

Master thesis submitted to obtain the degree of Master in Biology,
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Environmental Changes in a High Arctic Ecosystem

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**Botanic Garden
Meise**



As long as there is a hunger for knowledge and a deep desire to uncover the truth, microscopy will continue to unveil Mother Nature's deepest and most beautiful secrets.

Lelio Orci & Michael Pepper (2002)

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This master thesis wouldn't have been possible without the support, energy and enthusiasm of many people.

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1 June 2014

EVELINE PINSEEL

International collaborations

This master thesis consists of 2 separate sections. The second is part of a detailed multiproxy paleolimnological analysis of a lake in Petuniabukta (Spitsbergen – Svalbard) performed by researchers from the Czech Republic, Germany and Belgium.

The diatom analysis of the sediment core taken for the paleolimnological study is performed by the author of this master thesis. Dr. Daniel Nývlt (Masaryk University, Brno & Czech Geological Survey, Brno, Czech Republic) is responsible for the sedimentology, stratigraphy, geochemistry, geomorphology and the multi-proxy record interpretation. Jan Kavan (University of South Bohemia, České Budějovice, Czech Republic) carries out the physical, limnological and hydrological analysis. The botanic macroremains will be investigated by Alexandra Bernardová (University of South Bohemia, České Budějovice, Czech Republic). Matěj Roman and Daniel Vondrak (Charles University in Prague, Czech Republic) are responsible for the sediment magnetism and the chironomid analysis respectively. Support for the cyanobacterial, ecological and limnological analysis is given by Dr. Linda Nedbalová and Dr. Kateřina Kopalová (Charles University in Prague, Czech Republic). Pollen analysis is performed by Dr. Lisa Schüller (Bayreuth University, Germany). With respect to this master thesis, the major part of these analyses has not yet been finished. Therefore, the author of this thesis will only focus on the diatom analysis of the sediment core.

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Abstracts

English abstract

Changes in the freshwater diatom diversity of Petuniabukta (Spitsbergen, Svalbard Archipelago) are investigated on a spatial and temporal scale in an attempt to reduce the taxonomic and ecological uncertainty when applying diatoms as (paleo) environmental proxies in the Arctic.

To investigate the spatial scale, the diatom flora in littoral samples of 40 freshwater bodies was analysed for diatoms using light and scanning electron microscopy. A total of 315 taxa belonging to 58 genera has been found. Of these, 234 taxa were identified upon species, subspecies, variety or forma level. The identity of the other taxa is uncertain or only known up to the genus level. Several taxa are with certainty new to science and a new species, *Gomphonema svalbardense*, has already been described. Important taxa include *Achnanthydium* sp1 (*Achnanthydium minutissimum* s.l.), *Rossithydium petersenii* and *Diatoma tenuis*. Cluster analysis and DCA ordination allowed separating the observed diatom communities in 4 different assemblages which were explained by differences in environmental characteristics, such as the presence of streams, moss vegetation, glaciers and sea spray.

For the temporal scale, the diatom succession in a ~ 6000 year old sediment core from Garmaksla Lake was studied. Based on a CONISS cluster analysis and a broken stick analysis 8 zones were distinguished. Two taxa dominate throughout the core: *Staurosira venter* and *Amphora affinis*. Dominance of *A. affinis* in the lower part of the core could indicate more mesotrophic and warmer conditions compared to the overlaying by *S. venter* dominated zones which presumably correspond with colder, oligotrophic conditions. Unprecedented changes occur in the top layers of the core with a distinct increase in productivity and diversity. These recent changes are attributed to climate warming as a result of the end of the Little Ice Age, ~ 100 – 150 years ago, and, more recently, human induced environmental changes.

Dutch abstract

Veranderingen in de zoetwater diatomeeën diversiteit in Petuniabukta (Spitsbergen, Svalbard Archipel) werden onderzocht op een spatiale en temporele schaal in een poging om de taxonomische en ecologische onzekerheid bij het gebruik van diatomeeën in (paleo)ecologische studies in Arctische gebieden te reduceren.

Om de ruimtelijke schaal te onderzoeken werd de diatomeeënsamenstelling in littorale stalen van 40 meren en poelen geanalyseerd met behulp van licht- en rasterelektronenmicroscopie. Een totaal van 315 taxa behorende tot 58 genera werd gevonden. Hiervan werden 234 taxa geïdentificeerd tot op soort, ondersoort, variëteit of forma niveau. De identiteit van de overige taxa is onzeker of enkel gekend tot op genus niveau. Verschillende taxa zijn met zekerheid nieuw voor de wetenschap en een nieuwe soort, *Gomphonema svalbardense*, werd reeds beschreven. Belangrijke taxa zijn *Achnanthydium* sp1 (*Achnanthydium minutissimum* s.l.), *Rossethidyum petersenii* en *Diatoma tenuis*. De geobserveerde diatomeeëngemeenschappen werden in vier verschillende gemeenschappen verdeeld op basis van een cluster analyse en DCA ordinatie. Omgevingskenmerken, zoals de aanwezigheid van beekjes, mos vegetatie, gletsjers en spatwater van de zee, werden aangegeven als verklaring.

De temporale schaal werd onderzocht door de diatomeeënsuccessie in een ~ 6000 jaar oude boorkern van het meer Garmaksla te bestuderen. Een CONISS cluster analyse en *broken stick* analyse lieten toe 8 zones te onderscheiden. Twee taxa domineren in de boorkern: *Staurósira venter* en *Amphora affinis*. Dominantie van *A. affinis* in het onderste gedeelte van de boorkern zou kunnen wijzen op meer mesotrofe en warmere condities in vergelijking tot de bovenliggende door *S. venter* gedomineerde zones die vermoedelijk overeenstemmen met koudere, meer oligotrofe condities. Ongeziene veranderingen treden op in de toplagen van de boorkern met een sterke toename in productiviteit en diversiteit. Deze recente veranderingen worden toegeschreven aan klimaatsopwarming als gevolg van het einde van de Kleine IJstijd ~ 100 – 150 jaar geleden en, recenter, door anthropogeen geïnduceerde omgevingsveranderingen.

Abstract in Layman's terms

Diatoms, unicellular algae characterised by a siliceous cell wall, are excellent indicators for (past) environmental changes in Arctic regions due to their specific ecological preferences and the good preservation of their cell walls in lake sediments during several thousands years. However, this application is hampered by our limited knowledge concerning the diversity and ecology of diatoms in Arctic regions. To improve our knowledge, changes in diatom diversity are investigated between different lakes (spatial scale) and in a sediment core of one of these lakes (temporal scale) in Petuniabukta (Spitsbergen, Svalbard Archipelago, Arctic Region).

To investigate the spatial scale, the diatom flora in samples collected in 40 different freshwater bodies was analysed using light and scanning electron microscopy. A total of 315 taxa belonging to 58 genera has been found. Several of these taxa are new to science and a new species, *Gomphonema svalbardense*, has already been described. Statistical analysis allowed separating the observed diatom communities in 4 different groups. These were explained by differences in environmental characteristics, such as the presence of streams, moss vegetation, glacial influence and sea spray.

For the temporal scale, changes in the diatom composition in a ~ 6000 year old sediment core from Garmaksla Lake were studied. Two taxa dominate throughout the core: *Staurosira venter* and *Amphora affinis*. Dominance of *A. affinis* in the lower part of the core could indicate more nutrientrich and warmer conditions compared to the overlaying by *S. venter* dominated layers which presumably correspond with colder, nutrientpoor conditions. Unprecedented changes occur in the top layers of the core with a distinct increase in diatom productivity and diversity. These recent changes are attributed to climate warming as a result of the end of the Little Ice Age, ~ 100 – 150 years ago, and, more recently, human induced environmental change.

1 Introduction

1.1 Diatoms

1.1.1 General introduction

Diatoms are unicellular, diploid, eukaryotic algae, characterised by a yellow-brown pigmentation and a siliceous cell wall [9]. Most diatoms are photosynthetic autotrophic, although some species are known to be (facultatively) heterotrophic [163]. The diatom cell wall is composed of 2 halves of slightly different sizes, the valves, interconnected by several linking structures: the girdle elements or cingulum [167]. Valves and cingulum together form the frustule [9] (Figure 1). The silica in the cell wall ensures the rigidity of the cell wall and contributes highly to the fossilisation of diatom valves [9]. Furthermore, diatom classification, species delineation and identification of living and dead material depend mainly upon the detailed valve structure (Figure 1) [9, 167].

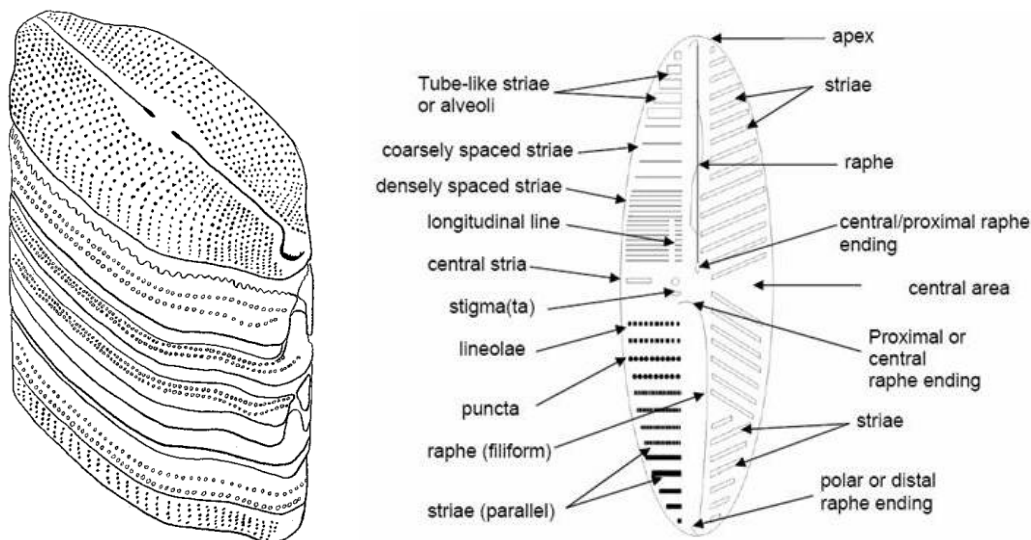


FIGURE 1. Frustule of a raphid diatom showing the valves and girdle elements (left) and the detailed valve structure of a raphid diatom (right). (Left figure taken from Round et al. [167], right figure taken from www.ces.iisc.ernet.in, consulted on the 7th of September 2013).

Most diatoms reproduce both sexually and asexually. During the vegetative cell division, daughter cells are produced so that each daughter cell receives one old mother valve and one new, but smaller, valve which is formed within the old one. This result in a gradual decrease in population mean cell size until a critical limit is reached and cell size is restored by sexual reproduction. During this process parent cells produce male and female gametes that, after fertilisation, give rise to an auxospore that subsequently develops into a single, maximally sized, cell. This initial cell differs morphologically from the asexually generated cells. In some taxa, the reduction of the valve size below the critical cell size is sufficient to trigger sexual reproduction, whilst other taxa additionally need certain environmental conditions [9, 90, 163].

Diatoms are the most species-rich group of algae on Earth [125]. Estimates of the total number of species vary between 20,000 [71] and 200,000 [125], although the range of 30,000 – 100,000 seems most likely [128]. Moreover, many extinct species are known from fossil material [163]. Diatoms first appeared during the early Jurassic and became abundant during the Cretaceous period about 100 million years ago [163, 177]. The most recent classification of the eukaryotes irrefutably classifies the diatoms in the 'Stramenopiles', the heterokont protists [1]. In this group, the diatoms are placed next to the Chrysophyceae and Xanthophyceae *inter alia*. Adl *et al.* [1] further subdivides the diatoms in 2 main groups: Coscinodiscophytina and Bacillariophytina. The Bacillariophytina are characterised by a bipolar or multipolar, sometimes circular, valve outline, whilst the Coscinodiscophytina always have a circular or sometimes elliptical valve outline. Within the Bacillariophytina, 2 main groups are recognised by Adl *et al.* [1]: the Bacillariophyceae, distinguished by a bipolar valve outline and raphe structure (i.e. a groove in the valve, Figure 1), and the Mediophyceae, with their bipolar, multipolar or circular valve outline and no raphe.

1.1.2 Ecology

Diatoms are always free-living, either as single cells or colonial. Parasitic taxa have never been observed [9, 163]. They are ecologically widespread, influence the global cycling of several elements, in particular carbon and silica and are estimated to contribute to at least 40 % of the oceanic net primary production [125] and 20 – 25 % of the world net primary production [222].

Diatoms occur in a large number of terrestrial and aquatic (freshwater, brackish and marine) environments [125] where they occupy 2 principal habitats: open water (planktonic) and moist or submerged surfaces (benthic) [167]. The benthos can be subdivided in the epilithon (attached to stones), the epiphyton (attached to plants), the epipsammon (attached to sand grains) and the epipelon (associated with mud) [9]. The plankton can be categorised in euplankton or holoplankton (taxa that spend their whole life-cycle in the water column), meroplankton (taxa that spend part of their life-cycle as benthos) and tychoplankton (taxa that have their true habitat in the benthos but which can occasionally survive in the water column) [9]. In lake ecosystems, most planktonic species are meroplanktonic, surviving unfavourable conditions by entering in a resting phase [9]. The distribution of diatoms in lakes depends both on the available habitats and on the combination of prevailing physical (e.g., temperature, light, ice cover and turbulence), chemical (e.g., nutrients, pH, dissolved organic carbon (DOC) and salinity) and biological (e.g., competition, parasitism and grazing) conditions [9]. Due to their ecological preferences, diatoms are often applied in stratigraphic correlation, ecological monitoring and paleoecological reconstructions [184].

1.1.3 Biogeography

Diatoms are found on all continents ranging from Antarctica to the Arctic region in various terrestrial and aquatic habitats [125, 167]. Until recently, many diatom 'species' have been regarded as ubiquitous [218] since the dispersal of microscopic organisms (cell size < 1 mm) was expected not to be restricted by geographic boundaries, as is the case for macro-organisms [49]. The key to their dispersal would be their immense population sizes, believed to strongly affect the changes of successful dispersal over longer distances [6, 46]. As a consequence, local extinction would occur rarely or not at all [46]. Therefore, the presence of diatoms on a certain location would only be affected by the prevailing ecological conditions and not by geographic boundaries, indicating that the absence of a certain species on a certain location would be the result of unsuitable ecological conditions only: '*everything is everywhere*' but '*the environment selects*' [6]. However, recent evidence suggests that diatoms and protists in general might not follow this rule. Vyverman *et al.* [219] show, based on a global freshwater diatom genus data set, the existence of a latitudinal gradient in local and regional genus richness that is highly asymmetric between both hemispheres. Whilst local species richness can be explained by habitat availability, regional diatom communities and connectivity between nearby habitats, differences in regional genus richness are mainly the result of isolation processes, contradicting the ubiquity hypotheses and its unlimited dispersal [6, 49, 219]. Moreover, in order to be able to disperse over long distances, diatoms should be resistant to the associated unfavourable conditions, such as desiccation, abrupt temperature changes and UV irradiance [190]. Studies show that most diatoms, freshwater taxa in particular, are very sensitive to unfavorable conditions, indicating that frequent long distance dispersal is very unlikely [188, 190]. All results are confirmed by the recent findings of high levels of endemism among diatoms, particular in isolated areas such as the (sub)-Antarctic, e.g., Sabbe *et al.* [172], Spaulding *et al.* [191] and Van de Vijver, *et al.* [206, 208, 210]. In summary, we can conclude that the ubiquity hypothesis presumably doesn't hold for diatoms, as their communities are controlled by similar processes as those controlling macro-organism communities, such as allopatric speciation [218].

1.1.4 Taxonomy

Traditionally, the study of the valve morphology in Light Microscopy (LM) is used as main criterion for diatom identification and species delineation [125]. Therefore morphometric characteristics, such as valve size and stria density, are used together with other features, such as valve outline, striation pattern and shape of the central area (Figure 1) [125]. The development of Scanning (SEM) and Transmission Electron Microscopy (TEM) in the 1970s, allowed a more detailed study of the valve morphology, greatly contributing to species delineation [125]. However, the current diatom taxonomy is not without problems. In 1999, Mann [125] noted that '*the species taxonomy of diatoms*

is messy and lacks a satisfactory practical or conceptual basis, hindering further advances in all aspects of diatom biology'. This is mainly the result of changing interpretations of species boundaries based on morphological characters, notably alterations between a narrow and a broad species concept [125, 126]. Diatom taxonomists in the second half of the 20th century interpreted species boundaries much wider than in the previous decennia, lumping together many previously independently described taxa since they were considered conspecific [125]. These lumping activities were above all based on the opinion that the observed variation was intraspecific and the result of phenotypic plasticity [125]. Furthermore, force-fitting [204] has been widely applied by diatomists as most diatoms species were considered to be cosmopolitan according to the ubiquity hypothesis [49]. Therefore, many diatoms from e.g., Antarctica and the African continent were force-fitted into a European framework (Van de Vijver B. pers. comm.). However, since recent evidence suggested that this concept doesn't hold for diatoms [219], so-called cosmopolitan 'morphospecies' might in fact consist of various different, probably closely related, taxa [218]. Moreover, studies show that minor morphological differences often are associated with profound molecular differentiation and reproductive boundaries, e.g., the *Sellaphora pupula* (Kützing) Mereschkowsky-complex [127], and that the degree of phenotypic variation is mostly rather low [125]. Furthermore, molecular studies indicate that the degree of (pseudo)cryptic diversity in diatoms is high, e.g., the *Eunotia bilunaris* (Ehrenberg) Schaarschmidt-complex [217], the *Pseudo-nitzschia delicatissima* (Cleve) Heiden-complex [160], the *Pinnularia borealis* Ehrenberg-complex [189] and the *Hantzschia amphioxys* (Ehrenberg) Grunow-complex [189]. Additionally, traditional assessment of morphological features tends to underestimate the complexity of the variation pattern [125], what became clear out of morphometric studies [e.g., 211]. Therefore, diatomists recently adopted a narrower species concept that resulted in the splitting of many previously lumped taxa [126]. Today, most species delineation is still based on valve morphology in particular but additional ecological, molecular, physiological and reproductive behavioral data are increasingly collected to assess species boundaries [126]. Several diatomists argue for the use of this so-called unified species concept [126] in which evidence from different sources together will provide the information for species delineation [36]. In summary, we can conclude that valve morphology is a good indicator for species boundaries and identification with minor morphological differences mostly corresponding with species boundaries (Sabbe K. pers. comm.). However, additional information from other sources is recommended in particular in those species complexes that have shown to display (pseudo)cryptic diversity [125].

Additional problems are those associated with 'the load of the past'. Diatomists in the 19th and early 20th century have described hundreds of species, without knowing which underlying mechanisms caused the morphological variation they used to delineate species and without a good knowledge of the life cycle and its consequences on valve morphology, e.g., size reduction and shape alterations,

which resulted in erroneous assessed species boundaries [125, 126]. Often, only few, mostly not easily accessible, copies of these publications survive up to today [126]. Additionally, problems with lost or destroyed type material, severely affect the current taxonomy since those species names cannot be verified [126]. Moreover, most type material consists of permanent slides, whilst the original raw material is lost. This, however, doesn't allow morphological studies using SEM or TEM [126]. Worse, the type material of some species consists of drawings, often without any other information, e.g., most species of Grunow in Van Heurck [214] (Van de Vijver B. pers. comm.). These problems severely retard progress in diatom taxonomy.

1.1.5 Diatoms in High Arctic regions

Studies of the diatom flora from Spitsbergen are scarce (Table 1). The oldest study by Cleve [26] listed 71 diatom taxa from Kobbefjorden. Lagerstedt [106] distinguished 84 taxa in 16 unknown locations on Spitsbergen. Except for 7, all taxa previously distinguished by Cleve [26] were also listed by Lagerstedt. Zanon [227] reported on marine diatoms from Kobbefjorden but also listed 56 freshwater taxa. Hustedt [81] studied one sample of a mossbank near a glacierfront in Kongsfjord and found 30 diatom taxa. Krasske [105] reported 208 taxa in 33 samples (including brackish water) taken from various locations in West-Spitsbergen. Thomasson [200, 201] only reported 11 taxa. Up to today, the study by Foged [53] in 1964 remains the most extensive. He studied 209 samples from freshwater and both moss and humid soil habitats in West-Spitsbergen and Prins Karls Forland and distinguished a total of 572 taxa. In more recent years, studies have been carried out by Willén [223] on the diatoms of Spitsbergen (the region of Isfjorden Radio station), Picińska-Faltynowicz [152] on the diatoms of south-western part of Spitsbergen and Van de Vijver *et al.* [209] on the diatoms of the Brøgger Peninsula in Spitsbergen. They distinguished respectively 19, 157 and 131 taxa but only gave a limited amount of ecological information. Beyens & De Bock [12] reported on moss-dwelling diatoms of Edgeøya, Metzeltin & Witkowski [132] on the diatoms of Bjørnøya and Beyens & Van de Vijver [14] on the diatoms of Hopen Island. Six of the most recent studies [70, 79, 85, 87, 122, 226] were paleoecological studies, not contributing to diatom taxonomy or ecology, except for Jones & Birks [87] whom also gives ecological information aiming to develop transfer functions for several environmental factors. Apart from the studies listed in Table 1, several recent studies addressed cyanobacterial and algal communities, including diatoms, in Spitsbergen [e.g., 91, 93, 94]. However, these studies lack detailed information on diatoms and report only a very limited number of taxa, often identified up to genus level only. At last, in 2004 Van de Vijver *et al.* [205] described 3 new *Stauroneis* taxa from Spitsbergen in their revision of this genus in the Arctic and Antarctic regions. In summary, it is clear that the diatom flora of Svalbard is not well known as most studies were limited to a species overview giving some ecological background without focusing on diatom taxonomy.

TABLE 1. Overview of previous diatom studies on Svalbard. An extended version of this table is given in Appendix E (Table E1). Recent changes in genus boundaries have been implemented. The studies that focused on Spitsbergen are indicated with an asterisk. NS = not specified, UN = unknown by the author of this thesis.

Study	Locality	# Genera	# Taxa	# New taxa
Cleve (1867) *	Kobbefjorden	UN	71	UN
Lagerstedt (1873) *	Spitsbergen & Bjørnøya	UN	84	UN
Zanon (1929) *	Kongsfjord	UN	>56	UN
Hustedt (1937) *	Kongsfjord	UN	30	UN
Krasske (1938) *	West Spitsbergen	34	208	15
Thomasson (1958, 1961)	Nordautlandet	6	11	0
Foged (1964) *	Spitsbergen	52	572	43
Willén (1980) *	Spitsbergen	11	19	0
Picińska-Fałtynowicz (1988) *	Hornsund fjord	35	157	0
Beyens & De Bock (1989)	Edgeøya	30	119	0
Wohlfart <i>et al.</i> (1995)	Bjørnøya	NS	NS	0
Metzeltin and Witkowski (1996)	Bjørnøya	95	625	22
Van de Vijver <i>et al.</i> (1999) *	Brøgger Peninsula	36	131	0
Beyens & Van de Vijver (2000)	Hopen Island	30	116	0
Jones and Birks (2004) *	West Spitsbergen	NS	182	0
Guilizzoni <i>et al.</i> (2006) *	Kongressvatnet	NS	140	0
Holmgren <i>et al.</i> (2010) *	West Spitsbergen	NS	NS	0
Jiang <i>et al.</i> (2011) *	Ny-Ålesund	NS	NS	0
Luoto <i>et al.</i> (2011)	Nordautlandet	NS	NS	0

When taking into consideration the entire Arctic region as a whole, many other studies can be listed: e.g., Moore [134-136], Hickman [76], Douglas & Smol [40, 41], Van de Vijver *et al.* [212] and Antoniadou *et al.* [4] for the Canadian Arctic, Cleve [27] for Franz Josef Land, Lowe [120], Foged [58] and Hein [75] for Alaska, Foged [56] for Iceland and Østrup [140-142], Petersen [151], Foged [50-52, 54, 55, 57, 59, 60], Denys & Beyens [39], Van Kerckvoorde [215, 216] and Cremer [30, 31] for Greenland. A more extensive overview is given by Douglas & Smol [42]. These studies of Arctic diatoms provided the foundation for the investigation of ecological characteristics of freshwater diatoms which resulted in the development of several regional calibration sets [42].

1.2 Paleolimnology

1.2.1 Paleolimnology in High Arctic regions

Paleolimnology is the study of the origin and history of lakes based on lake sediments [77]. Environmental changes, such as alterations in temperature, precipitation, evaporation, erosion, ice cover, light availability, glacial extent and human influences, cause physical, chemical and biological responses in lake ecosystems that are registered in the lake sediments by means of biological, chemical and glacial remnants [8, 77]. Therefore, lake sediments contain valuable information about

the causes and consequences of environmental changes in lakes and their catchments [8, 77]. Paleolimnology is crucial in reconstructing past environmental changes in those regions that have never been monitored, such as the polar regions [77]. Moreover, both the Arctic and Antarctic are, due to their sensitivity to the effects of Global Change [168] and their potential to exert profound changes on the whole planet as result of positive feedback systems, important areas for paleolimnological research to better understand the causes and consequences of the present rapid climate and other environmental changes [77]. Without a good understanding of the past climatic changes over periods spanning several centuries to millennia, it is impossible to understand the causes and consequences of the current climatic changes and therefore studies using environmental/climatic proxies are crucial to give us insight in the past environment [181]. According to Birks *et al.* [17] Svalbard is especially an interesting area for paleolimnological research due to (1) its location; (2) its climate; (3) its high lake variation; (4) its restricted relatively well-known fauna and flora; (5) the limited human impact since the discovery in 1596; (6) its isolated position far away from major sources of atmospheric pollution; (7) the limited local atmospheric pollution, (8) its recent climate changes; and (9) its good accessibility, contrary to other Arctic regions.

1.2.2 Diatoms as environmental indicators

Due to their siliceous cell wall, diatom valves are often well-preserved in lake sediments for thousands of years [9], making them, together with their ecological preferences, ideal proxies in paleolimnological research [184]. According to Battarbee *et al.* [9] diatoms can be used to give an indication for various environmental factors, including physical characteristics such as lake water temperature, light conditions and water column transparency, turbulence and ice cover. Chemical factors are also of major importance, since diatoms can give indications of the nutrient availability in the water column, the pH, lake water salinity and the amount of DOC [9]. When inferring past climatic changes from diatom assemblages, paleophycologists use 2 different approaches: (1) diatoms are used to directly reconstruct the past climate assuming diatom communities to be directly related to temperature or variables that are linearly related to temperature, and (2) diatoms are used to infer a limnological parameter, such as lake ice cover or water chemistry, that is related to climate [181]. The second method is more often used since the first is rather controversial [181].

Diatoms are widely used as proxies for paleoecological studies in both marine and freshwater ecosystems, often in combination with various other environmental indicators. For the Subarctic and Arctic region, several studies using diatoms as a proxy can be listed, e.g., for Svalbard [70, 79, 85, 87, 122, 226], Greenland [149, 150], the Canadian Arctic [43, 47, 48, 92, 145, 148, 170, 178], Alaska [24], northern Russia [107], northern continental Norway [20] and northern Finland [174, 186, 187].

