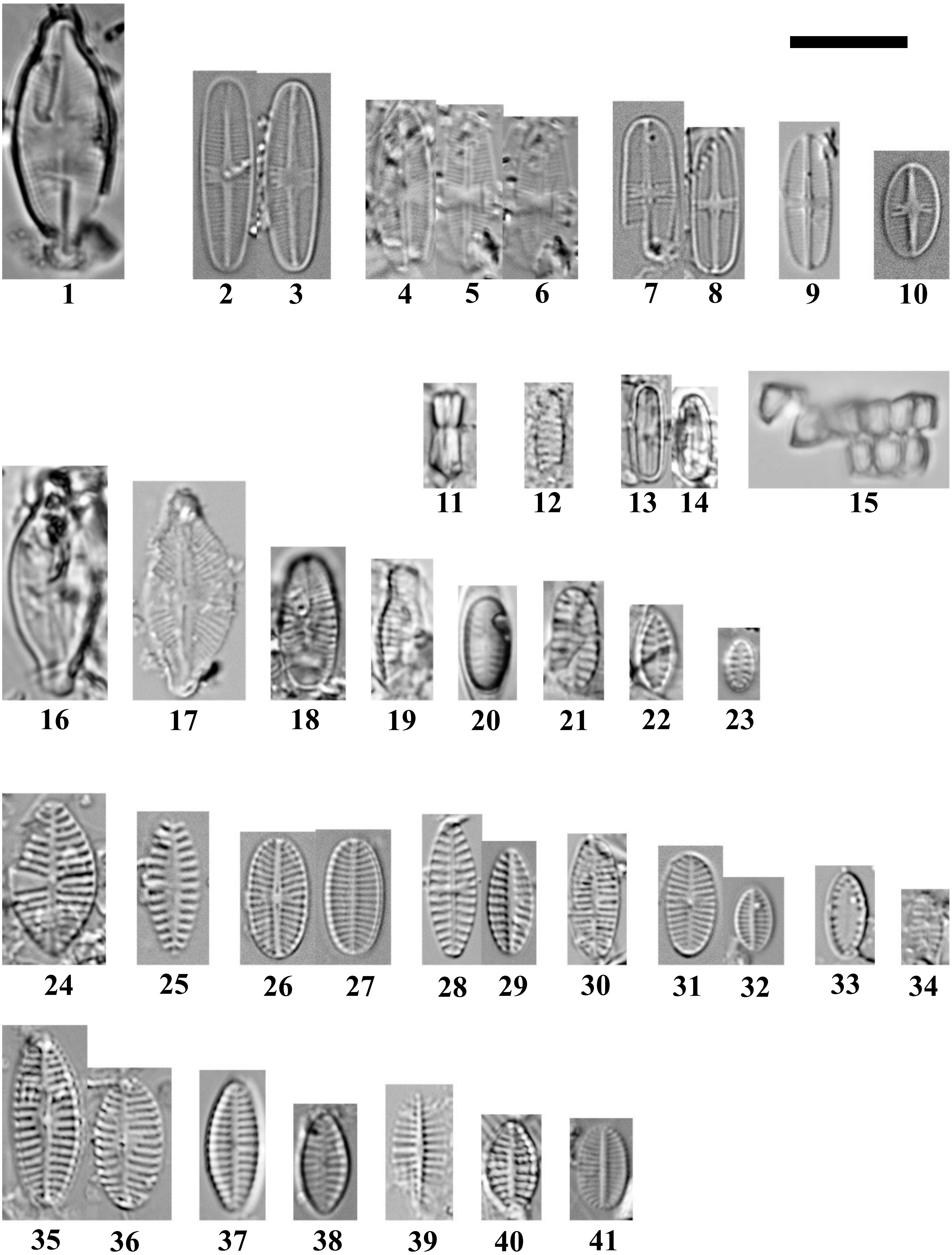


Plate 3. Fig. 1 *Stauroneis* sp2, Figs 2-3 *Psammothidium superpapilio*, Figs 4-6 *Psammothidium incognitum*, Figs 7-8 *Psammothidium* cf. *abundans*, Fig. 9 *Psammothidium confusoneglectum,* Fig. 10 *Psammothidium subatomoides*, Fig. 11 *Achnanthidium* sp1, Fig. 12*Staurosirella* sp1, Figs 13-14 *Humidophila inconspicua*, Fig. 15 *Humidophila* cf. *inconspicua*, Fig. 16 *Planothidium* sp15, Fig. 17 *Psammothidium rostrogermainii*, Fig. 18 *Planothidium* sp14, Fig. 19 *Planothidium* sp12, Fig. 20 *Planothidium* sp13, Fig. 21 *Planothidium* sp4, Fig. 22 *Planothidium* sp6, Fig. 23 *Planothidium* sp10, Fig. 24 *Planothidium dubium*, Fig. 25 *Planothidium* cf. *marginostriatum*, Figs 26-27 *Planothidium quadripunctatum*, Figs 28-29 *Planothidium wetzelectorianum*, Fig. 30 *Planothidum* renei, Figs 31-32 *Planothidum* cf. *renei*, Fig. 33 *Planothidium* sp7, Fig. 34 *Planothidium* sp5, Figs 35-36 *Planothidium* sp11, Fig. 37 *Planothidium* sp3, Fig. 38 *Planothidium* sp9, Fig. 39 *Planothidium* sp2, Fig. 40 *Planothidium* sp1, Fig. 41 *Planothidium* sp8. 10μm scale bar applies to all images.