1.2.3 Chrysophytes as environmental indicators

Chrysophytes, or golden brown algae, are a group of unicellular aquatic, mainly freshwater, algae characterised by a carotenoid pigmentation [228] that constitute another useful paleoenvironmental indicator [180, 228]. They are subdivided in 2 classes: the Chrysophyceae and the Synurophyceae [228]. In contrast to the Chrysophyceae which have only a single cell membrane, the Synurophyceae are characterised by a cell wall of siliceous scales [228]. All Chrysophytes produce siliceous stomatocysts, i.e. resting spores, to survive unfavourable conditions [228]. As in diatoms, these siliceous structures ensure long-term preservation of cysts and scales in lake sediments [180] and that, combined with their strict ecological preferences, makes them ideal indicators for paleolimnological research [228]. Chrysophytes have been used to infer changes in trophic status, temperature, pH, water-level, habitat availability, salinity and metal concentrations [228]. Since the same preparation techniques as those used for diatoms are also applied for chrysophytes, both algal groups can be used simultaneously in paleoecological studies [180]. A frequently used method is to assess the ratio of chrysophyte cysts to the total amount of counted diatom valves on the same microscopic slide [228]. Smol [180] argued that this ratio allows a fast and accurate indication of environmental conditions. In temperate regions, a low ratio indicates eutrophic conditions [180] and in polar regions, the ratio is used to gain information about ice cover and thus climate [228]. The ratio has also proven to provide information concerning lake water salinity [33].

1.3 Paleoclimate of Svalbard

The following section gives an overview of the current knowledge of the paleoclimate of Svalbard starting with the Last Glacial Maximum. When reading the following sections, one must always keep in mind that the proxies used in the cited studies mainly give a local climate signal which may result in an apparent overlap between subsequent periods of warming and cooling.

1.3.1 Last Glacial Maximum and end of the Weichselian

During the Last Glacial Maximum (LGM), Svalbard was almost entirely covered by the Barents Sea Ice Sheet: only the highest mountain peaks reached above the ice as nunataks [82, 109, 110]. The LGM on Svalbard is dated between 18,000 and 13,000 years ago [194], considerably later than the global date between 26,500 and 19,000 – 20,000 years ago [25]. The deglaciation of the Barents Sea Ice Sheet started around 15,000 years ago [109], although a significant ice sheet remained over Svalbard until 13,000 years ago after which deglaciation occurred rapidly [16, 108]. Whereas the Younger Dryas Stadial caused a significant cooling in the entire northern hemisphere between 12,500 and 10,000 years ago, this was considerably less pronounced on Svalbard [16, 194]. Up to now, no evidence has been found of glacier readvance in the western part of the archipelago [16, 194]. The

deglaciation of the western and northern parts of Spitsbergen began 13,000 – 12,000 years ago, whereas the ice sheets in the east melted about 10,500 years ago [62]. The deglaciation of Isfjorden started 12,500 years ago [196] and the central part of Spitsbergen was entirely ice-free about 11,200 – 11,300 years ago [7]. The entire archipelago was glaciated to the current extent about 10,000 years ago [108, 109, 124].

1.3.2 The early Holocene and the Holocene Climatic Optimum

During the early Holocene (8000 – 9000 years ago), glacier readvance occurred in the northern part of Billefjorden [96, 116]. This second cold period was named the Ebbadalen-Thomsondalen Stage and was most likely only a local phenomenon [96, 116].

During the Holocene Climatic Optimum, Svalbard was less glaciated than today [195]. Based on fossils of *Mytilus edulis* L., a thermophilous marine mollusk, this warm period was dated between 9500 – 3500 years ago and data of the bivalves *Modiolus modiolus* L. and *Zirphaea crispata* L. give an indication of a climatic optimum between 8700 – 7700 years ago [173]. Sediment data suggest 1.5 to 2.5 °C warmer summers during the Holocene climatic optimum compared to today [195] and Birks [15] demonstrates, based on plant macrofossils, an average 1 – 2 °C higher July temperature than today in the period between 8000 and 4000 years ago. During this warmer phase, thermophilous species, such as *M. edulis* and *Salix herbacea* L., probably were able to migrate northward and/or deeper landward [169, 173].

1.3.3 Medieval Warm Period and Little Ice Age

With the end of the Holocene Climatic Optimum glacier readvance marked a renewed period of cooling on Svalbard. For the Billefjorden region, this was dated on 3000 years ago [45] or, even earlier, c. 5470 years ago [7]. This cooling accumulated in the Little Ice Age (LIA), the coldest period during the late Holocene, AD (*anno domini*) 1600 – 1900 [83, 123, 198]. Gordiyenko *et al.* [66] suggested, based on ice core data, a two-phased LIA with the coldest periods around AD 1200 – 1500 and AD 1700 – 1900. Jones & Birks [87] interpreted marked changes in diatom assemblages AD 1200 in several sediment cores from the west-coast of Spitsbergen as a consequence of the onset of the LIA and a multi-proxy study of a lake near Ny-Ålesund gives an indication of a cold period AD 1420 – 1850/1890 [85]. Glacier readvance occurred during the LIA and most glaciers reached their maximal positions during the early [194] or even late 19th century [34, 84, 162]. However, the cooling that eventually accumulated in the LIA didn't take place in one clear-cut way: there are several indications for the existence of the Medieval Warm Period (MWP) on Svalbard. The MWP was a phenomenon in Europe and other regions at the borders of the North-Atlantic Ocean, before the LIA AD 900 – 1300, during which mean temperatures were higher than today [129]. Majewski *et al.* [123] found, based on sediment data and foraminifera from a sediment core of the Hornsund fjord on southwest

Spitsbergen, evidence for a warmer period around AD 1050, AD 1300 and AD 1500 – 1560. Both first data might correspond with the MWP. A multi proxy paleolimnological study of a lake in West Spitsbergen found a possible warmer period AD 1160 – 1255 [70]. Grinsted *et al.* [69] showed, based on the Lomonosovfonna ice core, glacier summer melt to be higher AD 1130 – 1200 compared to the 1990s, which is an evidence of an equally warm or even warmer MWP than present. When the MWP exactly ended on Svalbard is still unclear, but there are indications of glacier readvance in the 13th-14th century [66, 195]. The warmer periods AD 1500 – 1560 as described by Majewski *et al.* [123] and also indicated by Gordiyenko *et al.* [66], could represent a short period of warming just before the LIA or in a two-phased LIA.

1.3.4 End of the Little Ice Age till present

Multi-proxy evidence indicates that much of the Arctic started warming in the mid 19th century, considerably earlier than human induced global warming since AD 1920 [143, 185]. The end of the LIA is believed to have taken place around AD 1850 for the Arctic as a whole [143, 185], but occurred somewhat later on Svalbard at approximately AD 1890 – 1920 [34, 84, 85, 123, 198]. In general, the warming that marked the end of the LIA in the entire Arctic is thought to be related to a decreasing volcanic activity and associated sulphate release and an increase in solar irradiance coupled with feedbacks in the climate system [143]. The extended LIA on Svalbard presumably was the result of increased winter precipitation during the 18th and 19th century resulting in Svalbard glaciers to reach their maximal positions in the late 19th century, cooling down the lower parts of the atmosphere [7, 34, 84, 162]. This suggest that the late LIA on Svalbard wasn't extremely cold, but instead rather moist [34]. As a consequence of the end of the LIA, temperatures higher than at any time in the previous 500 years were reached on Svalbard [83] and the glaciers retreated again [194, 197]. In the Billefjorden region, the glaciers decreased in extent with 50 – 53.3 % [162].

The end of the LIA is believed to have strongly affected freshwater Arctic diatom communities. Paleolimnological records show relatively stable diatom assemblages during the last millennia [43]. Small shifts in diatom assemblages occurred but are most likely related to limited and/or long-term changes in the environment or the lakes itself. However, unprecedented changes occurred in the 19th century and continue up to now [43, 183, 185]. Paleolimnological records of 55 circumarctic lakes indicate a dramatic shift in species assemblages and ecological organisation since ~ 100 – 150 years ago [143, 185]. Ecological assessment of the observed taxa primarily indicate climate warming, i.e. decline of the ice cover, lengthening of the growing season, increased light availability, augmented nutrient supply and increase of epiphytic habitats associated with hydrological changes, as the driving factors for the observed changes, therefore marking the end of the LIA [148, 185]. In more recent decades, i.e. since AD 1920, anthropogenic induced climate change adds its effects and drove

the diatom communities even further away from their ecological state during the largest part of the Holocene [133, 185]. Other candidates for anthropogenic induced environmental change, such as ozone depletion and changes in lake water chemistry due to input of pollutants influenced the sensitive Arctic diatom communities from apart the second half of the 20th century [185]. This suggests that studying natural High Arctic diatom communities might already be impossible since they recently changed dramatically [143, 185].

Meteorological observations at Spitsbergen show an increase in annual temperature between AD 1912 and AD 1996, with a short cooling AD 1930 – 1960 [72]. The $\delta^{18}\text{O}$ values of ice cores show a similar trend [83]. The overall temperature increase since AD 1912 equals about 1 °C for Longyearbyen (the capital of Svalbard) [61]. However, annual mean temperatures in the beginning of the 21st century are still lower than those in the 1930s [61]. Whilst the total annual precipitation increased with 30 % AD 1912 – 1996 [72], corresponding with an increase of more than 2.5 % per decade, the snow fraction decreased [61]. These recent climate variations are thought to reflect changes in the atmospheric circulation associated with the North Atlantic Oscillation (NAO) with additional effects of sea ice, sea surface temperatures and climate warming [72].

1.4 Objectives

It is generally accepted that the current climate and environmental changes will have their greatest impact in Polar regions. Although diatoms are generally considered to be excellent bio-indicators for a broad array of environmental parameters, the use of diatoms as a proxy for environmental reconstructions in the Arctic region is hampered by the lack of detailed information regarding their occurrence and ecological preferences in this region, mainly due to historic force-fitting, incorrect identifications and the application of a too broad species concept. The main focus of this master thesis is to reduce the taxonomic and ecological uncertainty when applying diatoms as environmental proxies in the Arctic. For this, changes in the freshwater diatom diversity will be investigated on a spatial and a temporal scale.

First, the **actual diversity of freshwater diatoms** will be investigated in different lake types in the region of Petuniabukta on Spitsbergen, the largest island of the Svalbard Archipelago (spatial scale). The observed taxa will be identified following a fine-grained taxonomy using high-quality light and scanning electron microscopy, compared with historical records and their occurrence will be related to measured ecological parameters.

Secondly, an attempt will be made for an **environmental reconstruction** of a lake in the study area by examining the diatom succession in a sediment core of this lake (temporal scale). The environmental reconstruction will be made using recent literature data of the entire Arctic Region. ¹⁴C-dating will allow placing the environmental reconstruction in the correct time frame.

2 Material & Methods

2.1 Study area

2.1.1 Location

The High Arctic archipelago of Svalbard (76°30' – 80°30' N and 10 – 35° E), is the most northern inhabited region of the world. The archipelago, with a total area of almost 63,000 km², consists of the main island Spitsbergen (39,000 km²) together with more than 500 smaller islands of which Barentsøya, Edgeøya, Nordaustlandet and Prins Karls Forland are the most important. Additionally, the archipelago also includes Bjørnøya (74°30' N, 19°01' E) and Hopen Island (76°33' N, 25°07' E) [17]. Svalbard is located on the border between the Barents Sea, the Norwegian Sea and the Arctic Ocean [17, 195]. The west coast is influenced by an arm of the Gulf Stream, the Norwegian Current that, together with the associated cyclonic activity, provides western Svalbard with a milder climate and longer sea ice-free periods than is solely to be expected from its location. The eastern part of the archipelago is on the contrary influenced by cold northern currents. [17]. Glaciers cover about 60 % of Svalbard with the main ice-free areas located in the central and western part of the archipelago and the most extended glaciers in the northeastern part [17].

The present study was conducted in the region of Petuniabukta, Mimerbukta and Adolfbukta (78°40' – 78°44.5'N and 16°26' – 16°40'E) on Spitsbergen (Figure 2). This is the most northern part of Billefjorden, the inner branch of Isfjorden situated in the central part of Spitsbergen [97, 202]. Isfjorden is, together with Wijdefjorden, one of the principal fjords of the island [17]. In the study area, steep mountains with altitudes ranging between 265 and 935 m a.s.l. surround the fjord and a strandflat (a coastal lowland area) occurs along the entire coast line [97]. This strandflat is part of the lowland area that is found almost along the entire west coast of Spitsbergen [17]. Most lakes and almost all plant and animal life are restricted to this area [17]. About ten glaciers are located in Petuniabukta, among which the Nordenskiöld glacier is the biggest and the only tide-water glacier [202]. Pyramiden, a between 1910 and 1998 active Russian mining city, is situated along the western coast of Petuniabukta.

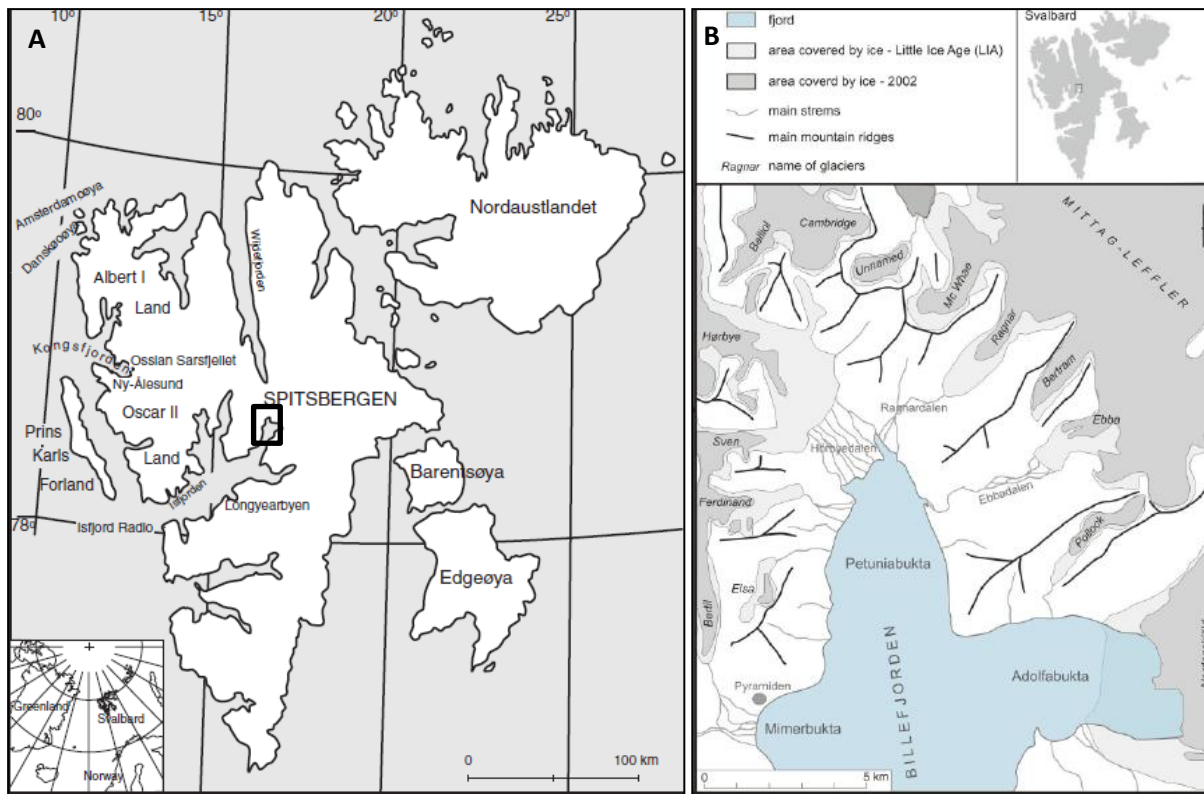


FIGURE 2. A) Svalbard archipelago, Bjørnøya and Hopen Island excluded, with indication of the study area. B) Petuniabukta, Mimerbukta and Adolfabukta. (Left figure taken from Birks *et al.* [17], right figure taken from Tomczyk & Ewertowski [202]).

2.1.2 Climate

The climate of Svalbard is classified as arctic-oceanic [17], but due to the different sea currents that influence the archipelago, a climate shift occurs from humid oceanic conditions in the west to colder and drier areas in the north and east [86]. Petuniabukta is situated in the maritime high Arctic climate zone, which is the climatically mildest part of Svalbard [97]. The annual mean temperature in Isfjord equals $-7.5\text{ }^{\circ}\text{C}$ and July is the warmest month with $5\text{ to }6\text{ }^{\circ}\text{C}$ in average [97]. A detailed analysis of the climate at Petuniabukta in the period 2008 – 2010 is given by Láska *et al.* [112].

The rain season in Spitsbergen lasts for 6 to 8 weeks and the mean annual precipitation equals 400 – 500 mm at the western coast and up to 200 – 300 mm towards the inland areas and the heads of the fjords such as Petuniabukta [17, 86, 162]. Both snow and rain can occur in every month of the year, but the main part of the precipitation falls as snow and the lower temperatures assure low evaporation rates. Snow covers the main part of western Svalbard between early September and the end of May or the beginning of June. The midnight sun is visible between the 21th of April and the 21th of August in Longyearbyen. This increases up to 141 days at 81°N . [17]. Permafrost is widespread in Spitsbergen: in coastal areas it occurs on depths of less than 100 m until more than 500 m deep at higher altitudes. In this way, liquid water stays on top of or nearby the ground surface. [17, 80]. During summer melt, the top layer melts. In Petuniabukta, the thickness of this active layer was found to vary between 30 and 250 cm [65].

2.1.3 Geology

The geology of the study area is strongly related to the north-south facing Billefjorden Fault zone (BFZ) that resulted in a complex unity of rock formations in the region [73, 197]. Four structural entities are present [197] (Figure 3): (1) the oldest consists of Precambrian metamorphic and volcanic rocks originated from the Caledonian Orogeny; (2) the Devonian sedimentary rocks are represented mostly by sandstones and mudstones (only represented on the western side of the BFZ); (3) the third entity dates from the Carbon and Perm and consists of sedimentary rocks such as sandstones, coal, conglomerates, mudstones, gypsum, anhydrites, limestones and dolomites; (4) the youngest structural entity is composed of Quaternary sediments like glacialine muds, sand, gravel, intertidal sediments, glacial and glacialfluvial terrestrial deposits in glacier marginal zones and sedimentary layers on mountain slopes. The main part of these deposits are younger than 10,000 years.

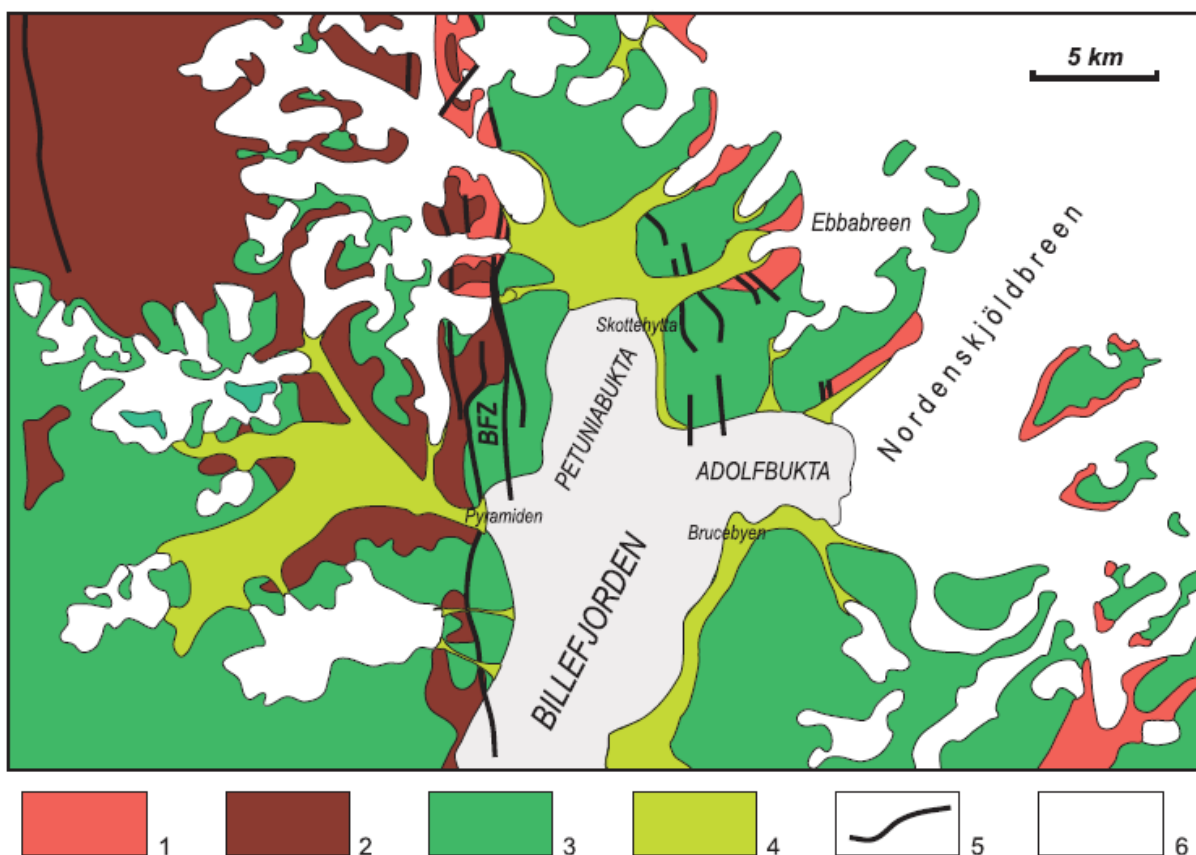


FIGURE 3. Simplified geological representation of Billefjorden according to Dallmann et al. [35]. Legend: 1 – Precambrian rocks; 2 – Devonian sedimentary rocks; 3; Carboniferous-Permian sedimentary rocks; 4 – Quaternary deposits; 5 – important fault zones; 6 – glaciers; BFZ – Billefjorden Fault Zone. Figure taken from Szczuciński & Rachlewicz [197].

During the early Holocene, the entire region rose due to glacio-isostatical uplift. The associated sea level drop amounts for more than 90 m, which led to the formation of several well-developed marine terraces, varying between 1 and 20 m height and mainly composed of sand and gravel, along the coast of Petuniabukta. Similarly, the development of alluvial fans and slope covers of which the

thickness can go up to 10 m could be noted during the Holocene [197]. Since the end of the LIA AD 1890 – 1920 [34, 84, 85, 123, 198], glaciers are retreating with speeds going from a few meters to 50 m per year resulting in the deposition of large quantities of glacial sediments, which give rise to huge lateral and terminal moraines [162, 197]. In these recently deglaciated areas, many small and bigger lakes developed. Except for Nordenskiöld, all glaciers in Petuniabukta end on land [202]. The meltwater of these glaciers is discharged towards the fjord by glacial rivers [197].

2.1.4 Flora & Fauna

Apart from some introduced species, Svalbard is home to 168 native plant species and to at least 373 bryophyte species, 606 lichens, 742 fungi and just over 1100 cyanobacteria and terrestrial, aquatic and marine algae [17, 144]. The vegetation of Svalbard is subdivided in the middle arctic tundra, the northern arctic-tundra and the polar desert zone [17, 157]. The northern arctic tundra zone is the main vegetation zone of western Svalbard, whereas the middle-arctic tundra vegetation is mainly restricted to the ends of the fjords and the polar desert zone is located only in the most northern parts of the archipelago and on altitudes above 100 m [17]. Due to erosion, extreme climatic conditions on exposed sites and recently deglaciated not yet colonised areas, large parts of Petuniabukta are not vegetated [157, 159], but those which are show a rather high diversity [157]. Important genera are *Carex* L., *Dryas* L. and *Silene* L. Some introduced species occur in the vicinity of Pyramiden [117]. Prach *et al.* [158] subdivided the vegetation of Petuniabukta in 5 categories.

The native herbivorous fauna of Svalbard is rather small, compared to other Arctic regions. No musk ox and native hares are found but an endemic subspecies of reindeer (*Rangifer tarandus* L. ssp. *platyrhynchus* Vrolik) occurs [17]. Some terrestrial bird species include the svalbard ptarmigan (*Lagopus mutus* Montin ssp. *hyperboreus* Sundevall) and the pink-footed goose (*Anser brachyrhynchus* Baillon) [17, 192]. The marine bird species are a.o. the little auk (*Alle alle* L.) and the puffin (*Fratercula arctica* L.) [192]. The terrestrial predators are represented by the polar fox (*Alopex lagopus* L.) and birds such as the great skua (*Stercorarius skua* Brünnich) [17, 192]. The top predator on Svalbard is the polar bear (*Ursus maritimus* Phipps) [192]. Wolves, owls, falcons and ravens are absent [17].

2.2 Sampling

2.2.1 Recent material

Recent samples of 39 lakes (for convenience, all water bodies are referred to as 'lakes') on 10 different localities (Figure 4) were taken in the Petuniabukta region between 23/07 and 26/08/2013. Epilithon and/or epipelon and, when mosses were present, epiphyton samples have been collected (Appendix E, Tables E2 and E3). Samples were stored in PVC tubes filled with 96 % ethanol for preservation. Lake water temperature, pH and conductivity were measured using a HANNA Combo pH/EC Tester (Appendix E, Table E4). Logistic constraints such as the absence of freezing equipment prevented the collection/measuring of more environmental parameters. Both GPS locations and altitude a.s.l. were noted (Appendix E, Tables E3 and E4). Additional environmental features such as the presence of bird feathers, guano or marine bivalve shells, the vegetation in and around the lake, the presence of cyanobacterial crusts and the presence of streams flowing in or out of the lake were noted as well (Appendix E, Table E5). Each lake and its surroundings have been photographically documented to allow further analysis of the environment. Three additional samples collected in the summer season of 2011 were analysed as well (Appendix E, Tables E2 and E6). These include the 40th lake on the 11th locality: Pyramiden (Figure 4). The chosen lakes in the study area differed in several characteristics regarding influence of biota (birds, reindeer), vegetation coverage in and around the lake, influence of small streams and surface runoff, age, type, surface area and distance to the sea (Appendix E, Table E4 and E5).

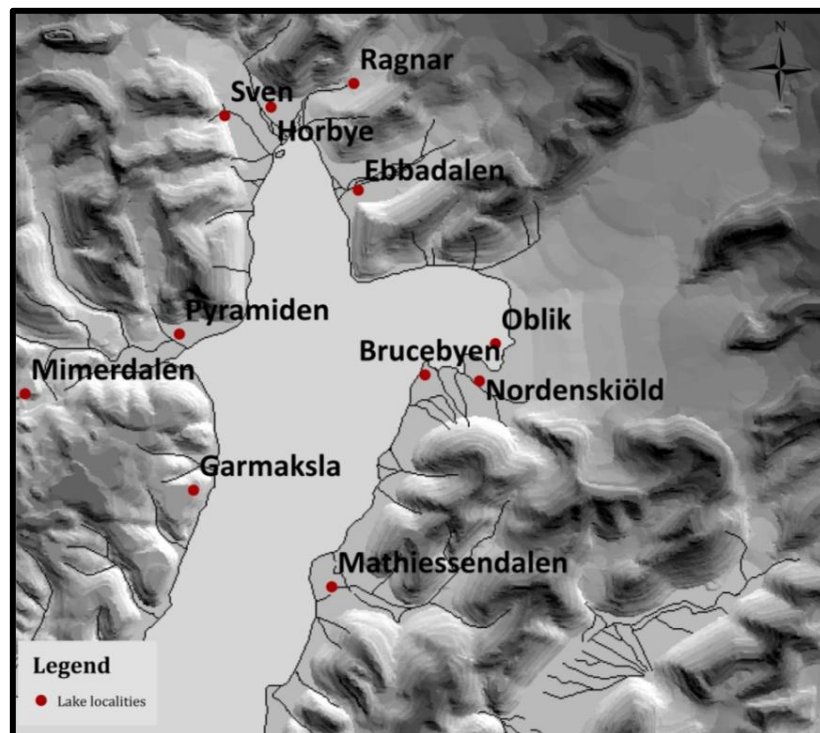


FIGURE 4. Lake localities in Petuniabukta, showing the fjord, the major rivers and mountains.

Basically, almost all lakes in the study area are to some degree related to glacier dynamics (Kavan J. pers. comm.). The lakes of Horbye, Sven and Nordenskiöld are all kettle lakes (Appendix D, Figure D1a) located in the (frontal) moraines of near-by glaciers, whereas the lakes of Ragnar are regarded as proglacial lakes (Appendix D, Figure D1b), dammed by the front moraine of the Ragnar glacier. All these lakes are rather young since they originated after the glaciers retreated since the end of the LIA at the beginning of the 20th century (Kavan J. pers. comm.). The Oblik Peninsula is located on the edge of the Nordenskiöld glacier, is connected with the glacier and is of a very young age (30 – 40 years), having originated after the glacier retreated (Nývlt D. pers. comm.). On this peninsula, several small lakes are located which are all in close vicinity of the sea. Furthermore, a large colony of arctic terns (*Sterna paradisaea*, Pontopiddan) is present on the peninsula. The Oblik lakes are all situated in tectonic faults that later have been eroded and remodeled by glacier erosion (Kavan J. pers. comm.) (Appendix D, Figure D1c). Garmaksla Lake (Figure 5) is believed to have originated after a landslide caused a depression and may be one of the oldest lakes in the study area (Kavan J. pers. comm.). It is located on a mountain, 308 m a.s.l., and can be considered a medium shallow lake with its maximal depth of 5 m. The lakes of Mimerdalen occur in depressions shaped by glacial erosion when the valley was still glaciated (Kavan J. pers. comm.) (Appendix D, Figure D1d). Currently, the dominant factor in the lake formation is snow erosion and accumulation during winter (Kavan J. pers. comm.). Both Garmaksla Lake and the Mimerdalen lakes are high altitude lakes characterised by relative short ice-free periods. The lakes at Brucebyen (Appendix D, Figure D1e) and Ebbadalen (Appendix D, Figure D1f) are located on raised marine terraces in close vicinity to the sea. The Ebbadalen lakes are situated in shallow depressions underlain by peat or mineral soils in permafrost terrain [229]. Since the marine terrace of Ebbadalen slightly slopes towards the sea, many small runoff streams are present during times of high discharge, connecting the lakes in this area [131]. The Mathiessendalen lakes are thought to be rather old marine terrace lakes (Appendix D, Figure D1g) or karst lakes (Appendix D, Figure D1h) (Nývlt D. pers. comm.) and strongly differ from each other in influence of biota, streams and the sea. The Pyramiden site is an artificial pond build in the second half of the 19th century for the water supply of the city of Pyramiden. Except for Garmaksla Lake, all lakes are situated on Quaternary deposits, either on strandflats or on glacial moraines. The bedrock of Garmaksla Lake, on the contrary, is composed of carbonate-rich dolomites and limestones. All lakes in the study area however experience to some extent influence of these carbonate-rich bedrocks since it is the main geological formation in the area [35, 197]. This could explain the overall alkaline pH of the surface waters in the area (input of base cations from the catchment) and suggests that most lakes also exhibit rather high concentrations of Ca²⁺ and Mg²⁺ [19].

2.2.2 Sediment core

Coring attempts during the summer season of 2012 revealed lack of sufficient sediment in almost all but one lake in the Petuniabukta area. Therefore, Garmaksla Lake (78° 36' 16.0" N and 16° 20' 14.7" E) was chosen to take a sediment core. Moreover, this lake is ideal for an environmental reconstruction of the region as it is estimated to be one of the oldest lakes in the study area and because of its isolated location on a high altitude, minimizing potential human influence. After a first attempt, 3 cores were retrieved from the sediment of Garmaksla Lake (Figure 5) on the 27th of July 2013 using an extended Kajak corer (UWITEC) handled from a small boat. The 3 cores had a length of 0.79 m, 0.66 m and 0.72 m. After compression, their lengths equaled 0.74 m, 0.63 m and 0.70 m respectively. To estimate the original position of the samples taken from the compressed cores, the original depth was recalculated using compression factors. In all figures and discussion the original depths are used. The longest core was chosen as the master core for all analyses. The other 2 cores will only be analysed for some geochemical data. Due to the liquid characteristics of the sediment, the cores were subsampled in the field after overview and detailed pictures were taken. Striking characteristics, such as the lamination of the cores, were noted. The sediment cores were subsampled in slides of 1 cm and the sediment was stored in black plastic bags and later stored in a cool way to prevent degradation.



FIGURE 5. Garmaksla Lake with indication (black arrow) of the estimated locations of the sediment cores (left) and detail of the first sediment core, i.e. the master core (right). Pictures taken by Kateřina Kopalová.

2.3 Sample preparation

2.3.1 Recent material

Diatom samples for LM observation were prepared following the method described in Van der Werff [213]. Small parts of the samples were cleaned by adding 37 % H₂O₂. Samples were subsequently heated to 80 °C during about 1 hour. Distilled water was frequently added to prevent the samples for boiling dry. The reaction was completed by addition of KMnO₄. The thereby formed black deposition was removed by adding small quantities of diluted HCl and H₂O₂. The possible present Fe³⁺ and chalk were removed by adding HCl (37 %). After centrifugation (3 times 10 minutes at 3700 x g) and subsequently dilution with distilled water to avoid excessive diatom valve concentrations on the slides, the cleaned solution was stored in 20 mL PVC bottles. Microscopic slides were made by adding 3 droplets of the cleaned solution on a cover slip covered with a thin layer of distilled water, dried subsequently at 40 °C until all water was vaporised and mounted in Naphrax[®].

Stubs were prepared for SEM analysis. Therefore, drops of the oxidised suspensions were filtered through polycarbonate membrane filters with a pore diameter of 1 µm. These filters were air-dried and subsequently fixed on aluminium stubs. The stubs were sputter-coated with a Gold-Palladium layer of 20 nm. All the samples, slides and stubs were stored in the Botanic Garden Meise.

2.3.2 Sediment core

All subsamples of the sediment core were dried in a stove at 50 °C during 24 h. The dried sediment was weighted and subsequently prepared as described in section 2.3.1. Prior to the centrifugation of the samples, *Lycopodium* spore tablets (Batch No. 483216, Department of Geology, Quaternary Sciences, Sölvegatan 12, SE-223 62 Lund, Sweden) were added together with hydrochloric acid to dissolve the chalk in the tablets. Before adding the tablets, the diatom density in the samples was estimated using LM. When few diatoms were present, 10 tablets were added whereas when many diatoms were present, 20 tablets were added. Addition of these tablets makes it possible to estimate the amount of diatoms in the original sample, which is an indication of diatom productivity. Subsequently, the samples were centrifuged (3 times 10 minutes at 3700 x g). Slide preparation followed the method as described in section 2.3.1. Whenever very low numbers of valves were present, 5 to 7 droplets of the cleaned solution were added to the cover slip to optimise the number of diatom valves on a slide.

2.4 Microscopic analysis

The microscopic slides were analysed using an Olympus BX51 microscope, equipped with Differential Interference Contrast (Nomarski) and the Colorview I Soft Imaging System. In every sample, 400 diatom valves were enumerated to obtain a representative idea of the species richness and

composition. In the sediment core, all layers were analysed in the top 20 cm of the core. Below 20 cm depth, 2 layers in every 3 were counted. Thirteen out of 16 samples in the lower part of the sediment core did not contain sufficient diatoms for counting and less than 400 (between 11 and 250, depending on the productivity) diatom valves were therefore identified in these samples (Appendix E, Table E7). After counting, slides were scanned to find rare taxa, not observed during the counts. Together with the diatom valves, chrysophyte cysts were counted (but not identified) to assess the chrysophyte/diatom ratio. During the analysis of the sediment core samples, the previously added *Lycopodium* spores were counted as well. Due to the fossil material in the sediment core, a considerable part of the diatom valves are fragmented. Frequently, fragmented valves were encountered in the recent samples as well. To get a representative idea of the data, it is however recommended to count the fragmented valves, since it might be a particular species that is mostly encountered as fragments [13]. To prevent one valve of being counted double, fragments were only counted when they fulfilled the following criteria [13]: (1) Raphid diatoms were only counted when the central area was entirely or almost entirely present, and (2) Araphid and centric diatoms were only counted when more than half of the valve was present.

For SEM, the stubs were studied in a ZEISS ULTRA SEM microscope at 3 kV at the National History Museum, London, UK and in the JEOL at the Botanic Garden Meise. Detailed photographs were taken to facilitate species identification. Books and articles used for species identification are listed in Appendix A. Additionally, examination of the type material of several taxa allowed confirming the identifications.

2.5 Radiocarbon dating

Two samples of plant macroremains (0.34 and 0.77 m depth) were chosen for preliminary dating of the core using ^{14}C -dating. Analysis was performed by the Poznan Radiocarbon Laboratory in Poland. The results were calibrated using the IntCal13 calibration dataset [164]. Based on the results, additional samples for various radiometric dating techniques, i.e. ^{14}C -, ^{210}Pb - and/or ^{137}Cs dating, will be chosen in the future. In respect of this master thesis, only the 2 first dates have been obtained however.

2.6 Data analysis

2.6.1 Recent material

The mean Chao2 richness estimator [22] and the incidence-based species richness estimator ICE [23] were calculated using the EstimateS program (version 9.0) [29]. These estimators allow assessing to which degree the investigated samples represent the diatom flora of the study area. The Shannon-

Wiener diversity index (ln-based) and Hill's evenness index were calculated in the statistical package MVSP 3.2 (Multivariate Statistical Package – Kovach Computer Services, 1993).

The different samples were assigned to several major diatom assemblages using 2 different techniques: cluster analysis and ordination. A cluster analysis based on Minimum Variance Strategy and with Squared Euclidian Distance as dissimilarity index was performed in MVSP 3.2. To assess the appropriate ordination model for the ordination, i.e. a linear (Principal Component Analysis, PCA) or unimodal (Correspondance Analysis, CA) model, a DCA (Detrended Correspondence Analysis) was first run in CANOCO (version 4.5) [199]. The total gradient length was larger than 2 SD, indicating a unimodal relationship between the parameters and species abundance data. Since the CA results however showed a clear arch effect, detrending was necessary and a DCA was run. Rare taxa were downweighted. The DCA results showed 3 outliers. These were removed from the dataset and the DCA was subsequently repeated. For all analysis, a square root transformation was performed. All statistical techniques used in this study are described in detail by Jongman *et al.* [88].

2.6.2 Sediment core

The diatom stratigraphy in the sediment core was visualised using Tilia 2.0.b.4. [68]. Therefore, only those taxa that reached an abundance of more than 1 % in at least one sample were retained. Stratigraphically constrained cluster analysis (CONISS) [67] on the entire data set in Tilia 2.0.b.4 was used to divide the diatom stratigraphy in several zones of which the significance was assessed by the broken stick model [10] in the rioja package [89] for R [161]. To visualise the clusters defined by the CONISS analysis, a PCA was run in CANOCO (version 4.5) since the total gradient length of the DCA was smaller than 2 SD, suggesting a linear model. Additionally, a DCA was run on the entire dataset (recent and sediment core samples) to assess the position of the sediment core relative to the recent lake samples. Previous to all analysis, a square root transformation was carried out.

The added *Lycopodium* spore tablets allowed estimating the productivity in the different samples as the number of diatom valves per gram dry material (Formula 1): the fewer spores are found on a certain amount of diatoms, the higher the productivity.

$$\text{Productivity} \left(\frac{\text{diatom valves}}{\text{g dry material}} \right) = \frac{\text{counted diatom valves} * \frac{\text{added } Lycopodium \text{ spores}}{\text{counted } Lycopodium \text{ spores}}}{\text{g dry material}} \quad (1)$$

Several diversity indices were calculated. The Shannon-Wiener diversity index (ln-based) and Hill's evenness index were computed in the statistical package MVSP 3.2 and the taxon turnover along the sediment core was calculated using Cody's β -diversity index [28].

3 Results

The results of the data analysis are subdivided into 2 separate sections: the recent material and the sediment core of Garmaksla Lake. The term 'taxon' is used to refer to the different diatom entities rather than 'species', since subspecies (ssp.), varieties (var.) and formas (f.) were also considered as taxa. In some cases additional abbreviations are used to indicate possible uncertainties concerning the identifications: 'aff.' (*affinis*: it bears some similarity to this taxon, but it is not conspecific) and 'cf.' (*confer*: it could be this taxon, but it is questionable). Other used abbreviations are 's.l.' (*sensu lato*: in a broad sense) and 's.s.' (*sensu stricto*: in a narrow sense).

3.1 Recent material

3.1.1 Taxon composition analysis

A total of 74 samples were examined of which 69 were used in the analysis (Appendix E, Table E2). 5 samples did not contain sufficient diatom valves for counting and were therefore removed from the data set (Appendix E, Table E2). A total of 315 taxa belonging to 58 genera were observed during the counts (total number of counted valves = 27,600) (Appendix F, Table F1). A full list of all diatom taxa can be found in Appendix B (Table B1) and Appendix C (Figures C1 – C14). Of these, 234 taxa were identified upon species, subspecies, variety or forma level. The identification of another 20 taxa is uncertain (indicated with 'cf.', 'aff.' or 'group'). Sixty taxa could only be identified up to the genus level and the identity of one taxon is at present entirely unknown (referred to as 'unidentified diatom'). Taxa identified upon genus level only, were referred to by their genus name followed by 'sp' and, in those genera that contained more than one unidentified taxon, a number.

The species richness estimators indicate the theoretically present number of taxa in the study area to amount to 382 (CHAO) or 377 (ICE). Therefore, the sampling effort scored 82 % (CHAO2) or 84 % (ICE) of all present taxa. The species accumulation curve is given in Figure 6. The taxon richness per sample (i.e. in the counts) varied between 8 and 60 taxa with a median value of 31 (Figure 7). The most taxon rich genera are *Nitzschia* Hassall (44 taxa), *Navicula* Bory de Saint-Vincent (31 taxa), *Encyonema* Kützing (18 taxa), *Stauroneis* Ehrenberg (17 taxa), *Pinnularia* Ehrenberg (16 taxa), *Cymbopleura* (Krammer) Krammer (15 taxa) and *Psammothidium* Bukhtiyarova & Round (13 taxa). Based on abundances, the following genera are the most important: *Nitzschia* (19.1 % of all counted valves), *Achnantheidium* Kützing (15.8 %), *Denticula* Kützing (6.8 %), *Navicula* (6.8 %) and *Rossithidium* Bukhtiyarova & Round (6.6 %) (Figure 8). The 11 most common genera together represent 79 % of all counted valves, but the remaining 47 genera determine more than 50 % of the diversity (Figure 8). Some genera, e.g., *Achnantheidium*, *Denticula*, *Rossithidium* and *Diatoma* Bory de Saint-Vincent highly contribute to the total number of valves but represent a low diversity indicating that a few taxa are

dominating (Figure 8). The most common taxa were *Achnanthydium* sp1 (15.4 %), *Rossethodium petersenii* (Hustedt) Aboal (6.5 %), *Diatoma tenuis* Agardh (5.7 %), *Nitzschia perminuta* (Grunow) Peragallo group 2 (4.1 %) and *Denticula tenuis* Kützing (3.8 %) (Table 2). *Achnanthydium* sp1 is the only taxon that was observed in all samples. The twelve most common taxa represented 50 % of all counted diatom valves and, on the other hand, the 100 least counted taxa (almost one third of all taxa) together accounted for only 1 % of all counted diatom valves. Forty-four taxa were never encountered during the counts, but were only found during scanning the slides for extra taxa.

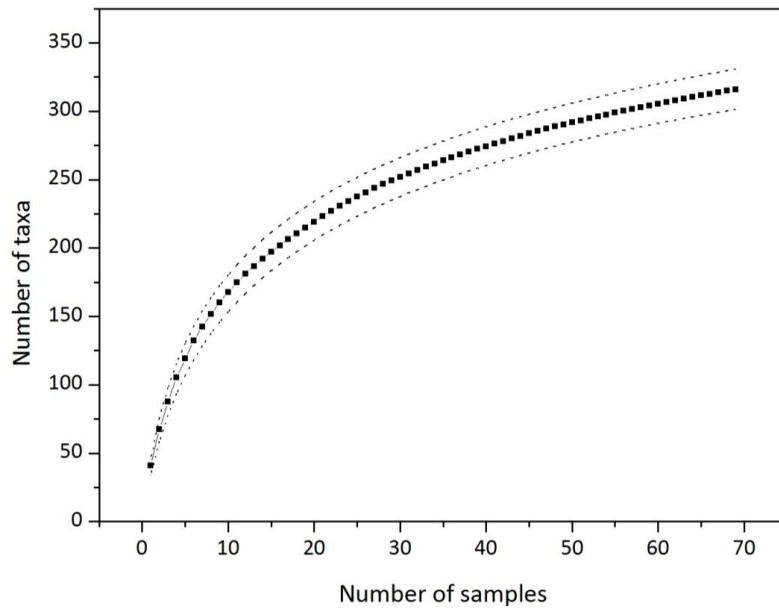


FIGURE 6. Species accumulation curve for the recent lake data with indication of the error margin.

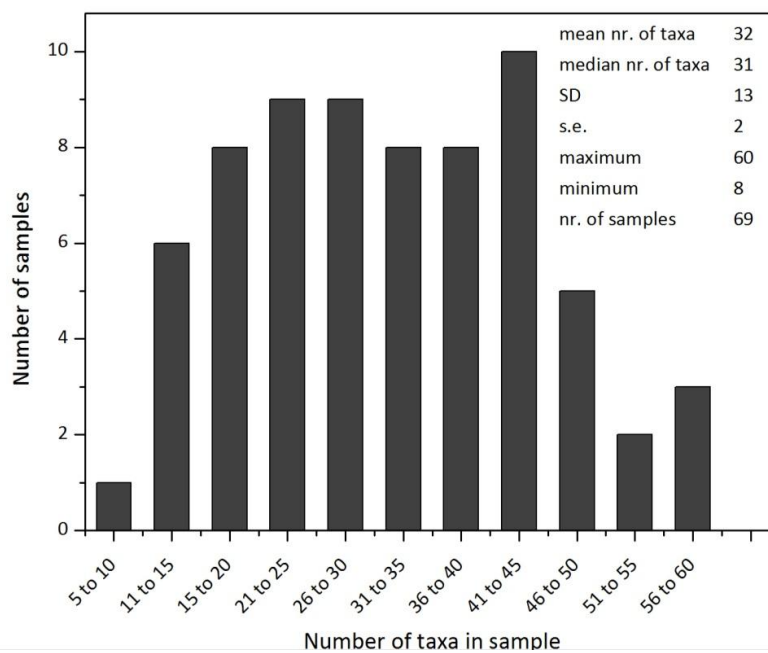


FIGURE 7. Distribution of the taxon richness per sample for the recent lake data. Only the taxa observed during the counts are taken into account. Legend: SD = standard deviation, s.e. = standard error

After thorough taxonomic analysis, at least 10 of the unidentified taxa can be considered new to science (Appendix B, Table B1: underlined taxa). It is however clear that near-future planned, more detailed analysis of the material using high resolution SEM microscopy and after consulting renowned taxonomic specialists for certain genera (e.g., *Navicula* and *Psammothidium*), more new taxa will need a formal description. One of the new taxa has already been described in the journal *Phytotaxa* during the course of this thesis: *Gomphonema svalbardense* Pinseel, Kopalová & Van de Vijver [153]. The publication of this taxon is included in Appendix G. Moreover, 9 other taxa, belonging to the genera *Achnanthydium*, *Cymbella* Agardh, *Cymbopleura* and *Encyonopsis* Krammer, will be described in the near future. The 3 new *Achnanthydium* taxa will be described in collaboration with several foreign scientists specialised in this particular genus (i.e. Dr. Paul Hamilton, Canadian Museum of Nature, and Dr. Ingrid Jüttner, National Museum of Wales), and all new cymbelloid taxa (*Cymbella*, *Cymbopleura* and *Encyonema*) will be the subject of one profound publication (Pinseel *et al.*, unpublished results).

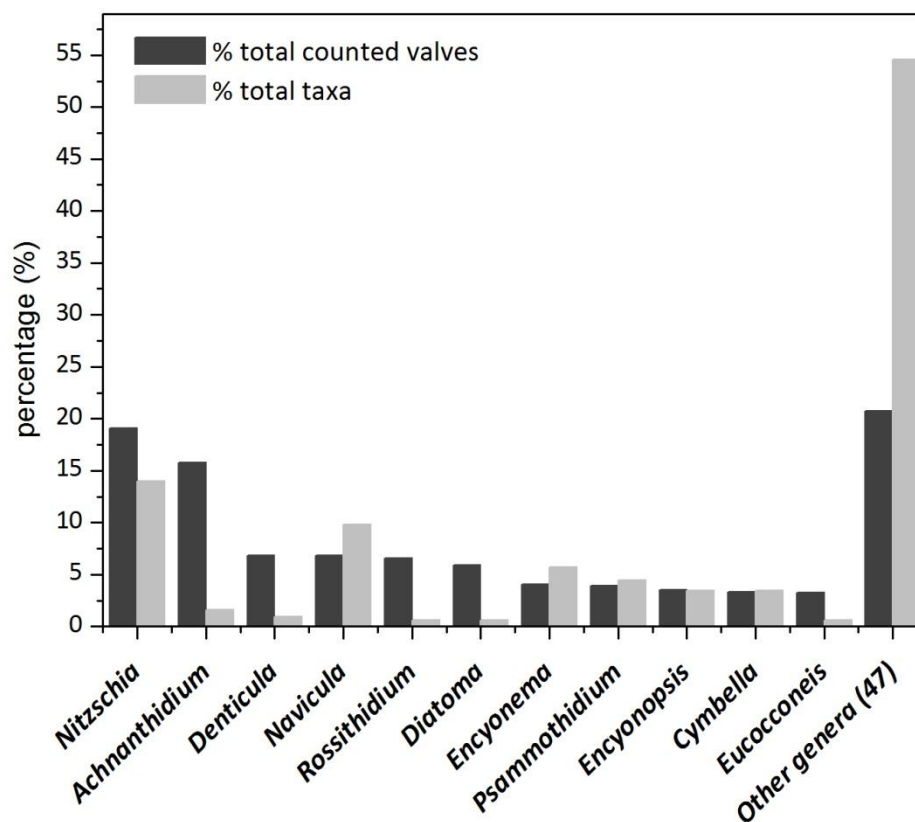


FIGURE 8. The relative abundance and the percentage of the total taxa for the most common genera of the recent lake data.

TABLE 2. Number of counted valves and relative abundances for the 20 most common taxa of the recent lake data.

Taxon	Total counted valves	% total counted valves
<i>Achnanthydium</i> sp1	4240	15.4
<i>Rossethidyum petersenii</i>	1788	6.5
<i>Diatoma tenuis</i>	1569	5.7
<i>Nitzschia perminuta</i> group 2	1123	4.1
<i>Denticula tenuis</i>	1051	3.8
<i>Denticula kuetingii</i> incl. var. <i>rumrichae</i>	788	2.9
<i>Nitzschia perminuta</i> group 1	642	2.3
<i>Nitzschia soratensis</i>	599	2.2
<i>Encyonopsis</i> sp5	489	1.8
<i>Cymbella botellus</i>	478	1.7
<i>Eucoconeis laevis</i> incl. var. <i>austriaca</i>	458	1.7
<i>Eucoconeis flexella</i>	443	1.6
<i>Nitzschia perminuta</i> group 4	429	1.6
<i>Psammothidium</i> sp1	428	1.6
<i>Nitzschia perminuta</i> group 3	427	1.5
<i>Encyonema minutum</i>	425	1.5
<i>Nitzschia perminuta</i> group 6	402	1.5
<i>Caloneis tenuis</i>	380	1.4
<i>Encyonema fagedii</i>	372	1.3
<i>Staurisirella</i> aff. <i>lapponica</i>	369	1.3
Other taxa	10700	38.8

3.1.2 Community analysis

Based on the cluster analysis and the DCA ordination, it was possible to divide the samples into 4 groups (Figures 9 and 10). The DCA explained 11.7 % and 5.7 % of the species variation on the first and second axis respectively and an additional 7.9 % was explained by the third and fourth axes together. These low values are typical for noisy data sets with a high number of zero values [193]. The detailed results of the DCA analysis are given in Appendix E (Table E8). Three samples were removed from the DCA since they were outliers (Appendix E, Table E2). Table 3 and Appendix D (Figures D2 and D3) give an overview of the most abundant taxa of the 4 assemblages and Appendix D (Figures D4 and D5) gives an overview of the distribution of several genera in the 4 assemblages. The percentages given in the following sections always indicate the average abundances.

The first assemblage (group A.1) is located on the right of the DCA diagram (black triangles) and is entirely composed of lakes on the Oblik Peninsula. In the cluster diagram, all samples of this locality are grouped together. The Oblik Peninsula lakes were characterised by a relatively young age (30 – 40 years), high glacial influence of the Nordenskiöld glacier, the presence of a colony of arctic terns and a possible influence of sea spray due to the short distances between the lakes and the sea. The

most important genera in this assemblage, in terms of abundances, were *Nitzschia* (44.8 %), *Navicula* (13.3 %), *Encyonema* (12.9 %) and *Achnanthydium* (10.6 %) (Appendix D, Figure D4). The most taxa rich genera were *Navicula* (16 taxa) and *Nitzschia* (11 taxa). The dominant taxa were *Nitzschia perminuta* group 2 (14.6 %) and group 1 (12.3 %), *Achnanthydium* sp1 (10.6 %), *Navicula* cf. *cryptocephala* Kützing (5.7 %), *Encyonema minutum* (Hilse) Mann (5.2 %) and *Encyonema fagedii* Krammer (4.8 %) (Table 3 & Appendix D, Figure D2). This assemblage will be referred to as the '*Nitzschia perminuta* assemblage'.