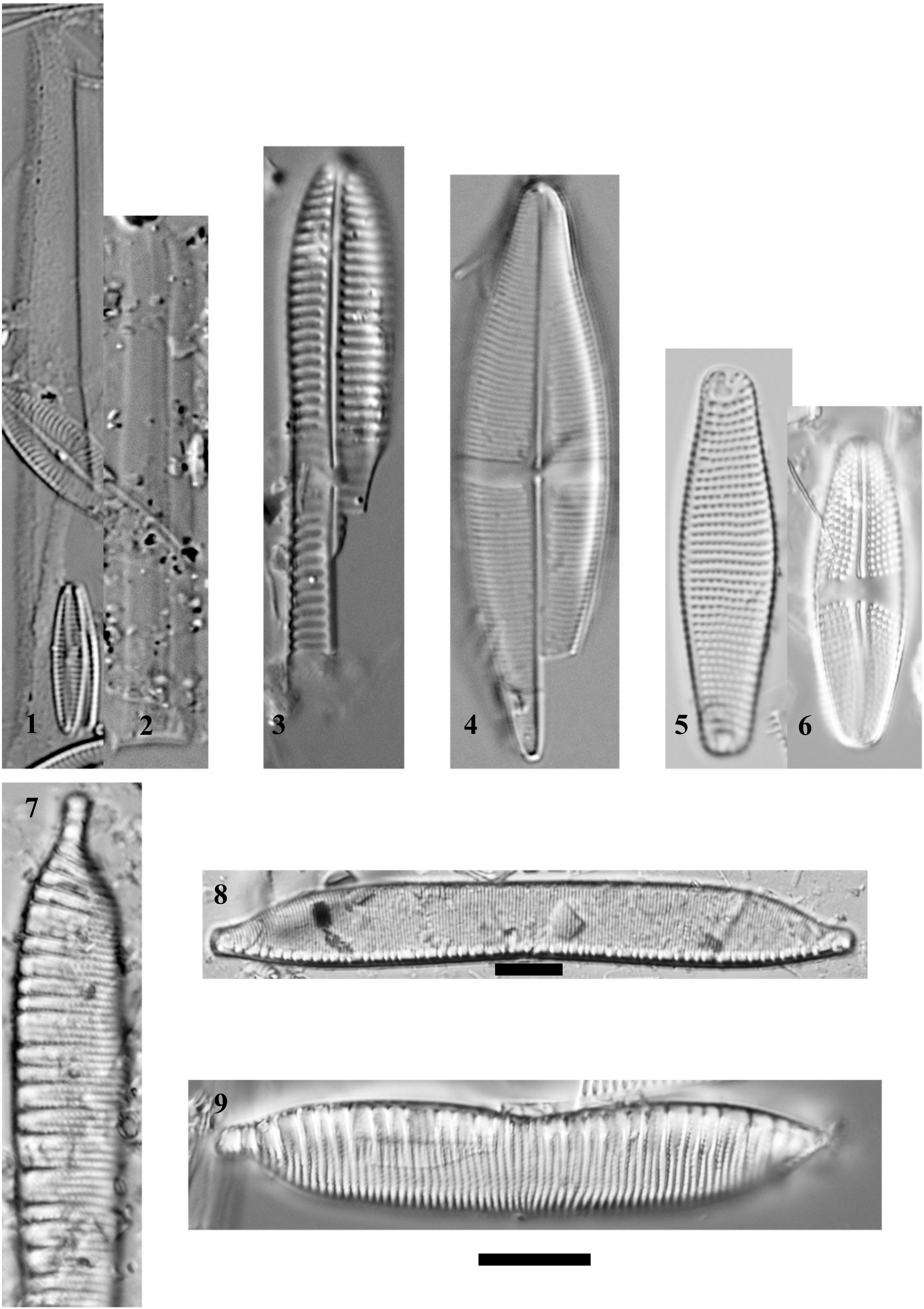


Plate 4. Figs 1-2 Elongated Pennate Frustule *incertae sedis*, Fig. 3 *Pinnularia* sp3, Fig. 4 *Stauroneis* sp1, Figs. 5-6 *Achnanthes taylorensis*, Figs. 7-9 *Hantzschia* sp1. Scale bar is 10µm. Inset scale bar for Fig. 8 (600x magnification) is 10µm.

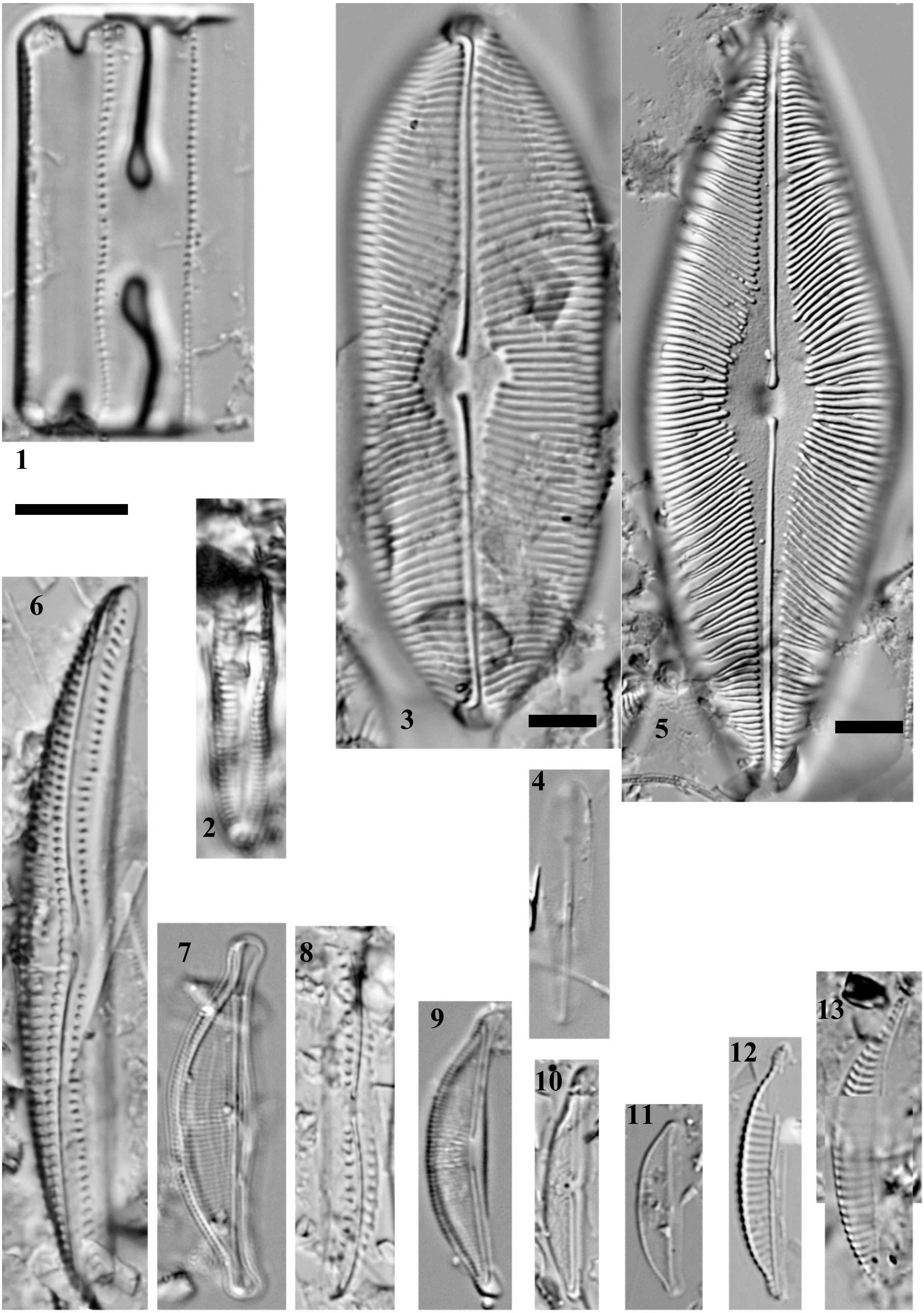
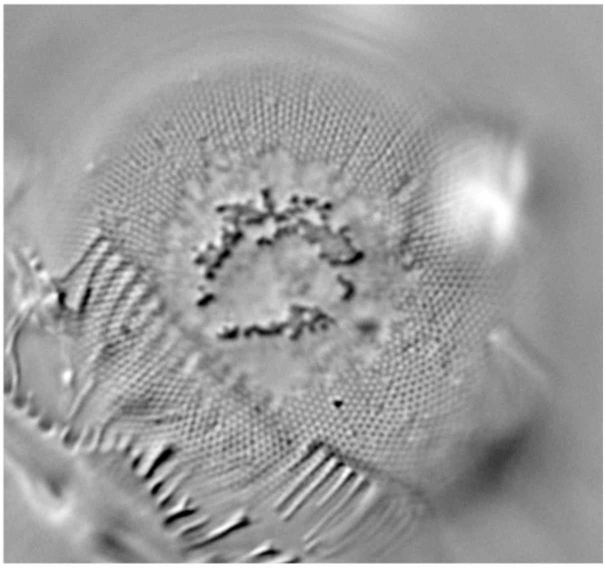


Plate 5. Fig. 1 Pennate Frustule *incertae sedis* 2, Fig. 2 Genus uncertain 2, Fig. 3 *Pinnularia* cf. *viridis*, Fig. 4 *Berkeleya* sp1, Fig. 5 *Pinnularia* sp4, Fig. 6 *Amphora* sp2, Fig. 7 *Amphora* sp1, Fig. 8 *Amphora* sp3, Fig. 9 *Halamphora* sp1, Fig. 10 *Halamphora* sp2, Fig. 11 *Halamphora* sp3, Fig. 12 *Halamphora* sp4, Fig. 13 *Halamphora* sp5. Central scale bar is 10µm. Inset scale bar for Figs 4-5 (600x magnification) is also 10µm.