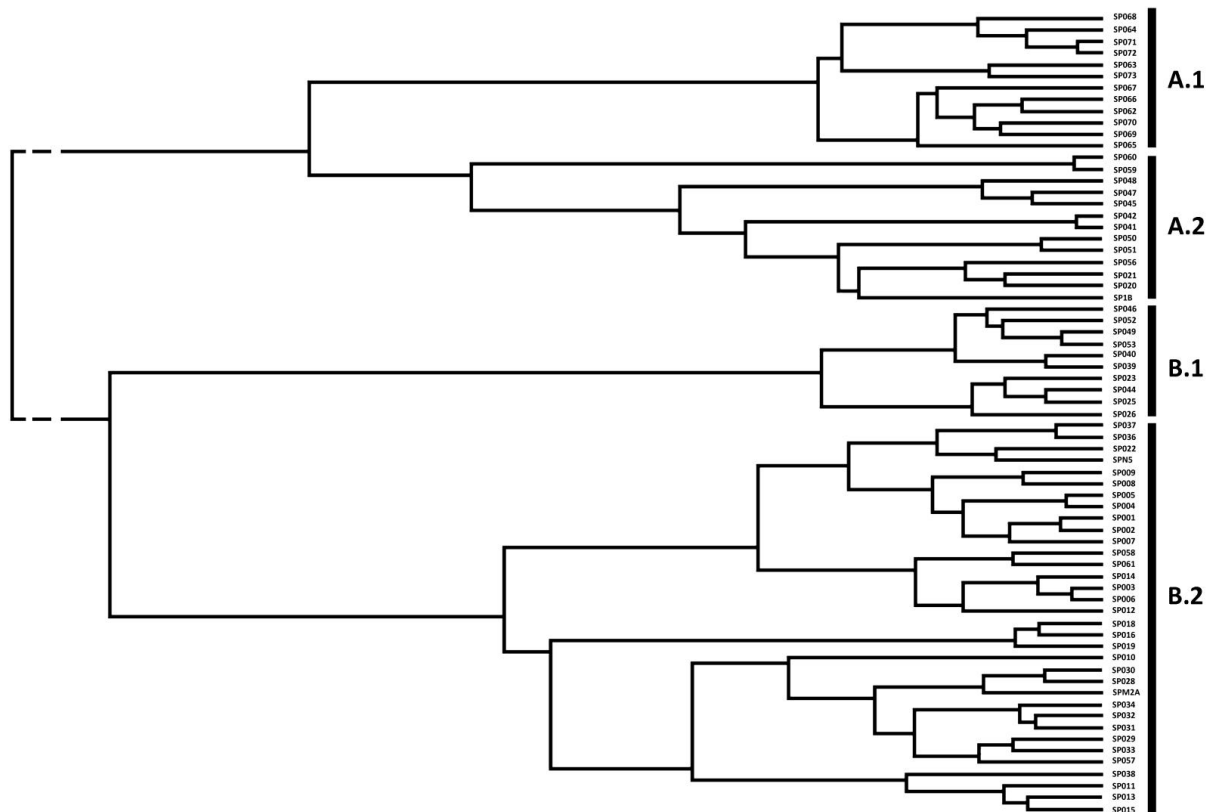


FIGURE 9. Cluster diagram of the recent lake samples. The 3 samples indicated as outliers in the DCA are shown, i.e. samples SP059 and SP060 in group A.2 and sample SP010 in group B.2. A bigger version of this graph is given in Appendix D (Figure D6).

The middle lower half of the ordination diagram is occupied by the second assemblage (group A.2) (green diamonds). Samples of several kettle lakes of the Horbye and Nordenskiöld localities, the proglacial lakes at Ragnar, the artificial lake at the deserted city of Pyramiden and a moss sample of one of the Mimerdalen lakes are located in this assemblage. Most samples in this assemblage are epilithon samples. Characteristic for most of these lakes is a clear water column combined with a sandy or stony substrate and limited to non-existing moss coverage. In none of these lakes, in- or outflowing streams were observed. The most abundant genera were *Psammothidium* (13.8 %), *Navicula* (12.4 %), *Achnanthydium* (8.9%), *Encyonopsis* (7.4 %) and *Eucoconeis* (Kützing) Meister (7.4 %) (Appendix D, Figure D4). The most diverse genera were *Nitzschia* (28 taxa), *Navicula* (18 taxa), *Pinnularia* (11 taxa) and *Psammothidium* (10 taxa). This assemblage was dominated by

Achnanthydium sp1 (8.3 %), *Encyonopsis* sp5 (7.0 %), *Psammothidium* sp1 (6.4 %) and *Eucoconeis flexella* (Kützing) Cleve (5.2 %) (Table 3 & Appendix D, Figure D2). Several taxa dominate in some samples, e.g., *Encyonopsis* sp5 and *E. flexella*, but are almost absent in others. The most striking characteristic of this assemblage is the overall presence of different *Psammothidium* taxa and therefore the second assemblage will be referred to as the ‘*Psammothidium* assemblage’.

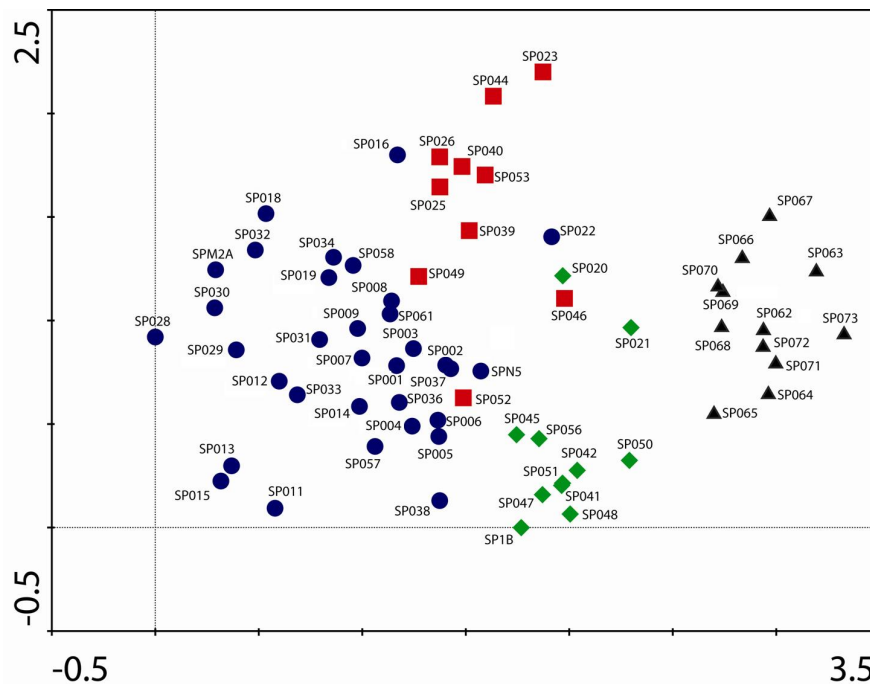


FIGURE 10. Detrended correspondence analysis (DCA) showing the position of the recent lake samples plotted on the first 2 axes of the DCA. The 3 outliers were removed. The separation of the different assemblages was based on the cluster analysis in MVSP. Black triangles = *Nitzschia perminuta* assemblage (group A.1), green diamonds = *Psammothidium* assemblage (group A.2), red squares = *Diatoma tenuis* assemblage (group B.1) and blue dots = *Denticula* – *Rosithidium* assemblage (group B.2). The explanation of the sample numbers is given in Appendix E (Table E2). A bigger version of this graph is given in Appendix D (Figure D7). A DCA biplot with indication of the most important taxa is given in Appendix D (Figure D8).

The third assemblage (group B.1) is situated in the middle upper half of the DCA diagram (red squares). Most samples in this assemblage are epilithon samples. Again, lakes of very different localities are represented: several kettle lakes nearby the Nordenskiöld, Horbye and Sven glaciers, the proglacial lakes at Ragnar glacier and a marine terrace lake at Mathiessendalen. Most lakes are characterised by a distinct current due to in- or outflowing streams or with environmental characteristics indicating the presence of temporary streams. The dominant genera were *Diatoma* (33.6 %), *Achnanthydium* (27.7 %), *Encyonopsis* (8.7 %) and *Nitzschia* (5.7 %) (Appendix D, Figure D4). *Nitzschia* (16 taxa), *Navicula* (13 taxa), *Psammothidium* (10 taxa) and *Encyonema* (8 taxa) were the most diverse genera. The most important taxa in terms of abundances were *Diatoma tenuis* (33.4 %), *Achnanthydium* sp1 (27.7 %) and *Encyonopsis subminuta* Krammer & Reichardt (5.4 %) (Table 3 & Appendix D, Figures D2 and D3). Based on its overall dominance, this assemblage is named the ‘*Diatoma tenuis* assemblage’.

TABLE 3. Summary of the main taxa in the different assemblages according to the cluster analysis. The symbols indicate for each assemblage the mean overall abundance of the taxa. Legend: ■ = > 5%, • = 2.5 – 5%, ○ = 1.5 – 2.5%, + = 0.5 – 1.5%.

	Group A.1	Group A.2	Group B.1	Group B.2
Number of samples	12	11	10	33
<i>Achnanthydium</i> sp1	■	■	■	■
<i>Nitzschia perminuta</i> group 1	■			
<i>Navicula</i> cf. <i>cryptocephala</i>	■			
<i>Encyonema minutum</i>	■			+
<i>Nitzschia perminuta</i> group 2	■	•	+	○
<i>Adlafia minuscula</i>	•			
<i>Encyonema silesiacum</i>	•			
<i>Nitzschia palea</i>	•	+		
<i>Navicula cincta</i>	•		+	
<i>Nitzschia linearis</i> var. <i>subtilis</i>	•	+	+	
<i>Encyonema fogedii</i>	•	+	+	+
<i>Psammothidium</i> sp1	+	■	+	
<i>Eucoconeis flexella</i>		■		○
<i>Encyonopsis</i> sp5		■	•	+
<i>Nitzschia perminuta</i> group 4	○	•		+
<i>Mayamaea</i> cf. <i>aliena</i>	+	•		
<i>Navicula bjoernoeyaensis</i>		•		
<i>Navicula pseudotenelloides</i>		•		
<i>Psammothidium marginulatum</i>		•		
<i>Nitzschia perminuta</i> group 6	+	•	+	○
<i>Nitzschia modesta</i>		•		+
<i>Encyonopsis subminuta</i>			■	
<i>Diatoma tenue</i>		+	■	○
<i>Eucoconeis laevis</i> incl. var. <i>austriaca</i>	+	○	•	+
<i>Rossithidium petersenii</i>	○	+	•	■
<i>Denticula kuetzingii</i> incl. var. <i>rumrichae</i>				■
<i>Denticula tenue</i>		○		■
<i>Caloneis tenue</i>		+		•
<i>Cymbella botellus</i>				•
<i>Staurosirella</i> aff. <i>lapponica</i>				•
<i>Nitzschia sorratensis</i>				•
<i>Nitzschia perminuta</i> group 3	○	○	+	○
<i>Navicula</i> sp5		○	+	+
<i>Gomphonema micropus</i>			○	
<i>Chamaepinnularia gandrupii</i>	+			
<i>Kobayasiella</i> sp	+	+		+
<i>Nitzschia liebethuthii</i>	+	+	+	+
<i>Nitzschia lacuum</i>		+	+	
<i>Cymbopleura angustata</i> var. <i>spitsbergensis</i>			+	+

The very left of the ordination diagram is occupied by the fourth assemblage (group B.2) (blue dots) and is composed of a mixture of samples of different localities, i.e. Garmaksla Lake, 2 of the Mimerdalen high altitude lakes, several of the kettle lakes of Sven and Nordenskiöld, the marine terrace lakes of Brucebyen and Ebbadalen and the karst lakes of Mathiessendalen. Most moss and several epilithon and epipelon samples are located in this assemblage. Several of these lakes are characterised by a moderate to extensive moss coverage on the lake's shores and, in case of Ebbadalen, also in the lake itself combined with an exuberant cyanobacterial mat. *Achnanthydium* (17.2 %) was the dominating genus in this assemblage in terms of abundances (Appendix D, Figure D4). Other important genera included *Nitzschia* (14.5 %), *Denticula* (12.7 %) and *Rossithidium* (11.2 %). Based on taxon diversity *Nitzschia* (32 taxa), *Cymbopleura* (14 taxa), *Encyonema* (13 taxa), *Psammothidium* (11 taxa), *Pinnularia* (11 taxa), *Caloneis* Cleve (11 taxa) and *Cymbella* (11 taxa) were the most important genera. Dominant taxa were *Achnanthydium* sp1 (17.0 %), *Rossithidium petersenii* (11.1 %), *Denticula tenuis* (7.1 %) and *Denticula kuetzingii* Grunow incl. var. *rumrichae* Krammer (5.6 %) (Table 3 & Appendix D, Figure D2). Based on their dominance, this assemblage will be named the '*Rossithidium-Denticula* assemblage'. Several other taxa such as *Cymbella botellus* (Lagerstedt) Schmidt, *Caloneis tenuis* (Gregory) Krammer and *Staurisirella* aff. *lapponica* (Grunow) Williams & Round, are almost restricted to this assemblage (Appendix D, Figure D2).

The previous paragraph showed that clear differences in dominant genera and taxa exist between the 4 assemblages. In this light, it is important to note that not all taxa/genera are equally abundant/present in nature resulting in some taxa/genera to have a higher probability to occur somewhere (in high abundances) just because they are generally more common. No correction was carried out to revise this and therefore assessing the less abundant genera is crucial when one wants to understand between assemblage differences. Using this idea, distinct dissimilarities between the different assemblages can be seen (Appendix D, Figures D4 and D5). The genera *Epithemia* Kützing, *Eunotia* Ehrenberg, *Hygropetra* Krammer & Lange-Bertalot, *Delicata* Krammer, *Staurisirella* Williams & Round, *Meridion* Agardh and *Brachysira* Kützing are (almost) entirely restricted to group B.2. *Adlafia* Moser, Lange-Bertalot & Metzeltin, *Chamaepinnularia* Lange-Bertalot & Krammer, *Craticula* Grunow and *Hantzschia* Grunow seem tightly associated with group A.1. Group B.1 is characterised by *Hannaea* Patrick and the genera *Muelleria* (Frenguelli) Frenguelli and *Stauroneis* seem most abundant in group A.2. On the other hand, some similarities between the different assemblages are striking. Groups A.2, B.1 and B.2 all show relatively higher abundances of *Cymbopleura* and *Amphora* Ehrenberg whereas these genera are largely absent in group A.1 and groups A.2 and B.2 both display relatively high occurrences of *Caloneis* when compared to the other groups. *Pinnularia* is less important in group B.1 than the other assemblages. The genera *Mayamaea* Lange-Bertalot and

Surirella Turpin are important in groups A.1 and A.2. The presence of several *Navicula* taxa typical for brackish to marine conditions (0.1 – 2.7 % of all counted valves) in group A.1 is striking.

Separation of the assemblages based on the collected environmental information proved to be difficult. Table 4 provides an overview of the median, minimal and maximal values of several biotic and abiotic parameters of the localities for the different assemblages. In most cases, the overlap between the different assemblages is high and the overall large standard deviations and standard errors (data not shown) point towards the difficulty to separate the assemblages based on these parameters. However, some issues can be noticed. Group A.1 seems to be associated with a slightly more alkaline pH compared to the other assemblages. Its mean number of taxa is similar to that of group B.1 and clearly lower than those of group A.2 and B.2. Group B.1 has both the lowest Shannon-Wiener diversity index and Hill's evenness index and is associated with the highest conductivity. The chrysophyte to diatom ratio seems somewhat lower in group B.1 compared to the other assemblages.

TABLE 4. Range (minimum and maximum) and median (between brackets) of several biotic and abiotic parameters given for each assemblage.

	Group A.1	Group A.2	Group B.1	Group B.2
Number of samples	12	11	10	33
Number of taxa	12 – 35 (23)	14 – 60 (40)	8 – 39 (24)	17 – 59 (39)
Shannon-Wiener index	1.72 – 2.89 (2.44)	1.92 – 3.42 (3.10)	0.58 – 2.90 (1.87)	1.32 – 3.41 (2.67)
Hill's evenness index	0.67 – 0.84 (0.78)	0.73 – 0.88 (0.80)	0.21 – 0.79 (0.62)	0.45 – 0.85 (0.73)
pH	8.7 – 10.9 (9.4)	8.2 – 8.7 (8.5)	7.4 – 9.2 (8.5)	8.1 – 8.9 (8.5)
Conductivity (µS/cm)	133 – 592 (300)	182 – 1948 (281)	180 – 1948 (428)	149 – 1222 (234)
Temperature (°C)	7.4 – 9.7 (8.5)	8.3 – 12.2 (8.7)	3.2 – 12.7 (8.2)	7.4 – 10.6 (8.5)
Altitude (m)	7 – 28 (20)	24 – 300 (71)	5 – 106 (52)	4 – 308 (62)
Distance to sea (m)	19 – 117 (46)	611 – 8820 (2690)	434 – 4990 (2540)	131 – 9470 (633)
Chrysophyte/diatom ratio	0.01 – 0.14 (0.04)	0.02 – 0.50 (0.04)	0.003 – 0.15 (0.01)	0 – 0.41 (0.03)

Three samples were removed from the DCA since they were considered outliers (Appendix E, Table E2). Two of these samples were from the same locality; a high-altitude lake known for its distinct changes in water level during the course of the year. The dominant taxa in these samples were *Humidophila perpusilla* (Grunow) Lowe *et al.* (39.9 %), *Humidophila paracontenta* (Lange-Bertalot & Werum) Lowe *et al.* (37.8 %) and *Gomphonema nathorstii* Foged (7.5 %). The third outlier was the top of the trial sediment core of Garmaksla Lake, dominated by *Staurosira venter* (Ehrenberg) Grunow (16.8 %), *Achanthidium* sp2 (15.0 %), *Amphora affinis* Kützing (13.0 %) and *Nitzschia fonticola* (Grunow) Grunow (10.5 %).

3.2 Paleolimnological analysis

3.2.1 Radiocarbon dating

The results of the ^{14}C -dating are summarised in Table 5.

TABLE 5. Results of the ^{14}C -dating of the master core of Garmaksla Lake. The calibrated ages (cal. yr. BP, i.e. BP = years before present; the year 1950) are given with 2 sigma errors (95 % probability that the real age lies in this interval).

Sample	Profile	Depth (cm)	Laboratory number	^{14}C yr. BP (± 1 sigma)	cal. yr. BP (± 2 sigma)		Dating method
GAR_32	G 2013/1	34.2	Poz-61448	2725 \pm 30	2816 \pm 55	2761-2871	AMS Poznań
GAR_72	G 2013/1	76.9	Poz-61450	4805 \pm 35	5536 \pm 66	5470-5602	AMS Poznań

3.2.2 General taxon composition

A total of 18,481 diatom valves were counted in 56 samples (Appendix F, Table F2). This resulted in the identification of 59 different taxa representing 29 genera (Appendix B, Table B2). Of these, 4 taxa and 1 genus were not observed in the recent lake samples (Appendix B, Table B2). The taxa richness per sample varied between 4 and 29 taxa with a median value of 14. The genera *Staurosira* (59.9 %), *Amphora* (19.2 %), *Achnantheidium* (5.9 %), *Cymbella* (3.8 %) and *Denticula* (3.5 %) dominated the samples in number of counted valves. The most diverse genera were *Nitzschia* (6 taxa), *Encyonopsis* (5 taxa) and *Encyonema* (5 taxa). The most common species were *Staurosira venter* (59.7 %), *Amphora affinis* (19.2 %), *Achnantheidium* sp2 (4.2 %) and *Cymbella* sp1 (3.7 %). *Amphora affinis* was observed in all samples and *Staurosira* sp was identified in all but one sample. These 2 taxa together accounted for 79 % of all counted valves. The 17 least counted taxa represented only 1 % all counted valves. 6 taxa were never encountered during the counts, but were only found during the scanning of the slides for extra present taxa.

Distinguishing *S. venter* from other, closely related, taxa using LM has been proven difficult due to the small valve size, the limited number of in LM discernable morphological characters and the considerable intraspecific morphological variation [147]. Confusion with *Staurosirella pinnata* (Ehrenberg) Williams & Round, a wide-spread taxon in the circumpolar Arctic, is especially common [4, 147]. Therefore, SEM was applied on selected samples of the sediment core to assess the identity of my specimens since both taxa can easily be separated based on the morphology of their areolae (chambered pores in the valve), i.e. elliptical for *S. venter* and lineolate for *S. pinnata* [4, 147]. Since all in SEM observed specimens showed elliptical areolae, assigning my specimens to *S. venter* is entirely justified.

3.2.3 Diatom stratigraphy

A CONISS cluster analysis allowed to distinguish 5 major zones in the sediment core (Zones A – E, Figure 11). A broken stick analysis suggested however the presence of 12 significant zones. Based on these results, there are arguments to subdivide zones A, B and E in 5, 3 and 2 subzones respectively. However, most samples in the lower part of zone B and the entire zone A did not contain sufficient diatom valves for analysis and therefore less than 400, varying between 11 and 250, diatom valves were enumerated in these particular samples. This increases the level of uncertainty concerning the derived species abundance data, in particular in those samples in which a very limited amount of diatom valves were counted (between 11 and 50). Thus, whenever valves of rare taxa were observed in these samples, their relative abundances are largely exaggerated resulting in distinct but apparent differences between different (subsequent) samples. This presumably explains the high number of significant zones in the lower part of the sediment core. Most of these zones are therefore not accepted in this study. The 2 lower zones in zone B are taken together and treated as a transition zone between zones A and B. Only 2 subzones are accepted in zone A and subzone A.1 represents the single lowest sample of the core since a distinct shift in the diatom assemblage to zone A.2 occurs in this sample and a total of 200 valves have been counted, making this observation reliable enough to separate this zone from the others.

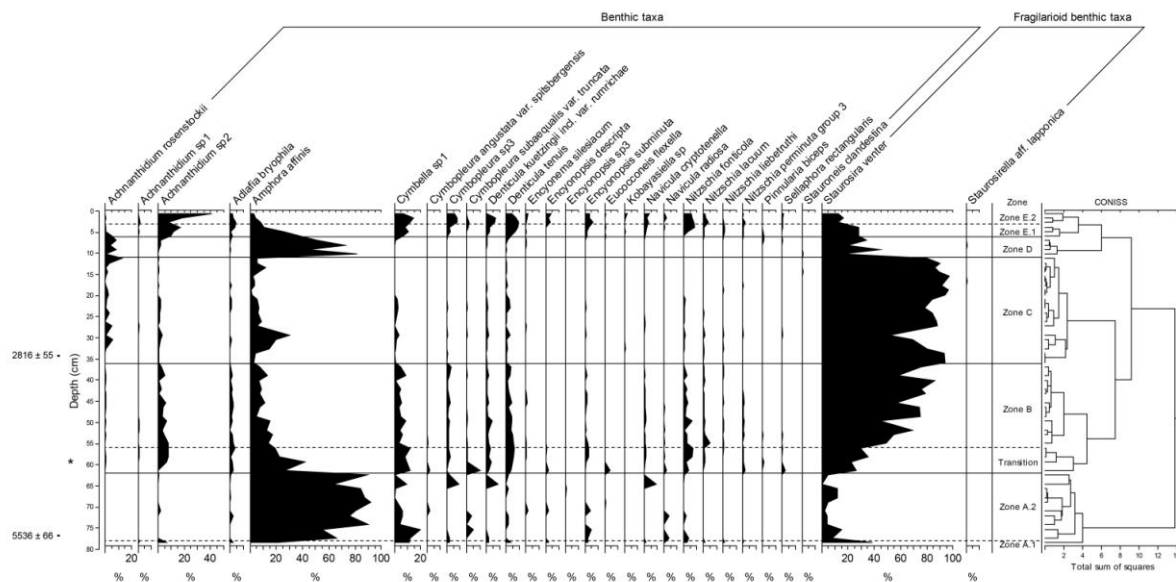


FIGURE 11. Diatom stratigraphy of the Garmaksla sediment core. The X-axis indicates the percentage of the total counted diatom valves. The zonation is based on the CONISS constrained cluster analysis and the broken stick significance test. In the layers below the asterisk (*) less than 400 diatom valves were counted in all samples except one (i.e. 67.8 cm depth). A bigger version of this graph is found in Appendix D (Figure D9). The scale bar of the X-axis is identical for all graphs. The indicated ages are expressed in 'cal. yr BP'.

The PCA explained 47.3 % and 26.5 % of the species variation on the first and second axis respectively and an additional 17.4 % was explained by the third and fourth axes together. Detailed results of the PCA analysis are given in Appendix E (Table E8). Figure 12 shows the results of the ordination with indication of the different zones as distinguished by the constrained cluster analysis. It is clear that distinct differences within the diatom stratigraphy exist since most zones do not overlap on the PCA biplot. Representation of the first PCA axis with respect to the core depth shows clear shifts in the diatom communities throughout the core (Figure 13). The PCA results on the combined dataset of the recent lakes and the sediment core showed that the entire sediment core can be considered an outlier relative to the recent lake samples indicating that the diatom assemblage in the sediment core never closely resembled those of the recent lake samples throughout the history of the core. The following paragraphs give a short overview of the different subsequent zones. The thereby given percentages indicate in all cases the average abundances of the taxa in a certain zone.

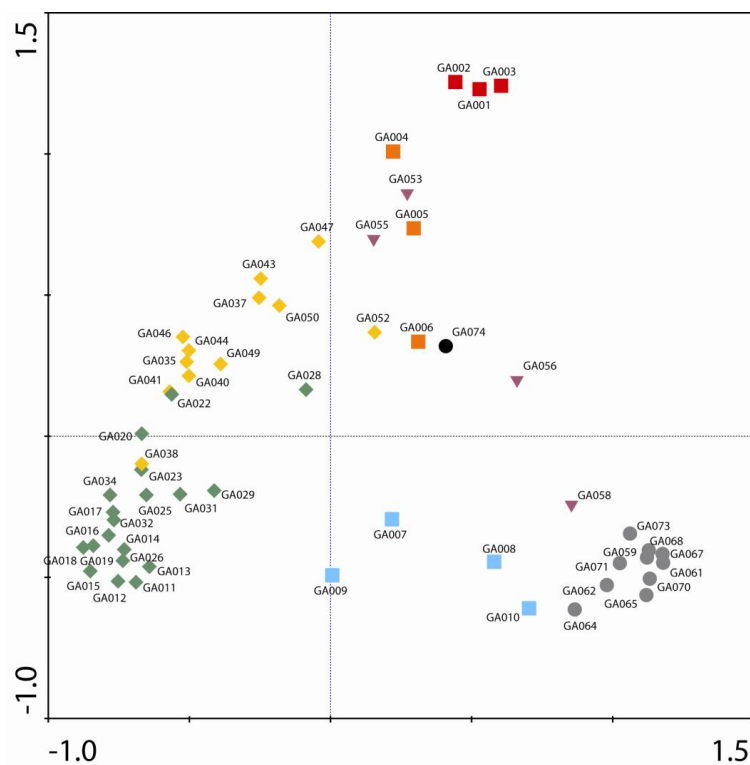


FIGURE 12. Principal Component Analysis (PCA) of the sediment core samples plotted on the first 2 axes of the PCA. The separation of the different groups is based on the CONISS constrained cluster analysis. Black = zone A.1, Grey = zone A.2, Purple = transition zone, yellow = zone B, green = zone C, blue = zone D, orange = zone E.1, red = zone E.2. Explanation of the sample numbers is given in Appendix E (Table E7). A bigger version of this graph is given in the Appendix D (Figure D10).