1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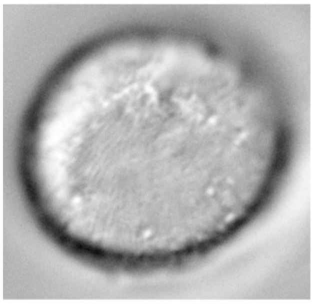
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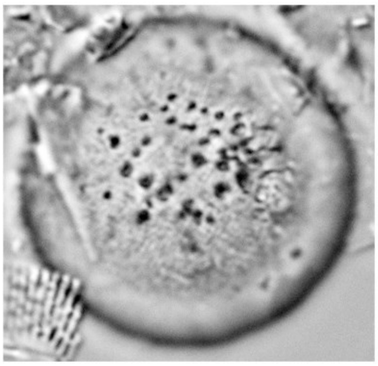
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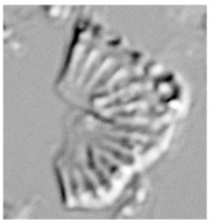
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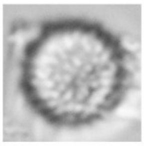
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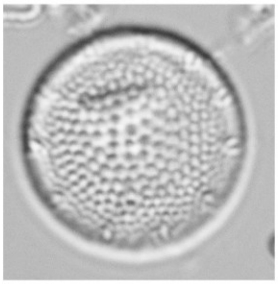
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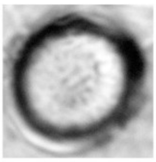
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Plate 6. Fig. 1-2 Centric sp5, Fig. 3 Centric sp2, Fig. 4 Centric sp6, Fig. 5 Centric sp4, Fig. 6 Centric sp3, Fig. 7 Centric sp1, Fig. 8 *Thalassiosira antarctica*, Figs 9-10 Centric unidentified. 10µm scale bar applies to all images.

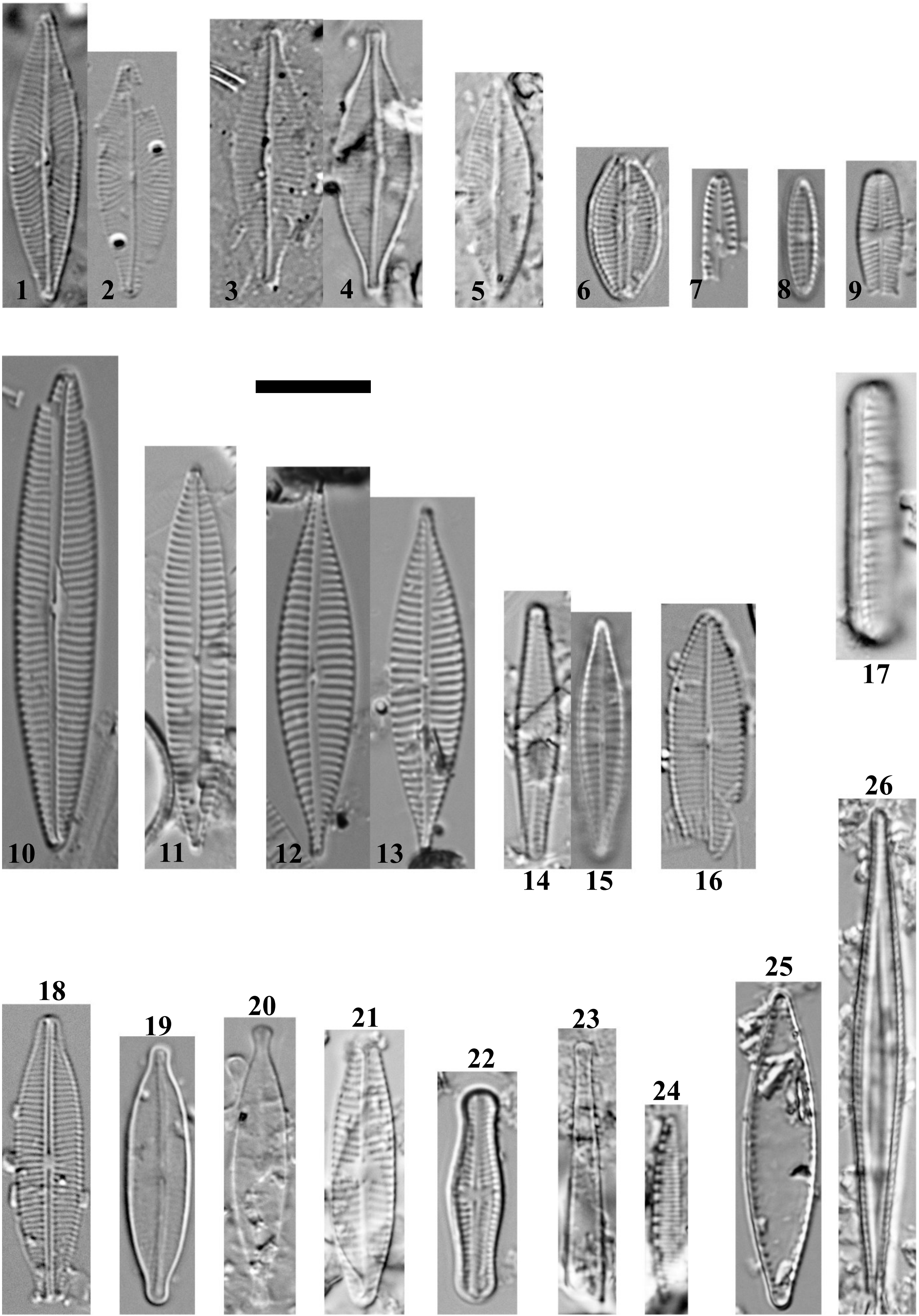

Plate 7. Figs 1-2 *Navicula* cf. *phylleptosoma*, Figs 3-4 *Navicula* cf. *gregaria*, Fig. 5 *Navicula phylleptosoma*, Fig. 6 *Navicula* cf. *ectoris* 2, Fig. 7 *Navicula* sp16, Fig. 8 *Navicula* cf. *perminuta*, Fig. 9 *Pinnularia* sp1, Fig. 10 *Navicula* sp12, Fig. 11 *Navicula* sp11, Figs 12-13 *Navicula* sp17, Figs 14-15 *Navicula shackletonii*, Fig. 16 *Navicula* sp18, Fig. 17 *Navicula* sp22, Fig. 18 *Craticula* cf. *submolesta* var 2, Fig. 19 *Craticula* cf. *submolesta* var 1, Fig. 20 *Craticula* cf. *antarctica*, Fig. 21 *Navicula* cf. *cremeri*, Fig. 22 *Pinnularia* sp2, Fig. 23 *Fragilaria* unidentifiable valve, Fig. 24 *Nitzschia* sp14, Fig. 25 *Nitzschia* sp13, Fig. 26 *Nitzschia* sp12. 10μm scale bar applies to all images.