Zone A: 79 to 62 cm.

Based on the broken stick analysis, the lowest zone is divided in 2 subzones, A.1 and A.2 of which subzone A.1 only represents one sample. The latter is characterised by high abundances of *Stausira venter* (38.0 %), *Amphora affinis* (21.0 %) and *Achnantheidium* sp2 (6.5 %). When compared to subzone A.1, subzone A.2 shows a distinct rise in the abundance of *A. affinis* (78.4 %) accompanied by a drop in the abundance of *S. venter* (6.6 %). *Cymbella* sp1 (6.0 %) becomes less important towards the upper parts of this zone. The number of taxa for zone A.2 varies between 4 and 8 with a median value of 5. In zone A.1, 20 taxa were observed. However, as previously indicated, most samples in this part of the core are very diatom poor and therefore less than 400 diatom valves were enumerated making the derived relative abundances of the diatom taxa, the conclusions drawn from them and the total number of observed taxa uncertain (when more diatom valves are counted, more taxa can logically be observed). Moreover, most valves showed indications of severe weathering and were in most cases highly fragmented. Therefore, the possibility exists that disproportional weathering of valves of different taxa could have resulted in the valves of some taxa to be more fragmented, or even entirely disappeared, than others. Hence, the diatom abundances shown in this lower part of the core need to be handled with care. These remarks equally apply for the lowest part (> 59.2 cm depth) of the transition zone.

Transition zone: 62 to 56 cm.

This zone represents a transitional phase between zones A and B. Throughout the entire zone, a gradual drop in the abundance of *A. affinis* and an accompanied rise in the abundance of *S. venter* are observed. In all other regards, the abundances of the other taxa are similar to zone B (see further). Fourteen to 25 taxa are present with a median value of 20.

Zone B: 56 to 36 cm.

Throughout this entire zone, a gradual increase in the abundance of *S. venter* is observed, with a mean overall abundance of 66.2 %. *A. affinis* (10.4 %) reaches distinct lower abundances when compared to the previous zones, except zone A.1. Several other taxa become more abundant since the transition zone and reach rather moderate abundances in zone B, e.g., *Cymbella* sp1 (5.0 %), *Achnantheidium* sp2 (4.0 %), *Denticula tenuis* (3.4 %), *Nitzschia fonticola* (2.2 %), *Cymbopleura* sp3 (1.5 %) and *Denticula kuetzingii* incl. var. *rumrichae* (1.4 %). Between 7 and 19 taxa, with a median value of 9 are present in this zone.

Zone C: 36 to 11 cm.

In this zone, *S. venter* clearly is the most dominant taxon with a mean abundance of 85.5 %. The abundances of *A. affinis* remain low, compared to the previous zones, with an average abundance of only 7.6 %. Figure 11 shows a recovery of *A. affinis* whenever the abundance of *S. venter* drops and vice versa. Of all other taxa present in this zone, only *Achnantheidium rosenstockii* Lange-Bertalot reaches an average abundance higher than 1 %. The number of taxa in the samples varies between 7 and 19 with a median value of 11.

Zone D: 11 to 6 cm.

A sudden and dramatic shift occurs between zones C and D with a distinct drop of *S. venter* (28.5 %) and a parallel increase of *A. affinis* (62.1 %). Most other taxa are almost absent in this layer with exception of *A. rosenstockii* (5.1 %). Between 8 and 16 taxa, with a median value of 11 are present in this zone.

Zone E: 6 to 0 cm.

The transition of zone D to E is accompanied by a sudden decline of *A. affinis* parallel to the still ongoing decline of *S. venter*. The top layers of the sediment core are among the most diverse of the entire core with a total of 40 different taxa. The most important taxa are *S. venter* (20.8 %), *Achnantheidium* sp2 (17.5 %) and *A. affinis* (14.6 %). Other taxa with relatively high abundances are *Cymbella* sp1 (9.8 %), *D. tenuis* (6.8 %), *N. fonticola* (5.3 %), *Cymbopleura* sp3 (4.3 %), *D. kuetzingii* incl. var. *rumrichae* (3.2 %), *Encyonopsis subminuta* (3.2 %), *Navicula cryptotenella* Lange-Bertalot (2.2 %), *Adlafia bryophila* (J.B.Petersen) Moser, Lange-Bertalot & Metzeltin (2.2 %), *Encyonopsis descripta* (Hustedt) Krammer (1.8 %) and *Nitzschia lacuum* Lange-Bertalot (1.5 %). Two subzones can be distinguished within zone E. The top zone (E.2, 3 to 0 cm) has higher abundances of *Achnantheidium* sp2 and lower abundances of *A. affinis* and *S. venter* than the other subzone (E.1, 6 to 3 cm). The average abundances of all other previously listed taxa are lower in zone E.1 compared to zone E.2 and *A. rosenstockii* becomes distinctly less important in zone E.2. The number of taxa in the layers of zone A.1 varies between 21 and 25 with a median value of 23, whilst zone A.2 shows 21 to 29 taxa with a median value of 25.

3.2.4 Productivity & Diversity

The overall diatom productivity in the sediment core is low. Around 5 cm depth an abrupt and dramatic increase in diatom productivity is observed. The Shannon-Wiener diversity, Hill's evenness and Cody's β -diversity indices overall show the same trends with the lowest values in zone A.2 and the highest in zone E.1 (Figure 13). The Cody's β -diversity index also shows some distinct peaks in zones B and C. As previously noted, the observed low diversity in the lower part of the core is (at least partially) attributed to the fact that less than 400 diatom valves were enumerated. The ratio of

chrysophytes to diatoms is nearly constant and low throughout the sediment core, with exception of some of the lower samples that show higher ratios (Figure 13). However, almost no chrysophyte cysts were observed and therefore no reliable conclusions can be drawn. As no detailed dating has been obtained by now, these results have to be treated with caution since correction for differences in sediment accumulation rates was impossible.

3.2.5 Lithology

Since all 3 cores were directly subsampled in the field, due to the fluid nature of the sediment, only a limited lithology, based on the field observations, of the cores is known (Figure 13). All 3 cores show homogeneous dark sediment in the upper layers. Deeper in all cores, finely laminated sediment with alternations of darker and lighter coloured regions is observed. The transition between the layers is approximately located on 6.5 cm depth for the master core and on 6 cm depth for both other cores. The overall appearance of the varved sediments seems rather organic. The deeper parts of all cores are characterised by dark, possibly more clayey, homogeneous sediment without visible layers. The transition from laminated to homogeneous sediment is observed on 0.40 m, 0.47 m and 0.38 m depth for the first (i.e. the master core), second and third core respectively.

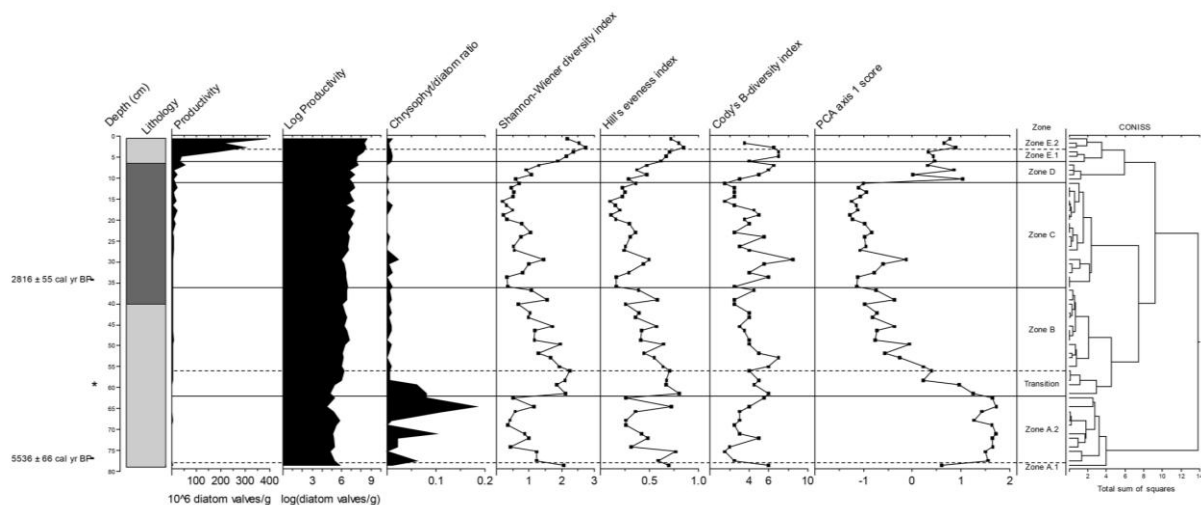


FIGURE 13. Lithology (light gray zones = homogeneous sediment, dark gray zone = varved sediment), productivity, chrysophyte/diatom ratio, Shannon-Wiener diversity index, Hill's evenness index, Cody's β -diversity index and the score of the first PCA axis as a function of the depth of the sediment core (master core). In the layers below the asterisk (*) less than 400 diatom valves were counted in all samples except one (i.e. 67.8 cm depth). A bigger version of this graph is found in Appendix D (Figure D11). A more detailed graph of the logarithm of the productivity is given in Appendix D (Figure D12).

4 Discussion

4.1 Recent material

4.1.1 Diatom diversity

The number of taxa found in this study is rather high compared to other studies of the diatom flora of Spitsbergen (Table 1). Only Foged [53] listed more taxa, but he studied distinctly more samples (209 versus 69 in this study) and covered a much larger part of Spitsbergen. Additionally to freshwater samples, Foged [53] also examined samples of humid soils and terrestrial mosses, habitat types that haven't been investigated in the present study. Since the environmental conditions in these habitats differ distinctly from those in freshwater ecosystems, other taxa are to be expected, partly contributing to the higher taxa number in Foged's study. This makes the current study the second largest diatom investigation on Spitsbergen ever, and the first to look to an area in such a detail since Foged's samples were scattered over many different localities. Comparison of this study with previous studies of the entire Svalbard Archipelago (Table 1) shows that, again, the number of taxa in this study is rather high. Only Metzeltin & Witkowski [132] list more taxa on Bjørnøya. They however also included marine littoral samples and their lake samples were scattered over a much larger area than those in this study. The main reason for the high diversity in this study is the application of a different species concept. Several authors of diatom studies on Svalbard [e.g., 87, 152, 209] applied a broad species concept instead of the currently emphasised much narrower species concept [125] and therefore lumped together many taxa that have been separated in the present study, such as the former *Cymbella microcephala* Grunow-complex.

A large amount of taxa were only identified up to the genus level (60) and the identification of 20 taxa is still uncertain. The identify of one taxon is entirely unknown. Moreover, several of these unidentified taxa are with certainty new to science. This is however not exceptional for studies in the Arctic region. For example, in 2008 Antoniadou *et al.* [4] also reported a large number of unidentified taxa from the Canadian Arctic which led to the description of 7 new taxa [5] and 4 new combinations [4]. Undersampling of many regions in the Arctic and the use of the current narrow species concept [125] can be cited as the main reasons for this observation. For example, in previous decades, several *Achnantheidium* species resembling *Achnantheidium minutissimum* (Kützing) Czarnecki were assigned to this taxon as *Achnantheidium* s.l. It was often referred to as the 'most common diatom in the world' [78]. However, recent evidence based on detailed LM and SEM showed that *A. minutissimum* s.l. actually represents a species complex of several tens of different species and consequently many taxa have been recently splitted from this complex [207]. One of the newly discovered *Achnantheidium* species (*Achnantheidium* sp1) in this study was formerly reported from the Arctic as *A.*

minutissimum [4], but detailed morphological comparison with the type material of *A. minutissimum* s.s. [139] and intensive contact with one of the authors of 'Diatoms of North America' [4] (i.e. Dr. Paul Hamilton) resulted in the conclusion that describing my specimens as a new species is entirely justified (Pinseel *et al.* unpublished results).

Taxa belonging to the genus *Nitzschia*, the most abundant and taxon rich genus in this study, proved to be rather difficult to identify. This is mainly the result of taxonomic difficulties within this genus, which is currently home to more than 1000 species names, both accepted and unaccepted, and an additional few hundred unchecked varieties and formas [63, 203]. The size of this genus and the limited number of in LM discernable morphological characteristics suitable for species identification make taxon delimitation in this group rather problematic resulting in an unstable taxonomy [203]. Krammer & Lange-Bertalot [102] distinguished a broad array of formas within *N. perminuta* s.l. and, additionally, problems with several designated lectotypes increase the vague character of this taxon, which is presumably a complex of many different species (Van de Vijver B. pers. comm.). To distinguish between morphologically different forms, several groups have been assigned of which 6 are thought to belong to *N. perminuta* s.l.. Antoniadou *et al.* [4] faced similar issues and also assigned several *Nitzschia* specimens to different self-defined groups within *N. perminuta* s.l.

In general, the diatom flora of this study shows a close similarity with those of several other Arctic studies [e.g., 4, 14, 209, 212, 215, 216]. However, comparison with most studies, excluding Antoniadou *et al.* [4], is difficult due to the taxonomic problems related to the different applied species concepts. Moreover, the authors of several recent studies in Spitsbergen [e.g. 87, 122] mainly based their species identifications on Krammer and Lange-Bertalot 1986 – 1991 [101-104], the freshwater diatom guide for Europe that applied a broad species concept making direct comparisons of my results with theirs difficult. Clearly, a revision on the diatom flora of the (High) Arctic is needed to improve both our fundamental knowledge concerning diatom diversity and biogeography but also to advance future (paleo)ecological research in the Arctic. Therefore large sampling campaigns are however needed. With this study, I hope to make a first contribution to this revision in respect to the Svalbard Archipelago.

4.1.2 Freshwater diatom communities

Four different assemblages were distinguished in this study. Separation based on abiotic parameters, such as pH and conductivity, proved to be difficult due to a large overlap in characteristics between the different localities. Clearly, other parameters than those measured in this study must be determining the diatom communities in Petuniabukta. Due to logistic constraints, it was impossible to collect more environmental data. Moreover, measurements were only carried out once for each locality and therefore presumably do not trustworthy reflect the actual physicochemical

characteristics of the water bodies. For example, Komárek *et al.* [97] demonstrated distinct temporal differences throughout the growing season in lake water chemistry (e.g., conductivity and ion concentrations) of the Ebbadalen lakes in Petuniabukta. Marked differences in taxa composition exist though and it is possible to link these dissimilarities with several environmental characteristics of the localities and the microhabitats of the samples using literature information.

The best defined assemblage is formed by all sampled waterbodies of the Oblik Peninsula in front of the Nordenskiöld glacier (group A.1). The most important taxa in this assemblage are *N. perminuta* group 1 and group 2. Since the taxonomic status of these taxa is not clear (see discussion about *N. perminuta*), the ecological preferences are also poorly known. Antoniadou *et al.* [4] argued that the large environmental range of their *N. perminuta* groups suggests very broad ecological preferences or wrong identifications, i.e. a larger taxon diversity than previously thought. Krammer & Lange-Bertalot [102] indicate *N. perminuta* as a cosmopolitan taxon with oligosaprobic preferences. Based on the dominance of these *Nitzschia* taxa in recently formed lakes, we can assume that these particular taxa are early colonisers indicating an early successional state and/or that this *N. perminuta* complex benefits from the supply of minerals, nutrients or sediment particles (e.g., silt) coming from the nearby Nordenskiöld glacier. The Oblik lakes distinctly differ in both characteristics from most other lakes and *N. perminuta* like taxa also reach rather distinct, but mostly lower, abundances in several other lakes, older than the Oblik locality, (e.g., Nordenskiöld, Sven, Ragnar and Garmaksla), adding more strength to both hypothesis. Next to *N. perminuta*, *Encyonema minutum* and *E. fogedii* are rather important in this assemblage. Both are benthic diatoms [4] and *E. minutum* is a typical indicator for oligotrophic water with moderate electrolyte content [4, 98], confirming the moderate conductivity measurements in most samples of this assemblage. Additionally, several taxa in group A.1 indicate the influence of sea spray, which logically follows out of the short distance to the sea. For example, *Navicula gregaria* Donkin, *Navicula phyllepta* Kützing and *Navicula meniscus* Schumann are typical for brackish or even marine conditions [4, 99]. *Navicula slesvicensis* Grunow, *Navicula phylleptosoma* Lange-Bertalot and *Navicula vaneei* Lange-Bertalot are often found in slightly brackish waters such as estuaries and lakes nearby the coast [99]. Several of these taxa (*N. gregaria*, *N. meniscus*) are restricted to this assemblage and the others clearly reach higher abundances compared to the other assemblages. In all cases, the total abundances are however low (0.1 – 1.1 % of all counted valves). A more abundant naviculoid in some samples of this assemblage (2.7 % of all counted valves) is *Navicula cincta* (Ehrenberg) Ralfs, a taxon typical for eutrophic, electrolyte rich to brackish waters [99]. The combined presence of all these taxa clearly indicates some influence of sea spray. This influence is however believed to be rather limited since the abundances of these taxa are low and the measured conductivity is moderate. It cannot be excluded that both *N. perminuta* taxa benefit from sea spray, (partly) explaining their high abundances in this assemblage since sea spray is

(nearly) absent in all other localities. The presence of aerophilic *Mayamaea* taxa in some samples could indicate seasonal lake level changes and high levels of organic matter [111, 137]. Within-assemblage differences could partially be related to differences in nutrient availability. For example, lakes with high abundances of *N. cincta*, an indicator of eutrophy, show low abundances of *E. minutum*, an indicator of oligotrophic conditions. Differences between lakes in the influence of the on the peninsula present arctic tern colony presumably play a role in these observations. In summary, the '*N. perminuta* assemblage' is associated with young lakes characterised by variable nutrient conditions, slight influence of sea spray, an alkaline pH (compare pH in Table 4) and a high glacial influence.

The B.1 group is the least species rich assemblage and is dominated by *Diatoma tenuis*, both in abundance and occurrence, a common cosmopolitan taxon found in several habitats, i.e. epiphyton, plankton and benthos [4, 32] and distributed in fresh to brackish waters [38] with a moderate to high conductivity [4]. It is an indicator for meso-eutrophic conditions and circumneutral to alkaline pH [32]. When comparing the different assemblages, group B.1 indeed seems to be associated with the highest median conductivity of all assemblages, but *D. tenuis* also dominates samples with moderate conductivity. A distinct character of most, but not all, lakes in this assemblage is however the presence of some water current due to incoming or outgoing streams or with environmental signs indicating the presence of temporary streams. This could indicate a preference of *D. tenuis* for a turbulent environment. However, Denys [38] regards the taxon as 'indifferent' in relation to currents and Van de Vijver *et al.* [212] reported a *D. tenuis* dominated assemblage from Nunavut (Canada) in a large lake with standing water. On the other hand, Antoniadou & Douglas [2] did observe *D. tenuis* in rather high abundances in tidally influenced Arctic streams and the taxon is known to reach rather high abundances in Swedish rivers, north of the Arctic circle (Van de Vijver & Jarlman, unpublished results). Moreover, *D. tenuis* is also in need of high oxygen concentrations [38] which can partly be attributed to currents that effectively mix the water column and ensure the constant supply of oxygen. Furthermore, *Hannaea arcus* (Ehrenberg) Patrick is almost restricted to this assemblage and was found in 4 out of 10 samples, in all cases samples taken in lakes with a distinct current. It is a typical taxon for small streams in the Arctic and Alpine region [2, 78]. As *H. arcus*, *Meridion circulare* (Greville) Agardh has often been recorded from the Arctic region, always in association with streams or lakes with incoming streams [e.g., 2, 4, 14, 58, 209]. In this study, *M. circulare* was restricted to some samples of the A.2 and B.2 groups that had been taken from small incoming streams or with lakes which show signs of temporary streams. This taxon was however never encountered in the '*Diatoma tenuis* assemblage', indicating that the presence of streams is not the only determining factor in shaping this assemblage, since not all samples from streams are dominated by *D. tenuis*. Another distinct character of this assemblage is the almost entire absence of epiphyton samples and

all epilithon samples are from lakes with a clear water column and, except for the marine terraces lake at Mathiessendalen, close to and influenced by glaciers. Presumably, the combination of these different factors with addition of possible unknown environmental characteristics, are determining this assemblage. In summary, the '*Diatoma tenuis* assemblage' looks to be principally associated with lakes characterised by currents or the presence of temporary streams, with a clear water column, glacial influence and no or very limited vegetation coverage.

The '*Psammothidium* assemblage' (group A.2) differs from all other assemblages by its (slightly) higher abundances of several *Psammothidium* taxa. All lakes in this assemblage have several common characteristics, i.e. the vegetation coverage is limited or non-existing, the water column is clear and there are no or very limited currents or streams. Most samples of this assemblage are epilithon and epipelon that could partially explain the presence of the freshwater genus *Psammothidium* since it is typically found on sand grains [166]. This assemblage is, compared to groups B.1 and B.2, also characterised by lower abundances of *Achnanthydium* sp1. This observation is however difficult to explain since it concerns a taxon new to science (see previous discussion around *A. minutissimum*) and recent studies indicate distinct ecological variations between different morphological groups within *A. minutissimum* s.l. [156], making ecological comparison with closely related taxa impossible. The presence of *Mayamaea* cf. *aliena* in several samples possibly indicates fluctuating water levels and eutrophic conditions [111, 137]. On the other hand, all samples showed a moderate conductivity, with exception of 2, which may point to more oligo- or mesotrophic conditions in most lakes. The identity of this taxon is however unsure so a reliable conclusion about its presence is difficult to draw. Other taxa vary also highly between samples, e.g., *Eucoconeis flexella* and *Encyonopsis* sp5, which presumably results of differences in microhabitat or other environmental factors. Furthermore, a distinct overlap in localities exists with the '*Diatoma tenuis* assemblage', e.g., all samples of the lakes of Ragnar and Horbye belong to one of these assemblages, suggesting that both assemblages are closely related to each other but differ in some characteristic since *D. tenuis* is almost entirely absent in group A.2. Therefore, the hypothesis is formulated that the presence of distinct streams or currents somehow separates groups A.2 and B.1, since the localities are similar for all other known aspects, and that incoming streams profoundly alter the lake's microhabitat and/or supply the lakes with minerals, nutrients, silt or other sediments that can influence diatom communities. In this light, differences in microhabitat may explain why different samples of the same stream influenced locality cluster separate in group B.1 and A.2.

The '*Denticula-Rossithidium* assemblage' (group B.2) is the biggest and most diverse assemblage in this study. Both prevailing *Denticula* species are benthic taxa typical for a littoral environment [119] and oligo- to mesotrophic conditions [78]. Next to several epilithon samples, most moss samples are located in this assemblage, which explains the findings of several typical moss-inhabiting genera

such as *Denticula*, *Eunotia*, *Epithemia* and *Hygropetra* (Van de Vijver B. pers. comm.). The high abundances of *R. petersenii* are likely to be associated with the vegetation as well since Antoniadou & Douglas [2] found the taxon to be mainly associated with aerophilic moss and minimum flow velocities what might be a reflection of its ability to tolerate periodic desiccation. Striking is the restriction of *Cymbella botellus* to this assemblage. This taxon has a circumarctic distribution and mainly occurs in cold, oligotrophic waters with very low electrolyte content [100]. Apart from this, its ecology is poorly known. In summary, the '*Denticula-Rossithidium* assemblage' is a typical littoral community found in lakes with small annual water level changes, no or limited flow velocities and, apart from a few exceptions, with a moderate to very good moss coverage on the lakes shore and occasionally also in the lake itself. When currents are present, *M. circulare* and/or *H. arcus* are observed.

Two outliers of the DCA analysis represent a distinct diatom assemblage in one of the Mimerdalen high-altitude lakes. This lake is characterised by high water-level fluctuations in the course of the year (Kavan J. pers. comm.) resulting in temporary desiccation of large parts of the lake and explaining the dominance of *Humidophila paracontenta* and *H. perpusilla* since *Humidophila* Lowe *et al.* species are typical for moist subaerial environments [121]. The third outlier represents the top of the trial sediment core taken at Garmaksla Lake. Since a detailed analysis of the sediment core is given in the second part of the discussion, no further description is given in this section. Furthermore, except for a few localities, only a small amount of chrysophyte cysts were observed, indicating that this algal group is, compared to diatoms, clearly less abundant in the sampled habitats in the study area. Finally, within-assemblage differences are presumably related to (small) differences in water chemistry, physicochemical characteristics, bedrock, vegetation type, glacial influence, etc. Differences in the microhabitat of the sampled diatom communities are thought to be extremely important in explaining why several different samples of one lake or lakes of the same locality cluster in different assemblages.

4.2 Paleolimnology of Garmaksla Lake

4.2.1 Radiocarbon dating

The radiocarbon ages obtained from plant macroremains suggest a maximum age of approximately 6000 years for the entire master core. However, caution has to be taken since Garmaksla Lake is sensible to the ^{14}C -reservoir effect, i.e. contamination of the lake's sediment by older carbon residues from the catchment area which dilute the lakes ^{14}C -concentration resulting in older assessed ages than is truly the case [221]. Preliminary dating of bulk sediment of a sediment core of Garmaksla Lake, taken during the 2012 summer season by researchers from the Centre for Polar Ecology, gave results varying between 12.4 and 15.9 ^{14}C ka BP for the entire core. Because of the glacial history of

the study area, combined with the length of the core, these ages are considered too old, as the whole area was covered by ice during this time. The reason for this overestimation is found in the catchment area and the bedrock of Garmaksla Lake, as it is entirely composed of limestone and dolomite [35, 197], i.e. sedimentary rocks rich of CaCO_3 and $\text{CaMg}(\text{CO}_3)_2$ respectively, resulting in contamination of the lake's sediment by older allochthonous carbon. The current radiocarbon dating done on plant macroremains is clearly less susceptible for the ^{14}C -reservoir effect since the obtained ages seem reliable when compared with similar sediment cores of Svalbard. However, the influence of the ^{14}C -reservoir effect cannot be fully excluded and therefore these ages should be considered as maximum ages whereas the sediment might be slightly younger (Nývlt D. pers. comm.). Future dating of the top sediments using ^{210}Pb - and ^{137}Cs , crossdating of ^{210}Pb -/ ^{137}Cs - and ^{14}C -ages to assess the radiocarbon reservoir, or luminescence dating of a new core should allow assessing the extent of the ^{14}C -reservoir effect. At the moment, the core is however interpreted in terms of the current observed ages, which is justified since they seem to occur, when compared with literature data, in the expected time frame.

4.2.2 Comparison with the recent material

Comparison with the recent lake samples covered in the first part of this thesis showed the entire sediment core to be an outlier in the recent lake dataset, indicating that the diatom communities in the sediment core never closely resembled those of the current littoral epilithic and epiphytic communities in the study area. This presumably is an effect of differences in the sampled habitat since the sediment core was taken in the centre of Garmaksla Lake and thus represents a benthic (and possibly partly planktonic) epipelagic diatom community. The observation that recent samples of epilithic and epiphytic diatom communities of Garmaksla Lake have not proven to be outliers strengthens this hypothesis. It was therefore impossible to design transfer functions for environmental variables using the recent lake samples. Only samples of the deepest parts of the other lakes in the study area could have been used, providing that the measured environmental variables would actually determine the sampled diatom communities. Due to logistic constraints, it was however impossible to sample these habitats. The sediment core will therefore be interpreted using the environmental preferences of the dominant taxa as reported in verified literature data. These findings however suggest that Garmaksla Lake never dried out nor developed an intense moss cover on the location of the sediment core since its communities never resembled these characteristic for those types of habitat.