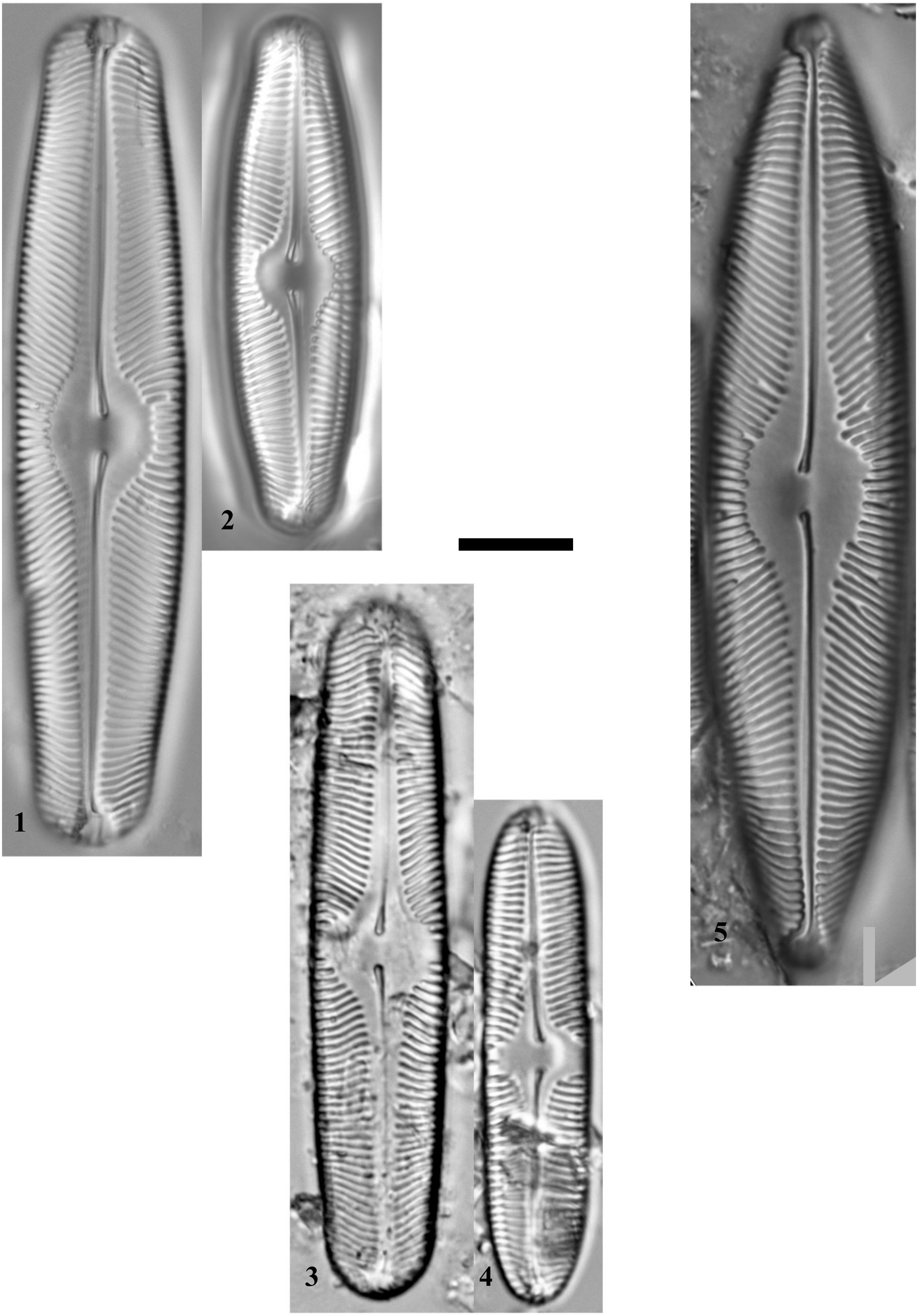

Plate 8. Figs 1-2 *Pinnularia australomicrostauron* morphotype 2, Figs 3-4 *Pinnularia australomicrostauron* morphotype 4, Fig. 5 *Pinnularia australomicrostauron* morphotype 5. 10µm scale bar applies to all images.

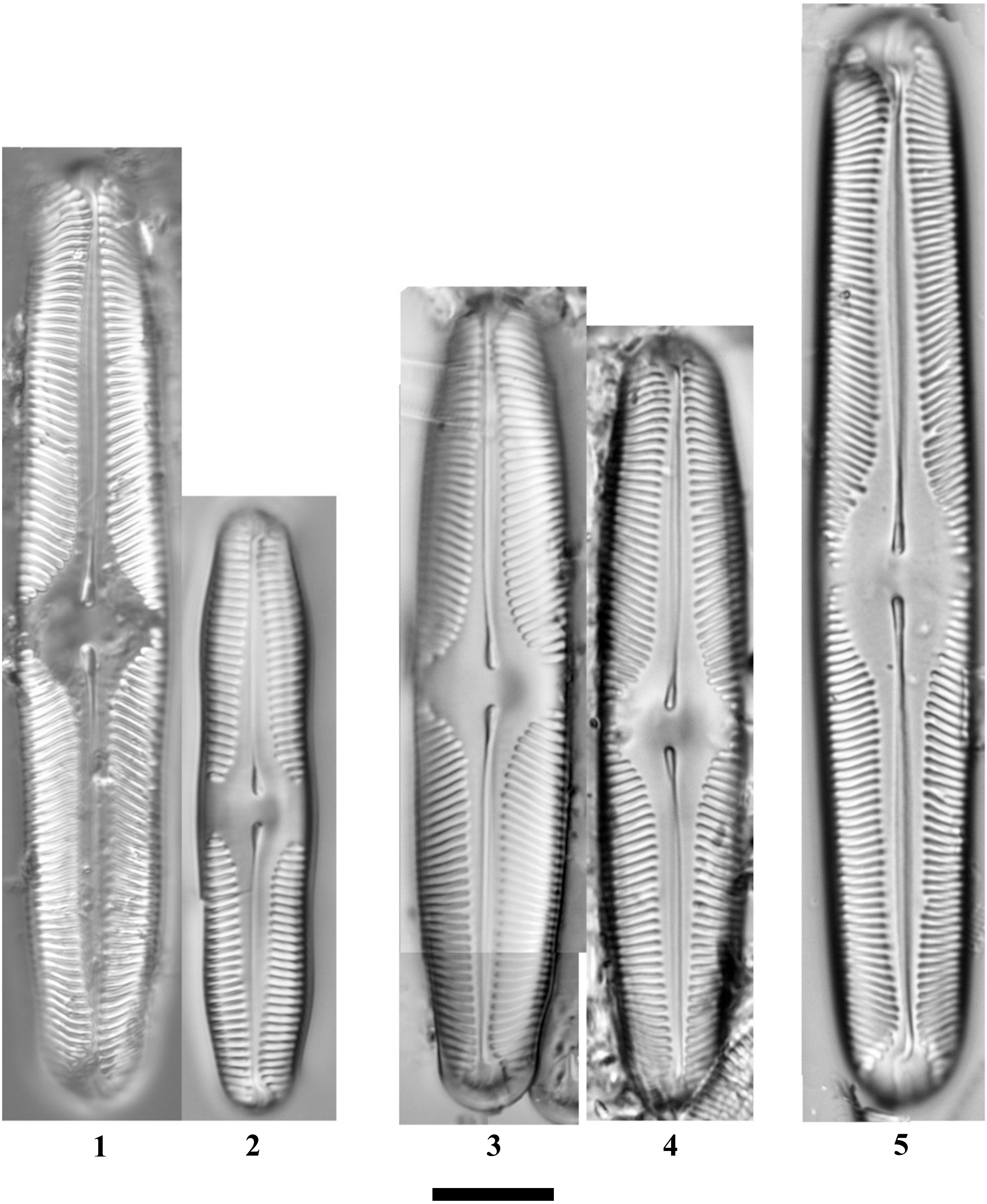

Plate 9. Figs 1-2 *Pinnularia australomicrostauron* morphotype 1, Figs 3-4 *Pinnularia australomicrostauron* morphotype 3, Fig. 5 *Pinnularia australomicrostauron* morphotype 6. 10µm scale bar applies to all images.