4.2.3 Ecology and taxonomy of selected taxa

One of the most striking characteristics of the sediment core is the alternation of 2 dominant taxa: *Amphora affinis* and *Staurosira venter*. Both taxa have gone through several taxonomic changes in

the last decades and have consequently been reported from the High Arctic region under different names. It is therefore recommended to take a closer look at the taxonomy and ecology of these taxa before the diatom stratigraphy itself is discussed.

The records of *S. venter* in Arctic and sub-Arctic tundra lakes are numerous. It is often found as one of the dominating taxa in sediment cores of lakes together with several other small benthic taxa belonging to the genera *Staurosira*, *Staurosirella* and *Pseudostaurosira* (*Fragilaria* s.l.) [e.g., 4, 24, 47, 48, 70, 87, 95, 107, 122, 146, 170, 178, 185]. All these genera previously belonged to the genus *Fragilaria*, which was split up based on some striking morphological differences [224]. Consequently, *S. venter* has also been reported from the High Arctic as *Fragilaria venter* Ehrenberg, *Fragilaria construens* var. *venter* (Ehrenberg) Grunow and *Staurosira construens* var. *venter* (Ehrenberg) Hamilton. As most other taxa belonging to *Fragilaria* s.l., *S. venter* is a typical indicator for environmental instability, such as changes in trophic status, salinity or climate [37]. Several authors suggested that blooms of small benthic *Fragilaria* s.l. are often associated with lakes in recently deglaciated areas, such as the expected conditions in many Late-Glacial and early Holocene lakes, thus indicating a pioneer role in these unstable environments [37, 74, 130]. Small benthic *Fragilaria* s.l. taxa have demonstrated the ability to take up nutrients from the sediment-water interface [176] and therefore possibly benefit more than other taxa from the release of inorganic nutrients from the bed material, associated with these young lakes [37, 74, 118]. Consequently, these taxa have a competitive advantage in oligotrophic lake environments and in lakes with long periods of ice cover and short growing seasons, i.e. in colder conditions [119, 146, 176]. Moreover, their dominance in these young postglacial lakes indicates a preference for alkaline conditions that typically develop due to the leaching of soluble base cations from recently deglaciated catchment areas rich of calcareous bedrock [20, 146].

Amphora affinis has long been considered a synonym of *Amphora copulata* Kützing but recent investigation of the type material of both taxa revealed that they represent separate species [113]. Additionally, *A. affinis* is commonly been confused with *Amphora libyca* Ehrenberg but recent typification of the original material of *A. libyca* indicated a distinct morphological separation from *A. affinis* [138]. Most records of *A. copulata* and *A. libyca* from the High Arctic can therefore be considered to represent *A. affinis* [113] but not all [e.g. 4]. Since many publications do not include a full list of pictures of the observed diatom taxa, it is difficult to assess which taxon has truly been observed in most studies. Due to these historic taxonomic confusions, the ecology of *A. affinis* is poorly known but it is generally believed to be a typical benthic taxon characteristic for mesotrophic to slightly eutrophic conditions combined with circumneutral to slightly alkaline water [113]. Compared to *S. venter*, *A. affinis* may therefore prefer (slightly) warmer conditions.

4.2.4 Paleolimnology

In High Arctic regions, climate changes are seen as the main drivers for environmental change in lake ecosystems, both through direct and indirect effects [18, 97, 175]. In respect of Garmaksla Lake, possible important indirect influences on the lake's ecosystem involve climate (temperature, precipitation and wind) driven changes in the catchment area influencing hydrology, erosion rate, vegetation coverage, soil development and permafrost. Glacial influence is very limited since no glaciers are nearby and the lake is believed not to receive any glacial meltwater today. Therefore, climate is seen as the major primary driver for the observed changes in the core. Following the previously described ecological preferences, it is possible to identify subsequent periods of cooling and warming. Small changes in the dominance of *A. affinis* and *S. venter* within these periods presumably reflect local to regional environmental changes. Since both *A. affinis* and *S. venter* are indicators for alkaline conditions and the current pH of the lake is still alkaline, a distinct acidification of the lake seems not to have occurred throughout the history of the lake. Based on the obtained ¹⁴C-ages and literature data of other paleoecological studies in the Arctic, an attempt is made to give some general hypothesis concerning the observed climate trends.

Warmer period between 79 and 62 cm depth

The most striking characteristic of this core section is the low productivity. Two main reasons can be put forward. The first is related to bad valve preservation, due to, for example, high alkaline conditions since this would dissolve the valves [64] or severe weathering as a result of high age. Since *A. affinis* is considered a taxon with circumneutral to slightly alkaline pH preference, a (highly) alkaline pH in this by *A. affinis* dominated region cannot be excluded. The second reason for explaining the low productivity involves unfavourable environmental conditions. Since *A. affinis* is believed to prefer slightly warmer and more mesotrophic conditions than *S. venter*, unfavourable conditions for diatom growth seem unlikely, but cannot be excluded. Severe weathering due to high age combined with highly alkalic conditions however seems most likely since most valves were highly fragmented, suggesting that diatom productivity in fact could have been high(er).

Since less than 400 valves were counted in most layers of this zone the derived diatom abundances, and mainly those of the less abundant genera, are not 100 % reliable. Most valves in these layers were extremely fragmented indicating severe weathering. Since more silicified taxa preserve better than less silicified taxa, observed relative proportions alterations due to weathering are possible. No information concerning the amount of silicification of the different taxa is known, but differences that might result in better preserved valves of *A. affinis* compared to other taxa can not be ruled out since *A. affinis* has strongly silicified valves as seen in SEM. Moreover, it is possible that much of the

actual former diversity in this layer has not been observed. Therefore, all derived conclusions concerning this core section always need to be handled with caution.

Assuming *A. affinis* to be the dominant taxon, this part of the core could represent a period of warmer, possibly more mesotrophic conditions compared to the overlying by *S. venter* dominated section of the core (see further). The most likely explanation for this warm period is the Holocene Climatic Optimum. Estimates of the timing and the extent of the Holocene Climatic Optimum on Svalbard differ between different studies, e.g., 9500 – 3500 years ago [173], 8000 – 4000 years ago [15] and Baeten *et al.* [7] and Elverhøi *et al.* [45] dated the end on c. 5470 and 3000 years ago respectively. Based on the current core, the end of the Holocene Climatic Optimum in Petuniabukta appears to be situated around 62 cm, when *S. venter*, an indicator of cold conditions, becomes more important (see next section), i.e. somewhere between 5536 ± 55 and 2816 ± 66 cal. yr. BP. Based on the currently known average sedimentation rate, it is estimated that the Holocene Climatic Optimum ended around 4900 cal. yr BP in the Garmaksla Lake area. This confirms data from the literature.

Colder period between 62 and 11 cm depth

This core section consists of 2 distinct phases: the first between 62 and 36 cm depth, characterised by a relatively high but decreasing diversity and gradually increasing abundances of *S. venter*, the second, between 36 and 11 cm, showing a lower, decreasing diversity and overall high abundances of *S. venter*. The productivity is higher than in the previous section, but still very low. Preservation problems in this core section cannot be ruled out since a distinct, but lower when compared with the deeper layers, number of valves showed clear signs of weathering and fragmentation. It is hypothesised that the increase of *S. venter* points towards a gradual cooling, culminating in a cold and oligotrophic period that reaches its maximum just before 11 cm depth. This possibly may represent the cooling marking the end of the Holocene Climatic Optimum that after a period of several thousand years reached its maximum in the Little Ice Age (LIA), AD (1200) 1600 – 1900, with the coldest periods observed in the late Holocene [83, 123, 198]. Based on the abundances of *S. venter* only, it is impossible to assess the actual starting point of the LIA and no evidence of a Medieval Warm Period is found. Moreover, it is possible that throughout a very cold period, no or only a limited amount of sediment was deposited due to prolonged ice cover, resulting in gaps in the diatom stratigraphy. In the future, more detailed dating, assessment of the sedimentation rates and additional information should allow gaining more insight in the timing of the events in this core section.

The presence of varved sediments from 40 cm depth until 6.5 cm depth, i.e. most of this zone, is striking. As no sedimentological information is known, it is difficult to assess the origin of these varves, but it is hypothesised that they are the result of differences in sedimentation between winter

and summer, i.e. during summer, snow melt runoff transports sediment particles in the lake. Of these, the coarsest will immediately settle on the lake's bottom, creating a summer layer. During winter conditions, when the lake is frozen and the water column is extremely quiet, fine particles, such as clay, are able to sedimentate resulting in a finer and darker winter layer. So-called clastic varves have been observed in several other lakes in Spitsbergen, e.g. Kongressvatnet [70], and may indicate prolonged ice cover and cold conditions [220], adding additional evidence for a cold period in this section of the core. Another explanation for this type of varves is seasonal deposition as a result of primary production during the growing season, alternated with decomposition in winter (Verleyen E., pers. comm.): organic varves [220]. No varves were observed below 40 cm, which may be the result of a turbulent sedimentation environment [85].

Recent environmental changes

The sudden and dramatic drop of *S. venter* at 11 cm depth announces profound changes in the diatom community which may indicate climate warming. The most recent climatic events on Svalbard believed to be able to cause this shift are the end of the LIA around AD 1890 – 1920 [e.g., 34, 84, 85, 123, 198] and, later, human induced climate warming since AD 1920 [143, 185]. In Petuniabukta, evidence of glacial retreat since AD 1900 has been observed [7, 162], indicating that a distinct climate change in the study area did happen in recent times. Moreover, numerous studies of sediment cores from (sub-)Arctic lakes report similar dramatic changes in diatom communities, often characterised by sudden declines of small *Fragilaria* s.l. taxa, approximately ~ 100 – 150 years ago [among others 3, 92, 115, 145, 148, 154, 170, 185] and the most distinct shifts were observed in the regions which have recently warmed the most [185]. Similar to this study, these shifts are often associated with increasing diversity and/or productivity [e.g., 3, 47, 85, 92, 115] and most, but not all [e.g., 154], were unprecedented in the remaining of the investigated cores indicating that the magnitude and speed of the observed changes have almost never been equalled in the previous centuries to even millenia [185]. In most studies, these recent shifts are attributed to the end of the LIA in the Arctic region, AD 1850 [143, 185], or later for Svalbard AD 1890 – 1920 [e.g., 34, 84, 85, 123, 198] and for the most recent layers the superposed effects of human influences since AD 1920 – 1950 [79, 143, 185]. However, this would mean 11 cm depth to correspond with the late 19th (or even a bit earlier, since distinct regional differences in climate change can occur) to early 20th century. Since 34 cm depth is dated at 2816 ± 66 cal yr. BP, suggesting an overall average sediment accumulation rate in the upper part of the core of about 0.012 cm/yr, a marked increase by an order of magnitude (i.e. 0.089 – 0.118 cm/yr in the upper 11 cm) in sediment accumulation rate should have occurred in the upper layers in order to explain this. This however seems possible when comparing with sediment accumulation rates of other sediment cores from Svalbard and the Arctic

as a whole since sedimentation rates often were distinctly lower during the early and mid Holocene, i.e. 0.01 – 0.02 cm/yr, with increasing sedimentation rates in the upper layers [e.g., 47, 48, 85, 107, 155]. Birks *et al.* [18] noted that sediment accumulation rates of lakes in Svalbard for the past century ranged between 0.02 – 0.10 cm/yr and that 150 years ago corresponds with the depth of 8 – 11 cm in most lakes of Southern Spitsbergen, not far from the current study area. Moreover, Holmgren *et al.* [79] even observed sediment accumulation rates ranging between 0.05 and 0.17 cm/yr in the upper layers of lakes in West Spitsbergen. In respect to Garmaksla Lake, a distinct rise in sediment accumulation rates during the past century is likely since the lake is located in a depression, on 2 sides enclosed by steep slopes. Increase of erosion rates in a warming climate inducing glacier, snowfield and permafrost melting, combined with these steep slopes may cause distinct increases in sediment import. Moreover, it needs to be considered that if the core is younger than currently believed, this would result in generally higher sediment accumulation rates than assessed at the moment, making the augmentation even more likely. In summary, the last 11 cm of sediment probably corresponds to the last ~ 100 – 150 years and will, in the remaining of this discussion, be interpreted in this way. Future dating should allow assessing if this interpretation can be maintained or should be rejected, but at the current state of the investigation, it's the most plausible scenario.

The currently observed warming, starting at 11 cm depth, took place in 2 different phases, the first characterised by a dramatic drop of *S. venter*, accompanied increase of *A. affinis*, rising diversity but still generally low productivity. The second phase, starting at 6 cm depth, consists of decreasing importance of *A. affinis* and increasing abundances of several other taxa, accompanied by an assumed dramatic increase in diversity and productivity. The latter may be related to warmer climate conditions and nutrient availability due to enhanced weathering in the catchment area [85]. The first shift is hypothesised to correspond with the initial end of the LIA AD 1890 – 1920 on Svalbard. It can however not be excluded that this shift already occurred earlier as a result of regional climate variation and/or since the late LIA on Svalbard was not extremely cold but rather moist instead [34]. On the other hand, the second warming phase may represent prolonged warming due to the end of the LIA presumably enforced by human impact through the increased greenhouse effect [92, 143] combined with ozone depletion [175] and atmospheric contamination by pollutants and fertilizers from global [11, 79, 83, 165, 175] and local origin, e.g., Longyearbyen and Pyramididen [131] since AD 1920 – 1950. As illustrated by diatom stratigraphies from Western Spitsbergen, 6 cm depth indeed may very well correspond with the beginning to middle 20th century [79]. Many studies argue that the extent of the currently observed diatom shifts can't be solely attributed to atmospheric contamination and therefore are mainly related to climate change [186]. The lack of distinct varves in these upper layers could also indicate rising temperatures and thus a more turbulent depositional environment. Several of the known taxa that increase in abundance in this zone are oligo- to

mesotrophic taxa indicating rather low, but possibly rising nutrient availabilities in Garmaksla Lake compared with the cold period that is dominated by *S. venter*. These nutrients most likely originate from increased erosion in the catchment area since the lake is not frequently visited by birds and no human activity is present in its catchment. Striking is the decline of *Achnantheidium rosenstockii* in the second phase. This taxon is typical for waters with high calcareous content [78]. In the study area, calcium originates from the limestone and dolomite bedrocks [35, 197]. During sample preparation, high chalk contents were observed in several of the intermediate layers but not in the uppermost layers, all together suggesting that the lake water recently became less calcareous. A possible explanation for this observation could be the input of acid precipitation which would react with the calcium, since Svalbard is known to receive low but significant amounts of acid precipitation [114] and recent changes in chrysophyte communities on Svalbard are thought to be associated with acid precipitation [11]. The carbonate rich bedrocks of Garmaksla Lake combined with an augmented input of base cations from the catchment as a result of enhanced weathering in a warming climate can explain the persisting alkaline pH of Garmaksla Lake, even when there is influence of acid rain [18]. Other reasons for the decline of *A. rosenstockii*, such as climate warming or competition, cannot be excluded however. At last, distinct temperature and precipitation fluctuations in the 20th century are known from instrumental records [72] and could explain the variations within the upper 6 cm of the core.

Comparison of the observed recent changes in taxon composition in the current investigated diatom stratigraphy with records of other Arctic lakes reveals some striking differences. Several deep lakes from Svalbard, Baffin Island, Ellesmere Island, northern Fennoscandia and central sub-Arctic Canada show abrupt shifts in the upper layers from typical benthic communities dominated by *Fragilaria* and *Achnanthes* Bory s.l. (i.e. previously a large genus that has been split up in several genera including *Psammothidium*, *Achnantheidium*, *Rossithidium*, *Euccoconeis* and *Planothidium* Round & Bukhtiyarova [e.g. 21, 166]) or by *Aulacoseira* Thwaites species dominated tychoplanktonic communities towards diatom assemblages dominated by planktonic, especially *Cyclotella* (Kützing) Brébisson, *Tabellaria* Ehrenberg and *Asterionella* Hassall, species [e.g., 47, 170, 171, 185, 186, 225]. This widespread shift towards a dominance of planktonic taxa is linked to reduced ice cover combined with a longer growing season and changes in thermal stratification [170, 185]. In several shallow Canadian (sub-)Arctic lakes, shifts occurred to diatom communities dominated by taxa typical for littoral environments and moss substrates, indicating habitat expansion of these taxa due to longer growing seasons resulting from climate warming [185]. With its maximal depth of approximately 5 meters Garmaksla Lake can be considered an intermediate shallow lake, but none of the previously described shifts corresponds with the observed changes in the diatom stratigraphy of Garmaksla Lake: planktonic taxa have not been observed and the diatom community in the current upper layers does

not agree with the littoral and epiphytic diatom assemblages found in the littoral zone of Garmaksla Lake. Contrary, the shift in Garmaksla Lake seems to correspond with a diversification of the benthic community. Garmaksla Lake is located on, for Spitsbergen, a rather high altitude (308 m a.s.l.) with extended ice cover throughout the year (ice free for maximum 3 months), which results in an at current state possible lower impact of climate warming compared to lakes with a shorter ice cover [47, 92]. Moreover, regional differences in the magnitude and extent of the general warming of the Arctic exist, which is illustrated by several lakes in regions, where no climate warming or even cooling is observed, such as certain areas of Greenland [e.g., 44, 149], and where consequently recent diatom shifts did not occur [e.g., 155]. Therefore it is hypothesised that the diatom community of Garmaksla Lake is due to prolonged ice cover still in a transitional/delayed phase compared to many other High Arctic lakes. Presumably, its communities are either going to a more planktonic community, though unlikely since no planktonic taxa have been observed, or to a more littoral community. Increasing abundances of for example *Denticula*, a genus typical for littoral environments could evidence the latter. Moreover, in the future a potential lowering water table may add further effects and result in a shift toward a more littoral community as many Arctic lakes are known to experience severe increases in evaporation due to the warming climate [182]. The extremely low observed chrysophyte abundances, a typical planktonic algal group [179], add additional evidence for a community with few planktonic algae.

For completeness, it is mentioned that input of allochthonous material by (subaquatic) landslides or mixing of subsequent layers might have occurred, affecting the stratigraphy and therefore also the previously described interpretation of the sediment core. At the current state, no evidence for a landslide is found since no oversized clasts or coarsegrained sediments were encountered in the sediment core. Moreover, it is unlikely that mixing of layers occurred between 40 and 6.5 cm depth since these layers show well-preserved and undisturbed varves. The homogeneous sediments of the lower layers however, could have experienced mixing. At the current state, no information concerning these processes is known. In summary, combining the diatom stratigraphy with the results obtained by several Czech and German research teams in the future will allow gaining more information concerning the observed environmental changes in the study area. More detailed dating, using a variety of dating techniques, will allow placing the observed changes in the right time frame. These findings might confirm or reject the proposed hypothesis. However, at present and focussing mostly on diatom communities, the in this master thesis elaborated explanation seems the most plausible.

5 Conclusion

The study of the recent lake samples revealed the presence of 315 different taxa of which one fourth could not be identified upon species or lower taxonomic level. Several of these taxa are with certainty new to science and one species, *Gomphonema svalbardense*, has already been described. Clearly, the diatom diversity of Spitsbergen is not well known indicating that a profound revision of the Arctic diatom flora is desired in order to improve both our fundamental knowledge and to advance future (paleo)ecological research.

Four separate diatom assemblages were distinguished. Separation of these assemblages based on the measured physicochemical parameters (pH and conductivity) proved to be difficult but it was possible to explain the assemblages by habitat differences. The '*Nitzschia perminuta* assemblage' is associated with young postglacial lakes with a limited influence of sea spray. The '*Diatoma tenuis* assemblage' occurs mainly in lakes with (distinct) currents due to in- or outflowing streams and with no or limited moss coverage. Since some small streams are also found in lakes of other assemblages, additional unknown ecological parameters presumably are of importance. The '*Psammothidium* assemblage' is found in lakes without vegetation, no or very limited currents and with a clear water column. The last assemblage is dominated by *Rossethidium petersenii* and *Denticula* taxa and is a typical littoral community of lakes with distinct moss coverage and with (slight) fluctuations of the water level.

The diatom stratigraphy of the sediment core of Garmaksla Lake was dominated by 2 taxa: *Staurosira venter* and *Amphora affinis*. Changes in their relative abundances suggest subsequent periods of warming and cooling whereas the warming observed in the upper layers is clearly unprecedented throughout the remaining of the core and is attributed to the end of the Little Ice Age, ~ 100 – 150 years ago, and, more recently, human induced environmental changes. This suggests that, in parallel with several other studies of Arctic sediment cores, Arctic diatom communities are rather dynamic, distinctly corresponding to environmental changes and that Arctic diatom assemblages currently move away from their ecological equilibrium of the past centuries to millennia. Since these findings only represent the diatom stratigraphy without additional information and detailed dating, the interpretation of this sediment core however needs to be handled with caution.

In the upcoming year, the results of the diatom stratigraphy will be combined with the biotic and geochemical analysis of several Czech and German research teams in order to provide a multi-proxy paleolimnological study of Garmaksla Lake. In an attempt to improve our knowledge concerning Arctic diatom diversity, all new species found in this study will be published by the author of this thesis. Moreover, renewed detailed analysis of the material with the aid of several renowned taxonomists will be carried out and might lead to additional publications.

6 References

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Appendix

Appendix A. Identification guides and articles for diatoms

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Appendix B. List of the diatom taxa

Recent material

TABLE B1. List of the diatom taxa (and DCA codes) of the recent lake samples from Petuniabukta, based on the sampling described in this study. The abundance (percentage of all counted valves) for each taxon is given. Legend: + = < 0.1%, - = taxon not observed during the count, but only during the scanning of the samples for extra taxa. The 20 most abundant taxa are indicated in bold and the 10 taxa new to science are underlined.

Abundance (%)	Taxon	Code
0.1	<i>Achnantheidium minutissimum</i> var. <i>jackii</i> (Rabenhorst) Lange-Bertalot	ACHNmija
-	<i>Achnantheidium rosenstockii</i> Lange-Bertalot	ACHNrose
15.4	<u>Achnantheidium sp1</u>	ACHNspe1
0.2	<u>Achnantheidium sp2</u>	ACHNspe2
0.1	<u>Achnantheidium sp3</u>	ACHNspe3
+	<i>Adlafia bryophila</i> (J.B.Petersen) Moser, Lange-Bertalot & Metzeltin	ADLAbryo
0.8	<i>Adlafia minuscula</i> Grunow	ADLaminu
+	<i>Alveovallum beyensii</i> Lange-Bertalot & Krammer	ALVEbeye
0.2	<i>Amphora affinis</i> Kützing	AMPHaffi
0.1	<i>Amphora inariensis</i> Krammer	AMPHinar
0.3	<i>Amphora lange-bertalotti</i> var. <i>tenuis</i> Levkov & Metzeltin	AMPHlabe
+	<i>Aneumastus tusculus</i> (Hustedt) Bukhtiyarova	ANEUtusc
0.2	<i>Brachysira neoexilis</i> Lange-Bertalot	BRACneox
0.1	<i>Brachysira zellensis</i> (Grunow) Round & Mann	BRACzell
0.1	<i>Caloneis alpestris</i> (Grunow) Cleve	CALOalpe
0.2	<i>Caloneis arctica</i> (Krasske) Lange-Bertalot	CALOarct
0.1	<i>Caloneis backmanii</i> Cleve-Euler	CALOback
0.2	<i>Caloneis falcifera</i> Lange-Bertalot, Genkal & Vekhov	CALOfalc
0.3	<i>Caloneis fasciata</i> (Lagerstedt) Cleve	CALOfasc
0.1	<i>Caloneis fusus</i> Hamilton & Antoniadis	CALOfusu
+	<i>Caloneis silicula</i> (Ehrenberg) Cleve	CALOsili
+	<i>Caloneis silicula</i> var. <i>intermedia</i> Mayer	CALOsivi
0.3	<i>Caloneis sublinearis</i> (Grunow) Krammer	CALOsubl
1.4	Caloneis tenuis (Gregory) Krammer	CALOtenu
0.1	<i>Caloneis thermalis</i> (Grunow) Krammer	CALOther
-	<i>Cavinula cocconeiformis</i> (Gregory) Mann & Stickle	CAVICocc
+	<i>Cavinula</i> sp	CAVISpe1
-	<i>Chamaepinnularia</i> cf. <i>evanida</i> (Hustedt) Lange-Bertalot	CHAMevan
0.2	<i>Chamaepinnularia gandrupii</i> (Petersen) Lange-Bertalot & Krammer	CRAMgand
-	<i>Craticula ambigua</i> (Ehrenberg) Mann	CRATambi
0.1	<i>Craticula minusculoides</i> (Hustedt) Lange-Bertalot	CRATminu
0.1	<i>Craticula molestiformis</i> (Hustedt) Lange-Bertalot	CRATmole
+	<i>Craticula submolesta</i> (Hustedt) Lange-Bertalot	CRATsubm
0.1	<i>Cyclotella antiqua</i> W.Smith	CYCLanti
-	<i>Cyclotella</i> cf. <i>comta</i> (Ehrenberg) Kützing	CYCLcomt
+	<i>Cyclotella ocellata</i> Pantocsek	CYCLocel

TABLE B1 – continued.