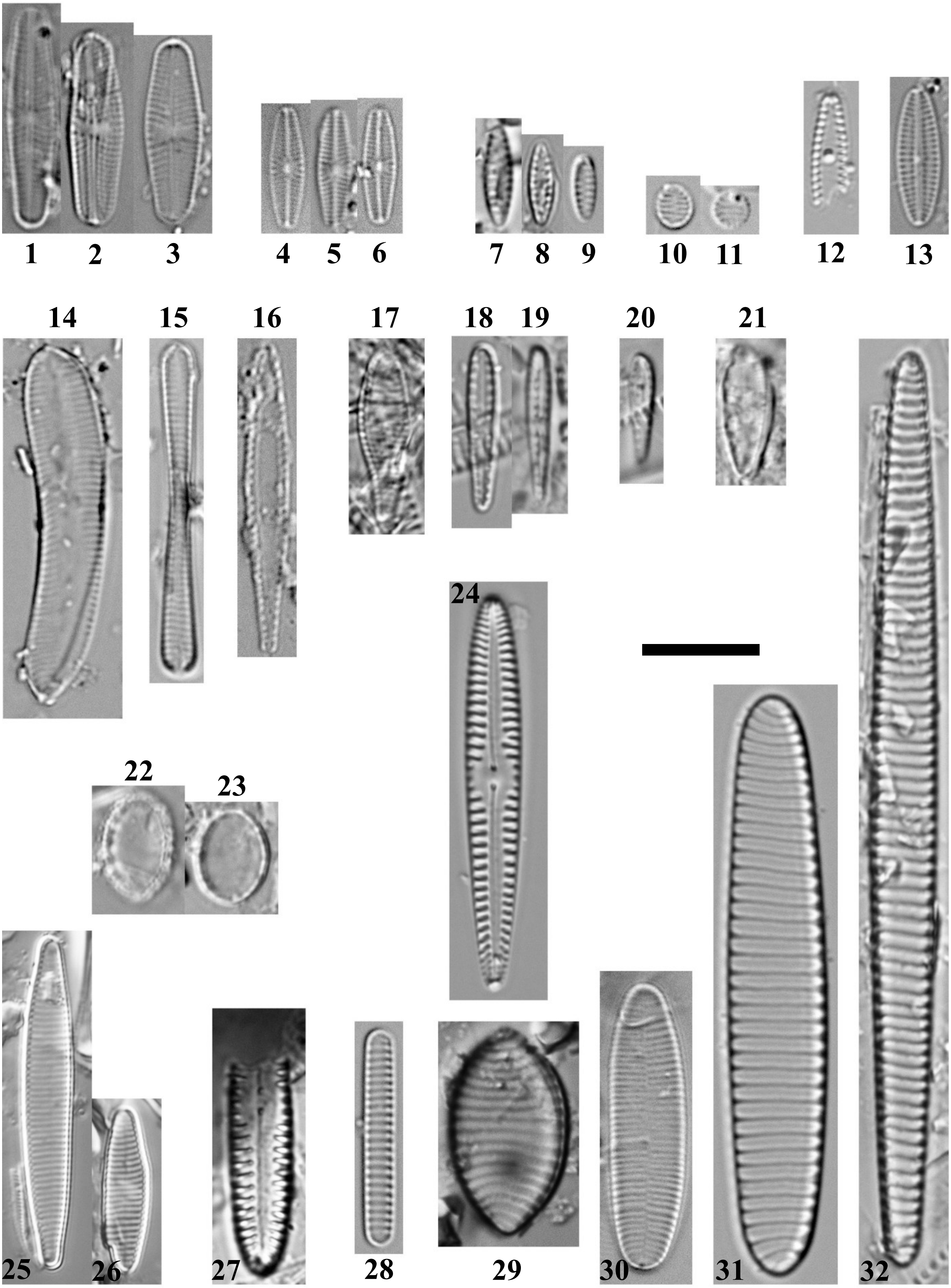

Plate 10. Figs 1-3 *Sellaphora seminulum*, Figs. 4-6 *Sellaphora* sp1, Figs 7-9 *Pseudostaurosira* sp1, Figs 10-11 *Nanofrustulum shiloi*, Fig. 12 *Staurosira* sp1, Fig. 13 *Microfissurata* sp2, Fig. 14 *Gomphonema* sp2, Fig. 15 *Gomphonema* sp3, Fig. 16 *Gomphonema* sp1, Fig. 17 *Gomphonema* sp4, Figs. 18-19 *Gomphonemopsis littoralis*, Fig. 20 *Gomphonemopsis* cf. *littoralis*, Fig. 21 *Gomphonema* sp6, Figs 22-23 *incertae sedis* Ellipsoid Pennate diatom, Fig. 24 *Gomphonema* sp5, Figs 25-26 *Stauroforma inermis*, Fig. 27 *Chamaepinnularia* sp1, Fig. 28 *Fragilariopsis vanheurckii*, Fig. 29 *Fragilariopsis rhombica*, Fig. 30 *Fragilariopsis* sp1, Fig. 31 *Fragilariopsis peragalloi*, Fig. 32 *Fragilariopsis sublinearis*. 10µm scale bar applies to all images.

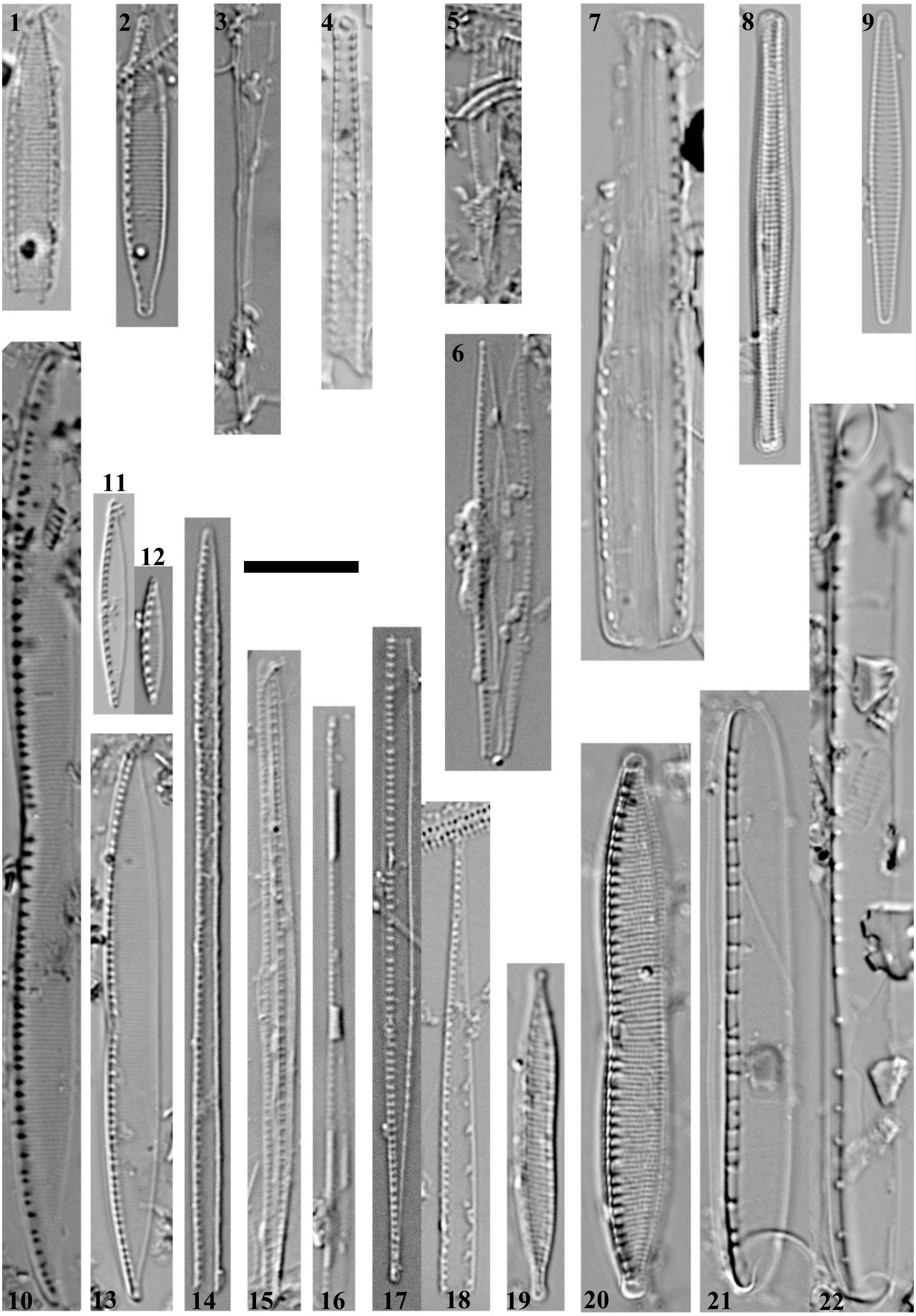

Plate 11. Fig. 1 *Nitzschia* sp8, Fig. 2 *Nitzschia* sp7, Fig. 3 *Nitzschia* sp3, Fig. 4 *Nitzschia* sp4, Fig. 5 *Nitzschia* cf. *gracilis*, Fig. 6 *Nitzschia gracilis*, Fig. 7 *Nitzschia* sp11, Fig. 8 *Synedra* sp1, Fig. 9 *Synedra* sp2, Fig. 10, 13 *Nitzschia* cf. *medioconstricta*, Figs 11-12 *Nitzschia* sp9, Fig. 14 *Nitzschia* sp10, Fig. 15 *Nitzschia* sp6, Fig. 16 *Nitzschia* sp5, Figs 17-18 *Nitzschia* cf. *lecointei*, Fig. 19 *Nitzschia* cf. *westiorum*, Fig. 20 *Nitzschia australocommutata*, Figs 21-22 *Nitzschia* sp2. 10µm scale bar applies to all images.

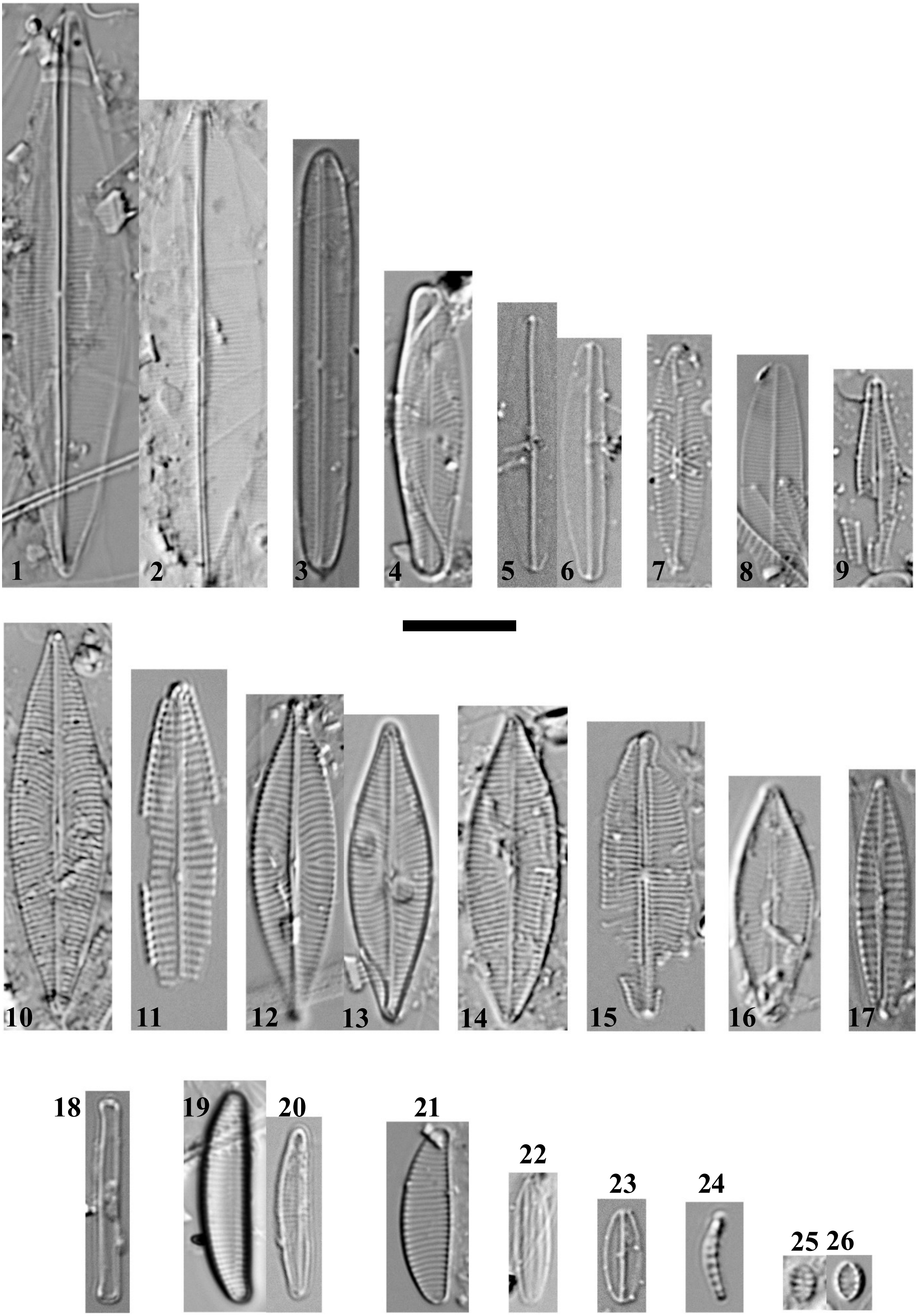

Plate 12. Figs 1-2 *Navicula* sp13, Fig. 3 *Navicula* sp21, Fig. 4 *Navicula* sp19, Figs 5-6 *Navicula* sp20, Fig. 7 *Navicula* sp15, Fig. 8 *Navicula* sp14, Fig. 9 *Navicula* sp7, Fig. 10 *Navicula* cf. *phyllepta*, Fig. 11 *Navicula* sp6, Figs 12-13 *Navicula* sp10, Fig. 14 *Navicula* sp9, Fig. 15 *Navicula* sp5, Fig. 16 *Navicula* sp4, Fig. 17 *Navicula* sp8, Fig. 18 *Catenula* sp3, Figs 19-20 *Eunotia* sp1, Fig. 21 *Eunotia* sp3, Fig. 22 *Astartiella* cf. sp1, Fig. 23 *Catenula* sp2, Fig. 24 *Eunotia* sp2, Figs 25-26 *incertae sedis* Pennate diatom < 5µm. 10µm scale bar applies to all images.