Abundance (%)	Taxon	Code
+	<i>Cyclotella pseudocomensis</i> Scheffler	CYCLpseu
-	<i>Cyclotella</i> sp1	CYCLspe1
-	<i>Cyclotella</i> sp2	CYCLspe2
0.1	<i>Cymbella arctica</i> (Lagerstedt) Schmidt	CYMBarct
1.7	<i>Cymbella botellus</i> (Lagerstedt) Schmidt	CYMBbote
+	<i>Cymbella cleve-eulerae</i> Krammer	CYMBclev
0.1	<i>Cymbella designata</i> Krammer	CYMBdesi
0.4	<i>Cymbella hantzschiana</i> var. <i>borealis</i> Krammer	CYMBhant
0.1	<i>Cymbella neocistula</i> Krammer	CYMBneoc
+	<i>Cymbella neoleptoceros</i> var. <i>tenuistriaca</i> Krammer	CYMBneol
0.3	<i>Cymbella weslawskii</i> Krammer	CYMBwesl
0.2	<u><i>Cymbella</i> sp sensu Antoniadès et al. 2008</u>	CYMBanto
0.4	<u><i>Cymbella</i> sp1</u>	CYMBspe1
+	<i>Cymbella</i> sp2	CYMBspe2
0.1	<i>Cymbopleura amphicephala</i> (Naegeli) Krammer	CYBPamph
+	<i>Cymbopleura anglica</i> (Lagerstedt) Krammer	CYBPangl
0.9	<i>Cymbopleura angustata</i> var. <i>spitsbergensis</i> Krammer	CYBPangu
0.3	<i>Cymbopleura broenlundensis</i> (Foged) Krammer	CYBPbroe
+	<i>Cymbopleura incerta</i> var. <i>incerta</i> (Grunow) Krammer	CYBPince
0.2	<i>Cymbopleura incerta</i> var. <i>spitsbergensis</i> Krammer	CYBPinsp
-	<i>Cymbopleura incertiformis</i> Krammer	CYBPinfo
0.2	<i>Cymbopleura oblongata</i> var. <i>parva</i> Krammer	CYBPoblo
+	<i>Cymbopleura subaequalis</i> s. l. Grunow	CYBPsuba
+	<i>Cymbopleura subaequalis</i> var. <i>truncata</i> Krammer	CYBPstr
+	<i>Cymbopleura tynnii</i> (Krammer) Krammer	CYBPtynn
+	<i>Cymbopleura venetaeformis</i> Hamilton & Antoniadès	CYBPvene
0.1	<i>Cymbopleura</i> sp1	CYBPspe1
0.1	<u><i>Cymbopleura</i> sp2</u>	CYBPspe2
0.1	<u><i>Cymbopleura</i> sp3</u>	CYBPspe3
0.2	<i>Delicata delicatula</i> (Kützing) Krammer	DELIIdeli
0.2	<i>Delicata spitsbergensis</i> Krammer	DELIspit
2.9	<i>Denticula kuetzingii</i> Grunow incl. var. <i>rumrichae</i> Krammer	DENTkuet
0.2	<i>Denticula subtilis</i> Grunow	DENTsubt
3.8	<i>Denticula tenuis</i> Kützing	DENTtenu
0.3	<i>Diatoma moniliformis</i> Kützing	DIATmono
5.7	<i>Diatoma tenuis</i> Agardh	DIATtenu
+	<i>Diatomella balfoeriana</i> Greville	DIMLbalf
-	<i>Didymosphenia geminata</i> (Lynbye) Schmidt	DIDYgemi
0.4	<i>Diploneis oblongella</i> (Naegeli) Cleve-Euler	DIPLoblo
+	<i>Diploneis oculata</i> (Brébisson) Cleve	DIPLocul
0.2	<i>Diploneis ovalis</i> ssp. <i>arctica</i> Lange-Bertalot	DIPLoval
0.1	<i>Diploneis parma</i> Cleve	DIPLparm
+	<i>Encyonema</i> aff. <i>aueri</i> (Krasske) Krammer	ENCYauer

TABLE B1 – continued.

Abundance (%)	Taxon	Code
+	<i>Encyonema elginense</i> (Krammer) Mann	ENCYelgi
1.3	<i>Encyonema fogedii</i> Krammer	ENCYfoge
+	<i>Encyonema hebridicum</i> (Gregory) Grunow	ENCYhebr
0.1	<i>Encyonema lange-bertalotii</i> Krammer	ENCYlabe
1.5	<i>Encyonema minutum</i> (Hilse) Mann	ENCYminu
+	<i>Encyonema obscurum</i> (Krasske) Mann	ENCYobsc
+	<i>Encyonema perminutum</i> Krammer	ENCYperm
0.8	<i>Encyonema silesiacum</i> (Bleisch) Mann	ENCYsile
-	<i>Encyonema silesiacum</i> var. <i>lata</i> Krammer	ENCYsila
0.2	<i>Encyonema</i> aff. <i>ventricosum</i> (C.Agardh) Grunow	ENCYvent
+	<i>Encyonema</i> sp1	ENCYspe1
+	<i>Encyonema</i> sp2	ENCYspe2
+	<i>Encyonema</i> sp3	ENCYspe3
+	<i>Encyonema</i> sp4	ENCYspe4
+	<i>Encyonema</i> sp5	ENCYspe5
+	<i>Encyonema</i> sp6	ENCYspe6
+	<i>Encyonema</i> sp7	ENCYspe7
+	<i>Encyonopsis cesatiformis</i> Krammer	ENCYcesf
+	<i>Encyonopsis cesatii</i> (Rabenhorst) Krammer	ENCYcesa
-	<i>Encyonopsis descripta</i> (Hustedt) Krammer	ENCYdesc
-	<i>Encyonopsis krammeri</i> Reichardt	ENCYkram
1.1	<i>Encyonopsis subminuta</i> Krammer & Reichardt	ENCYsubm
+	<i>Encyonopsis</i> cf. sp1 sensu Antoniadou <i>et al.</i> 2008	ENCYanto
0.2	<u><i>Encyonopsis</i> sp1</u>	ENCYspe1
0.1	<i>Encyonopsis</i> sp2	ENCYspe2
0.4	<i>Encyonopsis</i> sp3	ENCYspe3
+	<i>Encyonopsis</i> sp4	ENCYspe4
1.8	<u><i>Encyonopsis</i> sp5</u>	ENCYspe5
0.4	<i>Epithemia adnata</i> (Kützing) Brébisson	EPITadna
0.1	<i>Epithemia sorex</i> Kützing	EPITsore
-	<i>Epithemia turgida</i> Ehrenberg	EPITturg
1.6	<i>Eucocconeis flexella</i> (Kützing) Cleve	EUCOflex
1.7	<i>Eucocconeis laevis</i> (Østrup) Lange-Bertalot incl. var. <i>austriaca</i> (Hustedt) Lange-Bertalot	EUCOlaev
-	<i>Eunotia ewa</i> Lange-Bertalot & Witowski	EUNOewa_
0.2	<i>Eunotia minor</i> (Kützing) Grunow	EUNOmino
-	<i>Eunotia</i> sp	EUNOspe1
+	<i>Fallacia losevae</i> Lange-Bertalot, Genkal & Vechov	FALLlose
+	<i>Fistulifera saprophila</i> (Lange-Bertalot & Bonik) Lange-Bertalot	FISTsapr
0.2	<i>Fragilaria gracilis</i> Østrup	FRAGgrac
0.1	<i>Fragilaria tenera</i> (Schmidt) Lange-Bertalot	FRAGtene
0.3	<i>Fragilaria</i> sp1	FRAGspe1
0.5	<i>Fragilaria</i> sp2	FRAGspe2
+	<i>Fragilaria</i> sp3	FRAGspe3

TABLE B1 – continued.

Abundance (%)	Taxon	Code
0.2	<i>Frustulia</i> sp	FUSTspe1
+	<i>Geissleria paludosa</i> (Hustedt) Lange-Bertalot & Metzeltin	GEISpalu
+	<i>Geissleria</i> sp1	GEISspe1
+	<i>Geissleria</i> sp2	GEISspe2
-	<i>Gomphonema distans</i> (Cleve-Euler) Lange-Bertalot & Reichardt	GOMPdist
+	<i>Gomphonema kaweckanum</i> Metzeltin, Reichardt & Lange-Bertalot	GOMPkawe
+	<i>Gomphonema lagerheimii</i> Cleve	GOMPlage
0.4	<i>Gomphonema micropus</i> Kützing	GOMPmicr
0.2	<i>Gomphonema nathorstii</i> Foged	GOMPnath
+	<i>Gomphonema productum</i> (Grunow) Lange-Bertalot & Reichardt	GOMPprod
0.1	<u><i>Gomphonema svalbardense</i> Pinseel, Kopalová & Van de Vijver</u>	GOMP sval
+	<i>Gyrosigma acuminatum</i> (Kützing) Rabenhorst	GYROacum
0.2	<i>Halamphora dusenii</i> (Brun) Levkov	HALAduse
0.1	<i>Halamphora obscura</i> (Krasske) Levkov	HALAobsc
0.1	<i>Halamphora oligotrphenta</i> (Lange-Bertalot) Levkov	HALAolig
0.1	<i>Hannaea arcus</i> (Ehrenberg) Patrick	HANNarcu
+	<i>Hantzschia abundans</i> Lange-Bertalot	HANTabud
0.2	<i>Hantzschia amphioxys</i> (Ehrenberg) Grunow	HANTamph
+	<i>Hantzschia hyperborea</i> (Grunow) Lange-Bertalot	HANThype
+	<i>Hantzschia rhaetica</i> Meister	HANTrhae
+	<i>Hantzschia vivacior</i> Lange-Bertalot	HANTviva
-	<i>Hippodonta hungarica</i> (Grunow) Lange-Bertalot	HIPPhung
0.1	<i>Humidophila brekkaensis</i> (Petersen) Lowe, Kociolek, Johansen, Van de Vijver, Lange-Bertalot & Kopalová	HUMIbrekk
0.1	<i>Humidophila ingeaeformis</i> (Hamilton & Antoniadis) Lowe, Kociolek, Johansen, Van de Vijver, Lange-Bertalot & Kopalová	HUMIlinga
1.1	<i>Humidophila paracontenta</i> (Lange-Bertalot & Werum) Lowe, Kociolek, Johansen, Van de Vijver, Lange-Bertalot & Kopalová	HUMIpara
1.2	<i>Humidophila perpusilla</i> (Grunow) Lowe, Kociolek, Johansen, Van de Vijver, Lange-Bertalot & Kopalová	HUMIperp
0.1	<i>Humidophila</i> sp1 (sensu <i>Diademsis</i> sp1 Antoniadis <i>et al.</i> 2008)	HUMIanto
1.0	<i>Hygropetra balfouriana</i> (Grunow) Krammer & Lange Bertalot	HYGRbalf
1.0	<i>Kobayasiella</i> sp	KOBAspe1
+	<i>Luticola bilyi</i> Levkov, Metzeltin & Pavlov	LUTibily
-	<i>Luticola cohnii</i> (Hilse) Mann	LUTicohn
0.1	<i>Luticola frequentissima</i> Levkov, Metzeltin & Pavlov	LUTifreq
+	<i>Luticola quinquenoides</i> (Grunow) Levkov, Metzeltin & Pavlov	LUTiquin
+	<i>Luticola similis</i> Levkov, Metzeltin & Pavlov	LUTisimi
+	<i>Luticola triundulata</i> Levkov, Metzeltin & Pavlov	LUTitriu
+	<i>Luticola</i> sp1	LUTIspe1
+	<i>Luticola</i> sp2	LUTIspe2
+	<i>Luticola</i> sp3	LUTIspe3
+	<i>Mayamaea atomus</i> (Kützing) Lange-Bertalot	MAYAatom
0.6	<i>Mayamaea</i> cf. <i>aliena</i> (Krasske) Lange-Bertalot	MAYAalie

TABLE B1 – continued.

Abundance (%)	Taxon	Code
0.2	<i>Mayamaea permitis</i> (Hustedt) Bruder & Medlin	MAYAperm
0.8	<i>Meridion circulare</i> (Greville) Agardh	MERICirc
+	<i>Microcostatus krasskei</i> (Hustedt) Johansen & Sray	MICRkras
+	<i>Muelleria gibbula</i> (Cleve) Spaulding & Stoermer	MUElgibb
0.8	<i>Navicula arctotenelloides</i> Lange-Bertalot & Metzeltin	NAVIarct
0.8	<i>Navicula bjoernoeyaensis</i> Metzeltin, Witkowski & Lange-Bertalot	NAVIbjoe
0.5	<i>Navicula cincta</i> (Ehrenberg) Ralfs	NAVICinc
0.3	<i>Navicula cryptocephala</i> Kützing	NAVICrph
1.1	<i>Navicula cf. cryptocephala</i> Kützing	NAVICfrc
0.3	<i>Navicula cryptotenella</i> Lange-Bertalot	NAVICrte
0.5	<i>Navicula doehleri</i> Lange-Bertalot	NAVIdoeh
+	<i>Navicula expecta</i> Van Landingham	NAVIexpt
+	<i>Navicula gregaria</i> Donkin	NAVIgreg
+	<i>Navicula hanseatica</i> ssp. <i>circumarctica</i> Witkowski, Lange-Bertalot & Metzeltin	NAVIhans
-	<i>Navicula kefvingensis</i> (Ehrenberg) Kützing	NAVIkefv
0.1	<i>Navicula libonensis</i> Schoeman	NAVIlibo
+	<i>Navicula luciae</i> Witowski & Lange-Bertalot	NAVIluci
+	<i>Navicula meniscus</i> Schumann	NAVImeni
-	<i>Navicula peroblonga</i> Metzeltin, Lange-Bertalot & Nergui	NAVIpero
0.2	<i>Navicula phyllepta</i> Kützing	NAVIphta
0.3	<i>Navicula phylleptosoma</i> Lange-Bertalot	NAVIphto
0.5	<i>Navicula pseudotenelloides</i> Krasske	NAVIpseu
0.1	<i>Navicula radiosa</i> Kützing	NAVIradi
+	<i>Navicula slesvicensis</i> Grunow	NAVISles
+	<i>Navicula vaneei</i> Lange-Bertalot	NAVIvane
0.1	<i>Navicula vulpina</i> Kützing	NAVIvulp
+	<i>Navicula wiesneri</i> Pantocsek	NAVIwies
+	<i>Navicula</i> sp4 sensu Antoniadis <i>et al.</i> 2008	NAVIspe4a
0.1	<i>Navicula</i> sp1	NAVIspe1
+	<i>Navicula</i> sp2	NAVIspe2
+	<i>Navicula</i> sp3	NAVIspe3
0.1	<i>Navicula</i> sp4	NAVIspe4
0.7	<i>Navicula</i> sp5	NAVIspe5
0.1	<i>Navicula</i> sp6	NAVIspe6
-	<i>Navicula</i> s. l. sp.	NAVISlsp
0.1	<i>Neidium bergii</i> (Cleve-Euler) Krammer	NEIDberg
0.1	<i>Neidium decoratum</i> Brun	NEIDdeco
-	<i>Neidium distincte-punctatum</i> Hustedt	NEIDdist
+	<i>Neidium kozlowi</i> var. <i>densestriata</i> Foged	NEIDkode
+	<i>Neidium kozlowi</i> var. <i>elliptica</i> Mereschkowsky	NEIDkoel
+	<i>Neidium productum</i> (W.Smith) Cleve	NEIDprod
0.1	<i>Neidium spitsbergense</i> Foged	NEIDspit
-	<i>Nitzschia alpina</i> Hustedt	NITZalpi

TABLE B1 – continued.

Abundance (%)	Taxon	Code
-	<i>Nitzschia angustata</i> (W.Smith) Grunow	NITZanta
-	<i>Nitzschia angustatula</i> Lange-Bertalot	NITZanla
+	<i>Nitzschia archibaldii</i> Lange-Bertalot	NITZarch
0.1	<i>Nitzschia bacilliformis</i> Hustedt	NITZbaci
+	<i>Nitzschia bryophila</i> (Hustedt) Hustedt	NITZbryo
0.2	<i>Nitzschia clausii</i> Hantzsch	NITZclau
0.2	<i>Nitzschia communis</i> Rabenhorst	NITZcois
0.1	<i>Nitzschia commutata</i> Grunow	NITZcota
0.1	<i>Nitzschia debilis</i> (Arnott) Grunow	NITZdebi
-	<i>Nitzschia dissipata</i> (Kützing) Grunow	NITZdiss
0.2	<i>Nitzschia fonticola</i> (Grunow) Grunow	NITZfont
+	<i>Nitzschia graciliformis</i> Lange-Bertalot & Simonsen	NITZgrac
+	<i>Nitzschia</i> cf. <i>graciliformis</i> Lange-Bertalot & Simonsen	NITZcfgr
0.1	<i>Nitzschia hamburgiensis</i> Lange-Bertalot	NITZhomb
0.3	<i>Nitzschia lacuum</i> Lange-Bertalot	NITZlacu
+	<i>Nitzschia levidensis</i> var. <i>salinarum</i> Grunow	NITZlevi
1.0	<i>Nitzschia liebethuthii</i> Rabenhorst	NITZlieb
0.8	<i>Nitzschia linearis</i> var. <i>subtilis</i> Hustedt	NITZline
0.8	<i>Nitzschia modesta</i> Hustedt	NITZmode
0.6	<i>Nitzschia palea</i> Kützing (Schmidt)	NITZpale
0.3	<i>Nitzschia paleacea</i> Grunow	NITZpaea
2.3	<i>Nitzschia perminuta</i> (Grunow) Peragallo group 1	NITZper1
4.1	<i>Nitzschia perminuta</i> (Grunow) Peragallo group 2	NITZper2
1.5	<i>Nitzschia perminuta</i> (Grunow) Peragallo group 3	NITZper3
1.6	<i>Nitzschia perminuta</i> (Grunow) Peragallo group 4	NITZper4
0.1	<i>Nitzschia perminuta</i> (Grunow) Peragallo group 5	NITZper5
1.5	<i>Nitzschia perminuta</i> (Grunow) Peragallo group 6	NITZper6
+	<i>Nitzschia recta</i> Hantzsch	NITZrect
-	<i>Nitzschia sigma</i> (Kützing) W. Smith	NITZsigm
0.1	<i>Nitzschia sinuata</i> (Thwaites) Grunow	NITZsinu
2.2	<i>Nitzschia soratensis</i> Morales & Vis	NITZsorr
0.4	<i>Nitzschia subamphioxoides</i> Hustedt	NITZsuba
0.5	<i>Nitzschia suchlandti</i> Hustedt	NITZsuch
+	<i>Nitzschia thermaloides</i> Hustedt	NITZther
-	<i>Nitzschia vitrea</i> Norman	NITZvitr
0.1	<i>Nitzschia</i> sp1	NITZspe1
0.1	<i>Nitzschia</i> sp2	NITZspe2
-	<i>Nitzschia</i> sp3	NITZspe3
-	<i>Nitzschia</i> sp4	NITZspe4
-	<i>Nitzschia</i> sp5	NITZspe5
+	<i>Nitzschia</i> sp6	NITZspe6
+	<i>Nitzschia</i> sp7	NITZspe7
+	<i>Nitzschia</i> sp8	NITZspe8

TABLE B1 – continued.

Abundance (%)	Taxon	Code
+	<i>Pinnularia biceps</i> Gregory	PINNbice
0.3	<i>Pinnularia brebissonii</i> var. <i>acuta</i> Cleve-Euler	PINNbreb
+	<i>Pinnularia divergens</i> Schmidt	PINNdins
-	<i>Pinnularia divergentissima</i> (Grunow) Cleve	PINNdima
0.1	<i>Pinnularia frequentis</i> Krammer	PINNfreq
+	<i>Pinnularia ilkaschoenfelderae</i> Krammer	PINNilka
+	<i>Pinnularia</i> cf. <i>intermedia</i> (Lagerstedt) Cleve	PINNcfin
+	<i>Pinnularia isostauron</i> (Ehrenberg) Cleve	PINNisos
-	<i>Pinnularia krammeri</i> Metzeltin	PINNkram
+	<i>Pinnularia</i> cf. <i>marchica</i> Ilka Schönfelder	PINNmarc
0.1	<i>Pinnularia obscura</i> Krasske	PINNobsc
0.1	<i>Pinnularia</i> cf. <i>perinterrupta</i> Krammer	PINNcfpe
-	<i>Pinnularia pseudodivergentissima</i> Van de Vijver, Moravcová, Kusber & Neustupa	PINNpseu
-	<i>Pinnularia viridiformis</i> Krammer	PINNviri
+	<i>Pinnularia</i> sp1	PINNspe1
-	<i>Pinnularia</i> sp2	PINNspe2
+	<i>Placoneis amphibola</i> (Cleve) Cox	PLACamph
+	<i>Placoneis amphibola</i> f. <i>rectangularis</i> Foged	PLACamre
+	<i>Placoneis elginensis</i> (Gregory) Cox	PLAGelgi
+	<i>Planothidium fragilarioides</i> (Petersen) Round & Bukhtiyarova	PLANfrag
-	<i>Platessa rupestris</i> (Krasske) Lange-Bertalot	PLATrupe
+	<i>Psammothidium bioretii</i> (Germain) Bukhtiyarova & Round	PSAMBior
0.4	<i>Psammothidium broenlundense</i> (Foged) Hamilton, Antoniadis & Siver	PSAMBroe
+	<i>Psammothidium daonense</i> Lange-Bertalot	PSAMdaon
0.1	<i>Psammothidium grischunum</i> (Wuthrich) Bukhtiyarova & Round	PSAMgris
0.1	<i>Psammothidium helveticum</i> (Hustedt) Bukhtiyarova & Round	PSAMhelv
0.5	<i>Psammothidium kryophilum</i> (Petersen) Reichardt	PSAMkryo
0.7	<i>Psammothidium marginulatum</i> (Grunow) Bukhtiyarova & Round	PSAMmarg
+	<i>Psammothidium rossii</i> (Hustedt) Bukhtiyarova & Round	PSAMross
+	<i>Psammothidium scoticum</i> (Flower & Jones) Bukhtiyarova & Round	PSAMscot
0.1	<i>Psammothidium ventralis</i> (Krasske) Bukhtiyarova & Round	PSAMvent
1.6	<i>Psammothidium</i> sp1	PSAMspe1
0.4	<i>Psammothidium</i> sp2	PSAMspe2
-	<i>Psammothidium</i> sp3	PSAMspe3
6.5	<i>Rossithidium petersenii</i> (Hustedt) Aboal	ROSSpete
0.1	<i>Rossithidium pusillum</i> (Grunow) Round & Bukhtiyarova	ROSSpusi
+	<i>Sellaphora bacillum</i> (Ehrenberg) Mann	SELLbaci
-	<i>Sellaphora nana</i> (Hustedt) Lange-Bertalot, Cavacini, Tagliaventi & Alfinito	SELLnana
-	<i>Sellaphora pupula</i> (Kützing) Mereschkowsky	SELLpupu
+	<i>Sellaphora rectangularis</i> (Gregory) Lange-Bertalot & Metzeltin	SELLrect
+	<i>Stauroneis agrestiformis</i> Van de Vijver & Lange-Bertalot	STAUagre
+	<i>Stauroneis amphicephala</i> Kützing	STAUamph

TABLE B1 – continued.

Abundance (%)	Taxon	Code
+	<i>Stauroneis circumborealoides</i> Van de Vijver & Lange-Bertalot	STAUcircu
-	<i>Stauroneis clandestina</i> Lange-Bertalot & Van de Vijver	STAUclan
+	<i>Stauroneis francisci-josephi</i> Van de Vijver & Lange-Bertalot	STAUfran
-	<i>Stauroneis gelida</i> Van de Vijver & Lange-Bertalot	STAUgeli
+	<i>Stauroneis intricans</i> Van de Vijver & Lange-Bertalot	STAUintr
+	<i>Stauroneis lapponica</i> Cleve	STAUlapp
+	<i>Stauroneis</i> cf. <i>lundii</i> Hustedt	STAUcflu
-	<i>Stauroneis</i> aff. <i>obtusa</i> Lagerstedt	STAUafob
+	<i>Stauroneis reichardtii</i> Lange-Bertalot, Cavacini, Tagliaventi & Alfinito	STAUreic
0.1	<i>Stauroneis</i> aff. <i>subgracilis</i> Lange-Bertalot & Krammer	STAUafsu
+	<i>Stauroneis subhyperborea</i> Van de Vijver, Beyens & Lange-Bertalot	STAUsubh
+	<i>Stauroneis svalbardensis</i> Van de Vijver & Lange-Bertalot	STAUsva
+	<i>Stauroneis anceps</i> Ehrenberg sensu Foged 1964	STAUspan
+	<i>Stauroneis</i> sp1	STAUspe1
-	<i>Stauroneis</i> sp2	STAUspe2
+	<i>Stausira pseudoconstruens</i> (Marciniak) Williams & Round	STAUpseu
+	<i>Stausira robusta</i> (Fusey) Williams & Round	STAUrobu
0.3	<i>Stausira venter</i> (Ehrenberg) Grunow	STAUvent
1.3	<i>Stausirella</i> aff. <i>lapponica</i> (Grunow) Williams & Round	STAUafla
-	<i>Stausirella oldenburgiana</i> (Hustedt) Morales	STAUolde
+	<i>Surirella minuta</i> Brébisson	SURIminu
0.2	<i>Surirella terricola</i> Lange-Bertalot & Alles	SURIterr
+	<i>Ulnaria danica</i> (Kützing) Compère & Bukhtiyarova	ULNAdani
+	<i>Ulnaria delicatissima</i> (Schmidt) Aboal & Silva	ULNAdeli
+	Unidentified diatom	UNIDENTI

Sediment core

TABLE B2. List of the diatom taxa of the sediment core from Garmaksla Lake, based on the sampling described in this study. The abundance (percentage of all counted valves) for each taxon is given. Legend: + = < 0.1%, - = taxon not observed during the count, but only during the scanning of the samples for extra taxa. The 10 most abundant taxa are indicated in bold. Taxa that were only found in the sediment core and not in the recent lake samples are underlined. The numbers given to the unidentified taxa correspond with those of the recent lake samples.

Abundance (%)	Taxon
1.5	<i>Achnantheidium rosenstockii</i> Lange-Bertalot
0.2	<i>Achnantheidium</i> sp1
4.2	<i>Achnantheidium</i> sp2
0.8	<i>Adlafia bryophila</i> (J.B.Petersen) Moser, Lange-Bertalot & Metzeltin
19.2	<i>Amphora affinis</i> Kützing
+	<i>Brachysira neoexilis</i> Lange-Bertalot
-	<i>Caloneis</i> sp (<i>Caloneis tenuis</i> Gregory Krammer?)
+	<i>Cymbella botellus</i> (Lagerstedt) Schmidt
+	<i>Cymbella</i> sp sensu Antoniadis <i>et al.</i> 2008
3.7	<i>Cymbella</i> sp1
-	<i>Cymbopleura amphicephala</i> (Naegeli) Krammer
0.1	<i>Cymbopleura angustata</i> var. <i>spitsbergensis</i> Krammer
1.1	<i>Cymbopleura</i> sp3
0.2	<i>Cymbopleura subaequalis</i> var. <i>truncata</i> Krammer
+	<i>Delicata delicatula</i> (Kützing) Krammer
1.1	<i>Denticula kuetzingii</i> Grunow incl. var. <i>rumrichae</i> Krammer
2.4	<i>Denticula tenuis</i> Kützing
+	<i>Diploneis oblongella</i> (Naegeli) Cleve-Euler
+	<i>Encyonema</i> aff. <i>ventricosum</i> (C.Agardh) Grunow
-	<i>Encyonema fagedii</i> Krammer
+	<i>Encyonema minutum</i> (Hilse) Mann
+	<i>Encyonema obscurum</i> (Krasske) Mann
0.1	<i>Encyonema silesiacum</i> (Bleisch) Mann
+	<i>Encyonopsis cesatii</i> (Rabenhorst) Krammer
-	<i>Encyonopsis cesatiformis</i> Krammer
0.3	<i>Encyonopsis descripta</i> (Hustedt) Krammer
+	<i>Encyonopsis</i> sp3
0.9	<i>Encyonopsis subminuta</i> Krammer & Reichardt
0.1	<i>Eucocconeis flexella</i> (Kützing) Cleve
+	<i>Eucocconeis laevis</i> (Østrup) Lange-Bertalot incl. var. <i>austriaca</i> (Hustedt) Lange-Bertalot
+	<i>Eunotia minor</i> (Kützing) Grunow
+	<i>Geissleria</i> sp1
+	<i>Humidophila brekkaensis</i> (Petersen) Lowe, Kocielek, Johansen, Van de Vijver, Lange-Bertalot & Kopalová
+	<u><i>Humidophila</i> sp2</u>
0.1	<i>Kobayasiella</i> sp
+	<i>Luticola frequentissima</i> Levkov, Metzeltin & Pavlov

TABLE B2 – continued.