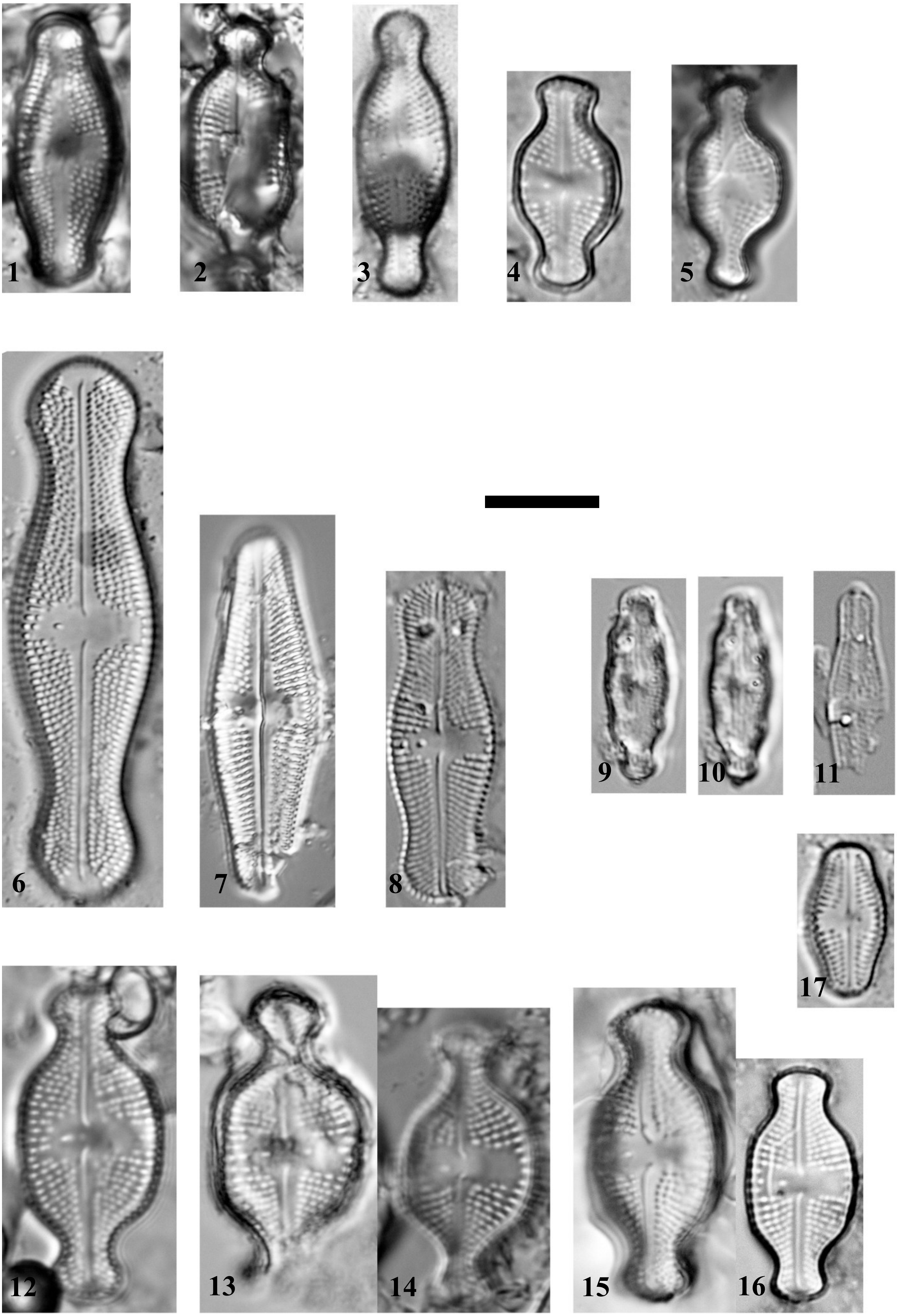

Plate 13. Fig. 1 *Luticola elegans*, Fig. 2 *Luticola* sp2, Fig. 3 *Luticola dolia*, Fig. 4 *Luticola* sp5, Fig. 5 *Luticola* cf. *katkae*, Fig. 6 *Luticola* cf. *transantarctica*, Fig. 7 *Luticola murrayi*, Fig. 8 *Luticola* cf. *gaussii*, Figs 9-10 *Luticola olegsakharovii*, Fig. 11 *Luticola* sp1, Fig. 12 *Luticola* sp4, Figs 13-14 *Luticola* sp3, Figs 15-16 *Luticola permuticopsis*, Fig. 17 *Luticola* cf. *muticopsis*. 10µm scale bar applies to all images.

Appendix 2

Curriculum vitae

JORDAN MICHAEL BISHOP
23 Old Town Highway, East Haven, CT, USA 06512
jordanmbishop87@gmail.com
+420 774 950 199

EDUCATION

Charles University, Prague, CZ. ABD-Defense 22 September 2020
Doctoral Candidate, Department of Ecology
Relevant Coursework: Ecology of Cyanobacteria & Algae, Stream Ecology, Phycology 1&2, Polar Ecology

University of Connecticut, Storrs, CT, USA
M.S. Ecology and Evolutionary Biology Department, GPA: 3.27/4.00
Relevant Coursework: Phylogenetics, Principles & Methods of Systematic Biology, Biological Collections, Fundamentals of Teaching & Learning

Connecticut College, New London, CT, USA
B.A. Environmental Studies, minor concentration within Biological Sciences, GPA: 3.65/4.00
Relevant Coursework: Biofuels, Freshwater Ecology, Plants, Protists and Fungi, Marine Ecology
Honors: Magna Cum Laude with honors & distinction, Barbara Shattuck Kohn '72 Environmental Studies Award, Sally L. Taylor Prize in Environmental Studies

Gateway Community College, New Haven, CT, USA
A.S. Natural Sciences and Mathematics, GPA: 3.92/4.00
Relevant Coursework: Microbiology, Anatomy & Physiology 1&2, General Chemistry 1&2
Honors: Phi Theta Kappa · Pfizer Science/Math Scholarship

PUBLICATIONS

Bishop, J., Wasley, J., Waterman, M.J., Kohler, T.J., Van de Vijver, B., Robinson, S.A. & Kopalová, K. (submitted *Antarctic Science*). Do water and nutrient availability influence the diatom communities found in mosses and lichens in the Windmill Islands, East Antarctica?

Bishop, J., Kopalová, K., Kohler, T.J., Van de Vijver, B., Roberts, D., McMinn, A. & Gibson, J. (In press *Diatom Research*). A re-investigation of lake sediment diatoms from the Vestfold Hills, Antarctica, using an updated, fine grained taxonomy.

Bishop, J., Kopalová, K., Darling, J.P., Schulte, N.O., Kohler, T.J., McMinn, A., Spaulding, S.A., Mcknight, D.M. & Van de Vijver, B. 2019. *Sabbea* gen. nov., a new diatom genus (Bacillariophyta) from continental Antarctica. *Phytotaxa*, 418(1), 10.11646/phytotaxa.418.1.2

Bishop, Jordan M. 2016. Examining valve shape variation in the freshwater diatom genus *Eunotia* over time and space. *Master's Thesis*. University of Connecticut.

Siver, P., Bishop, J., Lott, A. & Wolfe, A. 2015. Heteropolar eunotioid diatoms (Bacillariophyceae) were common in the North American Arctic during the middle Eocene. *Journal of Micropaleontology*, 34(2), 10.1144/jmpaleo2014-005

Bishop-Genovesi, J. 2014. Evaluating trends in valve shape in Eunotia by comparing fossil and modern species. Environmental Studies Honors Papers. *Undergraduate Honors Thesis*. Connecticut College.

PRESENTATIONS

Bishop, J., Wasley, J., Waterman, M., Kohler, T.J., Van de Vijver, B., Robinson, S. & Kopalová, K. 2020. Epiphytic diatom community shows larger response to bryophyte and lichen vegetation type than nutrient and water additions within Windmill Islands, East Antarctica. 18 March 2020. *13th European Diatom Meeting*. Cardiff, Wales. Poster Presentation.****COVID-19 Postponed

Bishop, J., Kopalová, K., Kohler, T.J., Van de Vijver, B., Roberts, D., McMinn, A. & Gibson, J. 2019. A re-investigation of historic materials from the Vestfold Hills in East Antarctica yields both endemic and cosmopolitan taxa across a number of lake ecologies. 25-30 August 2019. *7th European Phycological Congress*. Zagreb, Croatia. Poster Presentation.

Bishop, J., Kopalová, K., Darling, J.P., Schulte, N.O., Kohler, T.J., McMinn, A., Spaulding, S.A., Mcknight, D.M. & Van de Vijver, B. 2019. A unique new naviculoid diatom genus from Continental Antarctica. 27 March 2019. *12th Central European Diatom Meeting*. Belvaux, Luxembourg. Oral Presentation

Bishop, J. 2018. The state of the diatom flora of the Vestfold Hills within East Antarctica. 27 June. *25th International Diatom Symposium*. Berlin, Germany. Oral Presentation.

Bishop, J., Kopalová, K., Kohler, T.J., Van de Vijver, B. 2018. The *Navicula phyllepta* complex in the Antarctic Region. 27 June. *25th International Diatom Symposium*. Berlin, Germany. Poster Presentation.

Bishop, J. 2018. Evaluating valve shape variation within *Eunotia* across spatial and temporal scale using geometric morphometrics. 23 March. *Nederland-Vlaamse Kring Van Diatomisten (NVKD) Meeting*. Wetterskip Fryslân, Netherlands. Oral Presentation.

Bishop, J. 2017. Examining variation in valve shape with *Eunotia* across spatial and temporal scales. 23 March. *11th Annual Central European Diatom Meeting*. Prague, Czech Republic. Oral Presentation

Bishop, J. 2016. Examining valve shape variation in the freshwater diatom genus *Eunotia* over time and space. 20 May. *Master's Thesis Seminar*. University of Connecticut, Storrs, CT, USA. Oral Presentation

Bishop, J. 2015. Evaluating trends in valve shape of *Eunotia* by comparison of fossil and modern species. 17 August. *XPERT Summer School*. Amsterdam, Netherlands. Oral Presentation.

Bishop, J., Lewis, L., Siver., P. & Lizarralde, A. 2015. A proposed method to asses valve shape in *Eunotia* using morphology and phylogeny. 17-19 April. *54th Northeast Algal Society Symposium*. Syracuse, NY, USA. Poster Presentation.

Bishop, J., Siver., P. & Lizarralde, A. 2014.Valve shape in eunotiod diatoms: Comparing trends in modern and fossil species with an emphasis on Eunotia. 25-27 April. *53rd Northeast Algal Society Symposium*. Salve Regina University, Newport, RI, USA. Poster Presentation.

Bishop, J., Siver., P. & Lizarralde, A. 2013. Valve shape in Eunotia: comparing modern and fossil floras. 19-21 April. *52nd Northeast Algal Society Symposium.* Mystic, CT, USA. Poster Presentation.

FELLOWSHIPS & AWARDS

Charles University, Prague, CZ
Spring 2018-Present
- *Charles University Grant Agency (GAUK #1460218*)
  "Patterns and processes structuring freshwater diatom communities from Eastern Antarctica"

Fall 2016-Present
- *STARS Fellowship*

Botanic Garden Meise, Meise, BE
Spring 2018
- *Erasmus Trainingship*

The Academy of Natural Sciences at Drexel University, Philadelphia, PA
Spring 2015
- *McHenry Fellowship*

Northeast Algal Symposium, Syracuse, NY
Spring 2015
- *Student Travel Award*
- *Student Book Award*

University of Connecticut, Storrs, CT
Spring 2015
- *The Ronald Bamford Fund*

Fall 2014-Spring 2016
- *Multicultural Scholars Fellowship*

TEACHING

Teaching Assistant. University of Connecticut, Storrs, CT
Fall 2014 to Spring 2016
Course: *Principles of Biology II*

- Prepare lab lectures & lesson plan materials summarizing key concepts in weekly lab
- Administer weekly quizzes to assess learning comprehension of lab principles
- Create lab content from teaching assistants' workshops to better utilize teaching pedagogy
- Interface between student and instructor concerning course learning objectives and materials

Course: *Foundations of Biology*

- Instruct non-Biology major students in light microscopy and small-scale experiments
- Lead discussions in the application of scientific analysis to a broader audience

SKILLS SUMMARY

Lab & Field Technique: Water quality analysis using standard limnological methods, including Secchi Disk, Hydrolab, dissolved Oxygen & fluorescence meters, Chlorophyll extraction, Sediment preparations to preserve siliceous fossils, Flocam analysis, Recombinant DNA technology, Light & Scanning electron microscopy
Software: TpsDig, CANOCO, ArcGIS, R, Adobe Photoshop, Image J
Language: Basic proficiency in Italian

RESEARCH & ACADEMIC EXPERIENCE

Cryosphere Ecology Group, Department of Ecology, Charles University, Prague, CZ
Winter 2016 to Present
Doctoral Candidate

- Contributor: GACR-GJ16-17346Y - The Past Is The Key To The Future: Ecology And Holocene Development Of Freshwater Diatom Communities North Of The Antarctic Peninsula

Lewis Lab Group, Department of Ecology and Evolutionary Biology, University of Connecticut
Fall 2014 to Spring 2016
Graduate Assistant

- Phycological research including DNA techniques and single cell isolation
- Diatom ecology and morphological evolution using geometric morphometrics

Cross-disciplinary Palaeo-Environmental Research Training (XPERT)
Summer 2015
Institute for Biodiversity & Ecosystem Dynamics Summer School
University of Amsterdam, The Netherlands.

- Interpret paleontological records using multi-proxy data
- Workshop raw data for use in spatial modeling within R software

Biodiversity Research Collections, University of Connecticut
Summer 2015
Student Assistant

- Digitized herbarium records into online database
- Verified accuracy and validity of herbarium taxonomic metadata

Siver Lab Group, Department of Botany, Connecticut College
Summer 2012 to Spring 2014
Research Assistant

- Conducted research to identify flora within an Eocene maar lake
- Investigated morphological variance in fossil and modern diatoms and scaled chrysophytes
- Surveyed and sampled Connecticut water bodies, including rivers, lakes and bogs
- Cataloged and compared water and sediment samples from Canadian and American sites

Siver Lab, Freshwater Ecology, Department of Botany, Connecticut College Summers 2012 & 2013

Research Assistant
- Conducted research to identify flora within an Eocene maar lake
- Investigated morphological variance between fossil and modern samples of diatoms and scaled chrysophytes
- Surveyed and sampled Connecticut water bodies, including rivers, lakes and bogs
- Cataloged and compared water and sediment samples from Canadian and American sites