Abundance (%)	Taxon
-	<i>Navicula arctotenelloides</i> Lange-Bertalot & Metzeltin
0.6	<i>Navicula cryptotenella</i> Lange-Bertalot
0.2	<i>Navicula radiosa</i> Kützing
1.7	<i>Nitzschia fonticola</i> (Grunow) Grunow
0.5	<i>Nitzschia lacuum</i> Lange-Bertalot
0.2	<i>Nitzschia liebetruthii</i> Rabenhorst
0.2	<i>Nitzschia perminuta</i> (Grunow) Peragallo group 3
+	<i>Nitzschia perminuta</i> (Grunow) Peragallo group 6
+	<u><i>Nitzschia</i> sp9</u>
0.1	<i>Pinnularia biceps</i> Gregory
-	<i>Pinnularia brebissonii</i> var. <i>acuta</i> Cleve-Euler
+	<u><i>Planothidium lanceolatum</i></u> Brébisson ex Kützing
+	<i>Psammothidium broenlundense</i> (Foged) Hamilton, Antoniadis & Siver
+	<i>Psammothidium helveticum</i> (Hustedt) Bukhtiyarova & Round
+	<u><i>Pseudostaurosira brevistriata</i></u> (Grunow in Van Heurck) Williams & Round
+	<i>Rossethidium petersenii</i> (Hustedt) Aboal
0.1	<i>Sellaphora rectangularis</i> (Gregory) Lange-Bertalot & Metzeltin
+	<i>Stauroneis circumborealoides</i> Van de Vijver & Lange-Bertalot
0.2	<i>Stauroneis clandestine</i> Lange-Bertalot & Van de Vijver
0.1	<i>Staurosira pseudoconstruens</i> (Marciniak) Williams & Round
0.1	<i>Staurosira robusta</i> (Fusey) Williams & Round
59.7	<i>Staurosira venter</i> (Ehrenberg) Grunow
0.2	<i>Staurosirella</i> aff. <i>lapponica</i> (Grunow) Williams & Round

Appendix C. Pictures of the observed diatom taxa

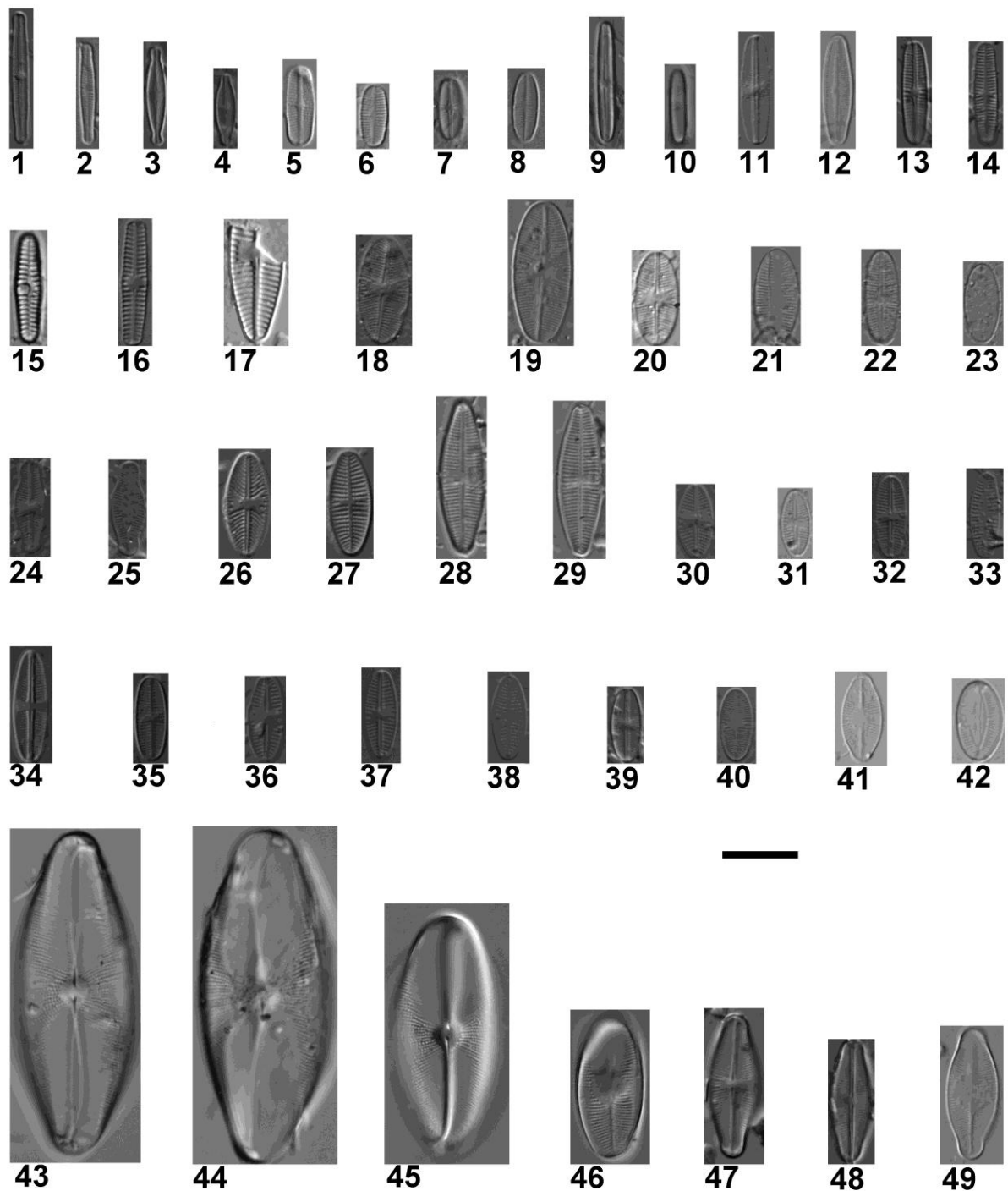


FIGURE C1. LM images. Monoraphidae. 1-2) *Achnanthydium* sp1, 3-4) *Achnanthydium minutissimum* var. *jackii*, 5-6) *Achnanthydium rosenstockii*, 7-8) *Achnanthydium* sp2, 9-10) *Achnanthydium* sp3, 11-12) *Rossithidium petersenii*, 13-14) *Rossithidium pusillum*, 15-16) *Planothydium fragilarioides*, 17) *Planothydium lanceolatum*, 18-19) *Psammothidium bioretii*, 20-21) *Psammothidium helveticum*, 22-23) *Psammothidium scoticum*, 24-25) *Psammothidium ventralis*, 26-27) *Psammothidium broenlundense*, 28-31) *Psammothidium kryophilum*, 32-33) *Psammothidium grischunum*, 34-35) *Psammothidium* sp1, 36) *Platessa rupestris*, 37-38) *Psammothidium* sp2, 39-40) *Psammothidium daonense*, 41) *Psammothidium rossii*, 42) *Psammothidium* sp3, 43-46) *Eucoconeis flexella*, 47-49) *Eucoconeis laevis* incl. var. *austriaca*. Scale bar = 10 μ m.

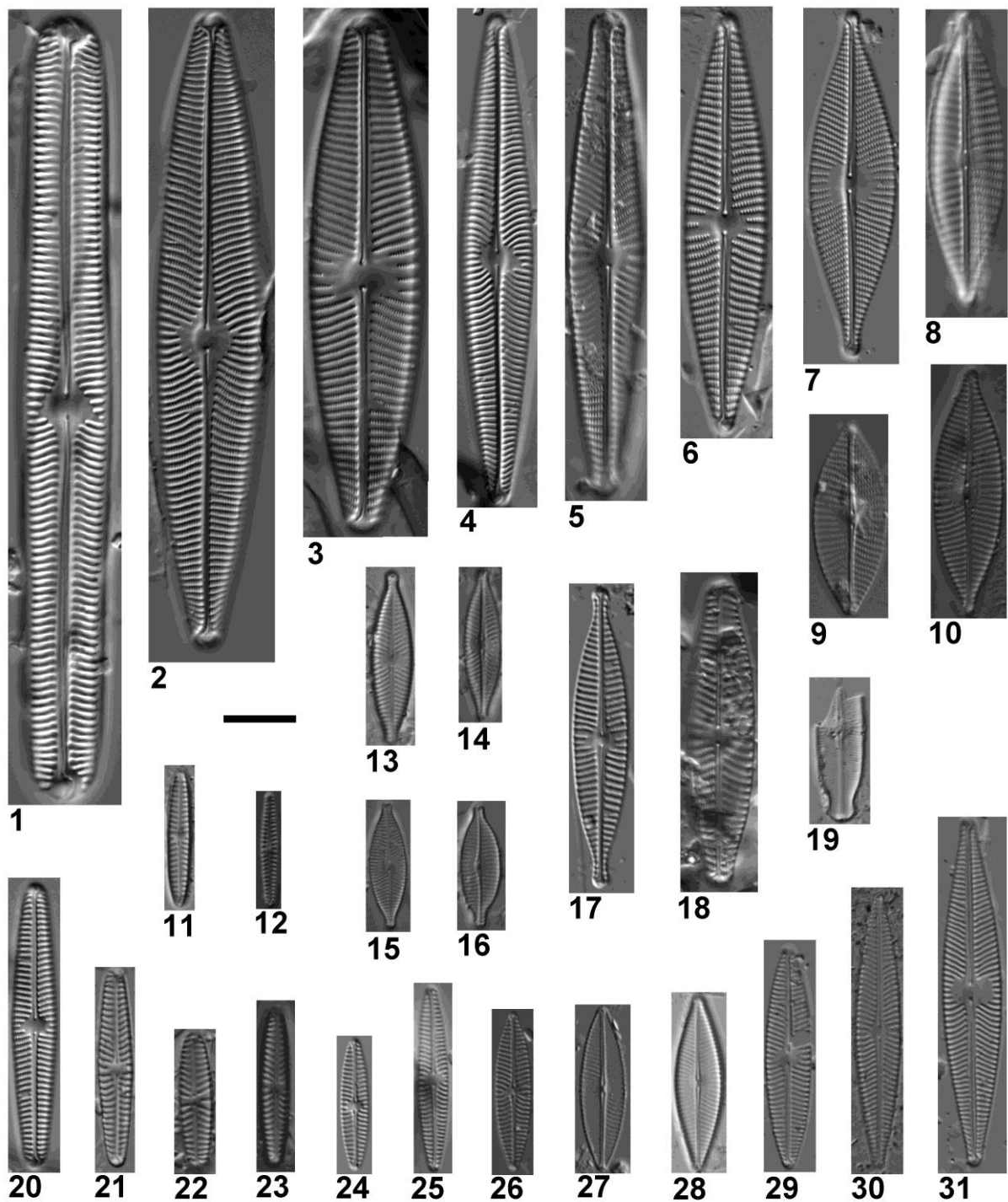


FIGURE C2. LM images. *Navicula*. 1) *Navicula peroblonga*, 2) *Navicula vulpina*, 3) *Navicula kefvingsensis*, 4) *Navicula radiosa*, 5) *Navicula* sp4 sensu Antoniadou et al. 2008, 6) *Navicula vaneei*, 7) *Navicula hanseatica* ssp. *circumarctica*, 8) *Navicula meniscus*, 9) *Navicula* sp3, 10) *Navicula luciae*, 11) *Navicula pseudotenelloides*, 12) *Navicula bjoernoeyaensis*, 13) *Navicula* sp6, 14) *Navicula* cf. *cryptocephala*, 15) *Navicula cryptocephala*, 16) *Navicula gregaria*, 17) *Navicula expecta*, 18) *Navicula slesvicensis*, 19) *Navicula* s. l. sp., 20) *Navicula libonensis*, 21) *Navicula wiesneri*, 22) *Navicula cincta*, 23) *Navicula doehleri*, 24) *Navicula arctotenelloides*, 25) *Navicula* sp4, 26) *Navicula cryptotenella*, 27) *Navicula phylleptosoma*, 28) *Navicula phyllepta*, 29) *Navicula* sp2, 30) *Navicula* sp5, 31) *Navicula* sp1. Scale bar = 10 μ m.

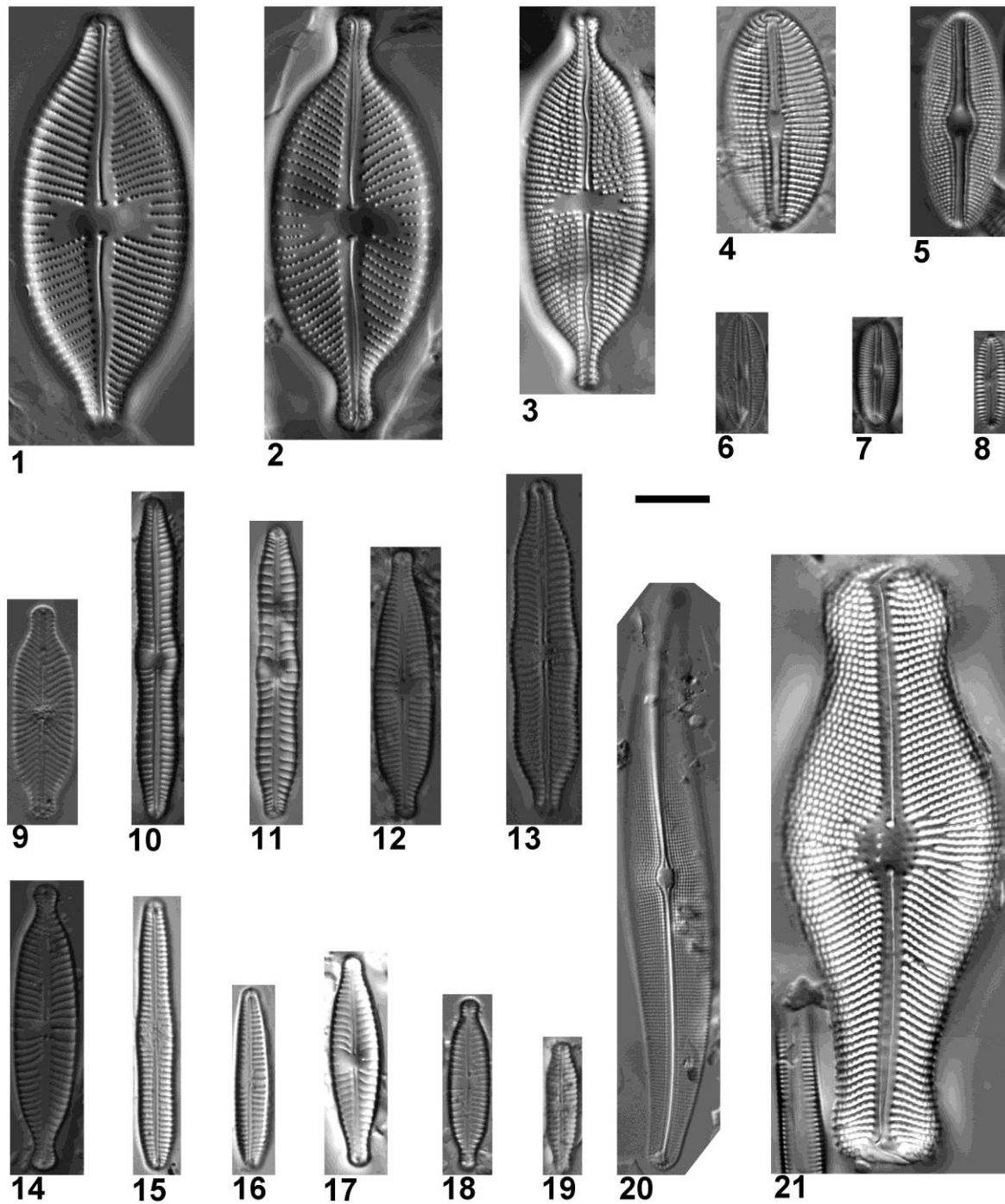


FIGURE C3. LM images. *Placoneis* – *Aneumastus* – *Diploneis* – *Diatomella* – *Gomphonema* – *Gyrosigma* – *Didymosphenia*. 1) *Placoneis amphibola*, 2) *Placoneis amphibola* f. *rectangularis*, 3) *Aneumastus tusculus*, 4) *Diploneis parma*, 5) *Diploneis ovalis* ssp. *arctica*, 6) *Diploneis oculata*, 7) *Diploneis oblongella*, 8) *Diatomella balfouriana*, 9) *Placoneis elginensis*, 10) *Gomphonema svalbardense*, 11) *Gomphonema distans*, 12-13) *Gomphonema nathorstii*, 14) *Gomphonema kaweckanum*, 15-16) *Gomphonema lagerheimii*, 17) *Gomphonema micropus*, 18-19) *Gomphonema productum*, 20) *Gyrosigma acuminatum*, 21) *Didymosphenia geminata*. Scale bar = 10 μ m.

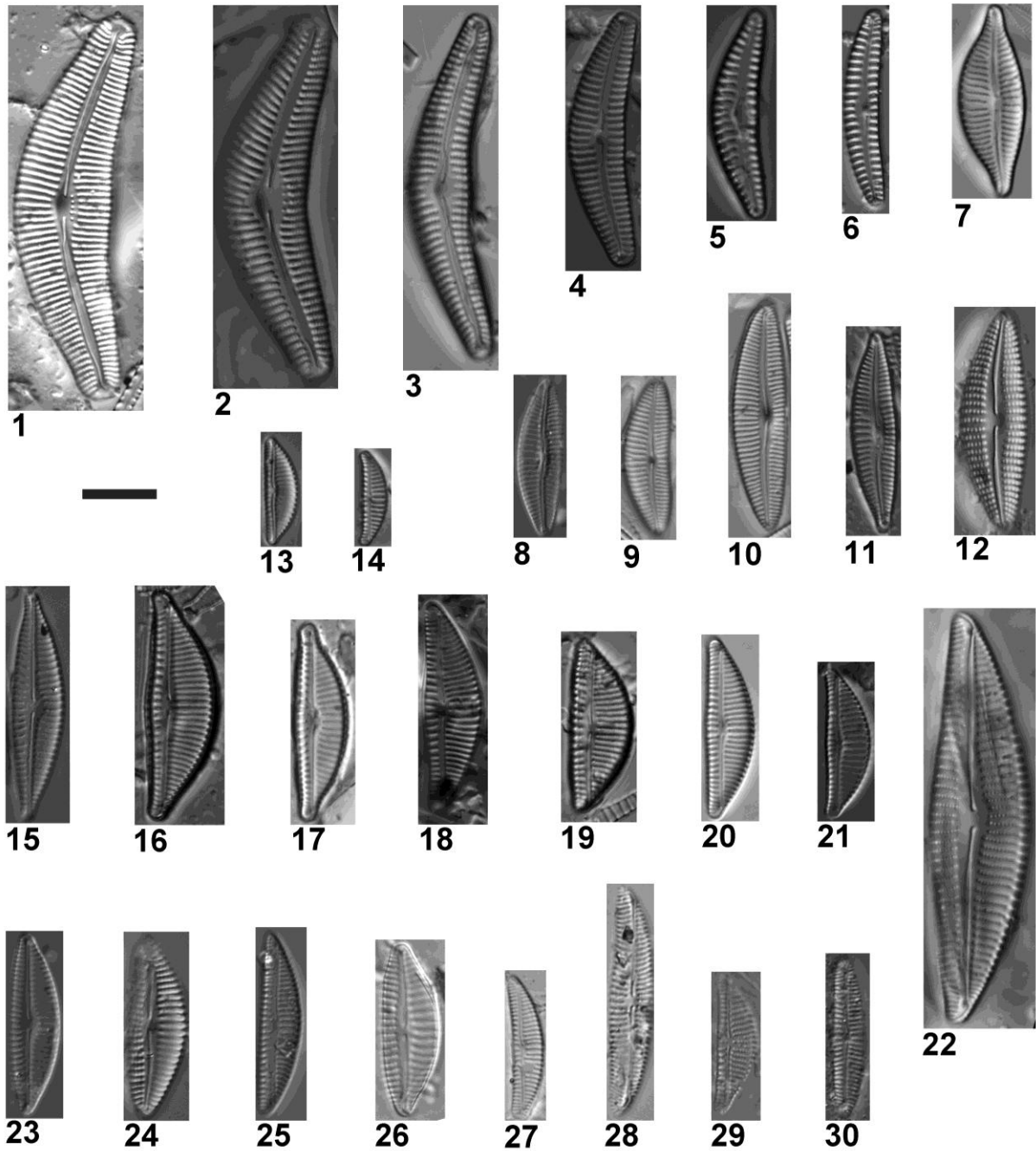


FIGURE C4. LM images. Cymbelloids (part 1). 1) *Cymbella arctica*, 2) *Cymbella neocistula*, 3) *Cymbella weslawskii*, 4) *Cymbella hantzschiana* var. *borealis*, 5) *Cymbella cleve-eulerae*, 6) *Cymbella botellus*, 7) *Cymbella designata*, 8) *Cymbella* sp2, 9-10) *Cymbella* sp1, 11) *Cymbella* sp sensu Antoniadou et al. 2008, 12) *Cymbella neoleptoceros* var. *tenuistriata*, 13) *Encyonema minutum*, 14) *Encyonema fogedii*, 15) *Encyonema hebridicum*, 16) *Encyonema lange-bertalotii*, 17) *Encyonema obscurum*, 18) *Encyonema silesiacum* var. *lata*, 19) *Encyonema silesiacum*, 20) *Encyonema perminutum*, 21) *Encyonema* aff. *ventricosum*, 22) *Encyonema elginense*, 23) *Encyonema* sp1, 24) *Encyonema* sp2, 25) *Encyonema* sp3, 26) *Encyonema* sp4, 27) *Encyonema* sp5, 28) *Encyonema* sp6, 29) *Encyonema* sp7, 30) *Encyonema* aff. *aueri*. Scale bar = 10 μ m.

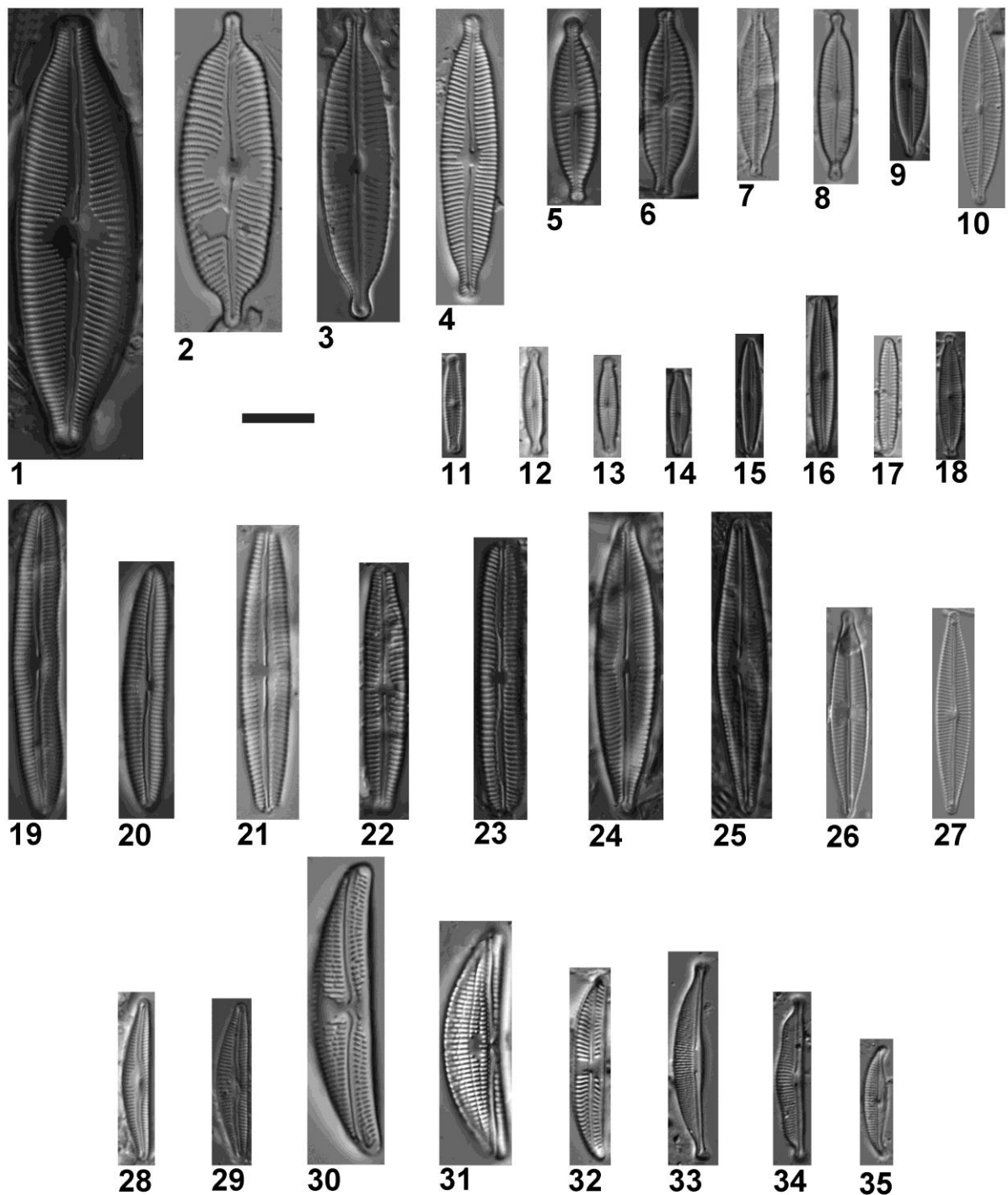


FIGURE C5. LM images. Cymbelloids (part 2) – Amphora – Halamphora. 1) *Cymbopleura tynnii*, 2) *Cymbopleura anglica*, 3) *Cymbopleura* sp2, 4) *Cymbopleura angustata* var. *spitsbergensis*, 5) *Cymbopleura* sp1, 6) *Cymbopleura amphicephala*, 7) *Cymbopleura* sp3, 8) *Cymbopleura broenlundensis*, 9) *Cymbopleura venetaeformis*, 10) *Encyonopsis descripta*, 11) *Encyonopsis* sp5, 12) *Encyonopsis* sp2, 13) *Encyonopsis* sp3, 14) *Encyonopsis* sp4, 15) *Encyonopsis krammeri*, 16) *Encyonopsis* sp1, 17) *Encyonopsis* cf. sp1 sensu Antoniadis et al. 2008, 18) *Encyonopsis subminuta*, 19) *Cymbopleura incerta* var. *incerta*, 20) *Cymbopleura incerta* var. *spitsbergensis*, 21) *Cymbopleura subaequalis* var. *truncata*, 22) *Cymbopleura subaequalis* s. l., 23) *Cymbopleura oblongata* var. *parva*, 24) *Cymbopleura incertiformis*, 25) *Encyonopsis cesatiformis*, 26-27) *Encyonopsis cesatii*, 28) *Delicata spitsbergensis*, 29) *Delicata delicatula*, 30) *Amphora affinis*, 31) *Amphora lange-bertalotii* var. *tenuis*, 32) *Amphora inariensis*, 33) *Halamphora oligotraphenta*, 34) *Halamphora dusenii*, 35) *Halamphora obscura*. Scale bar = 10 μ m.

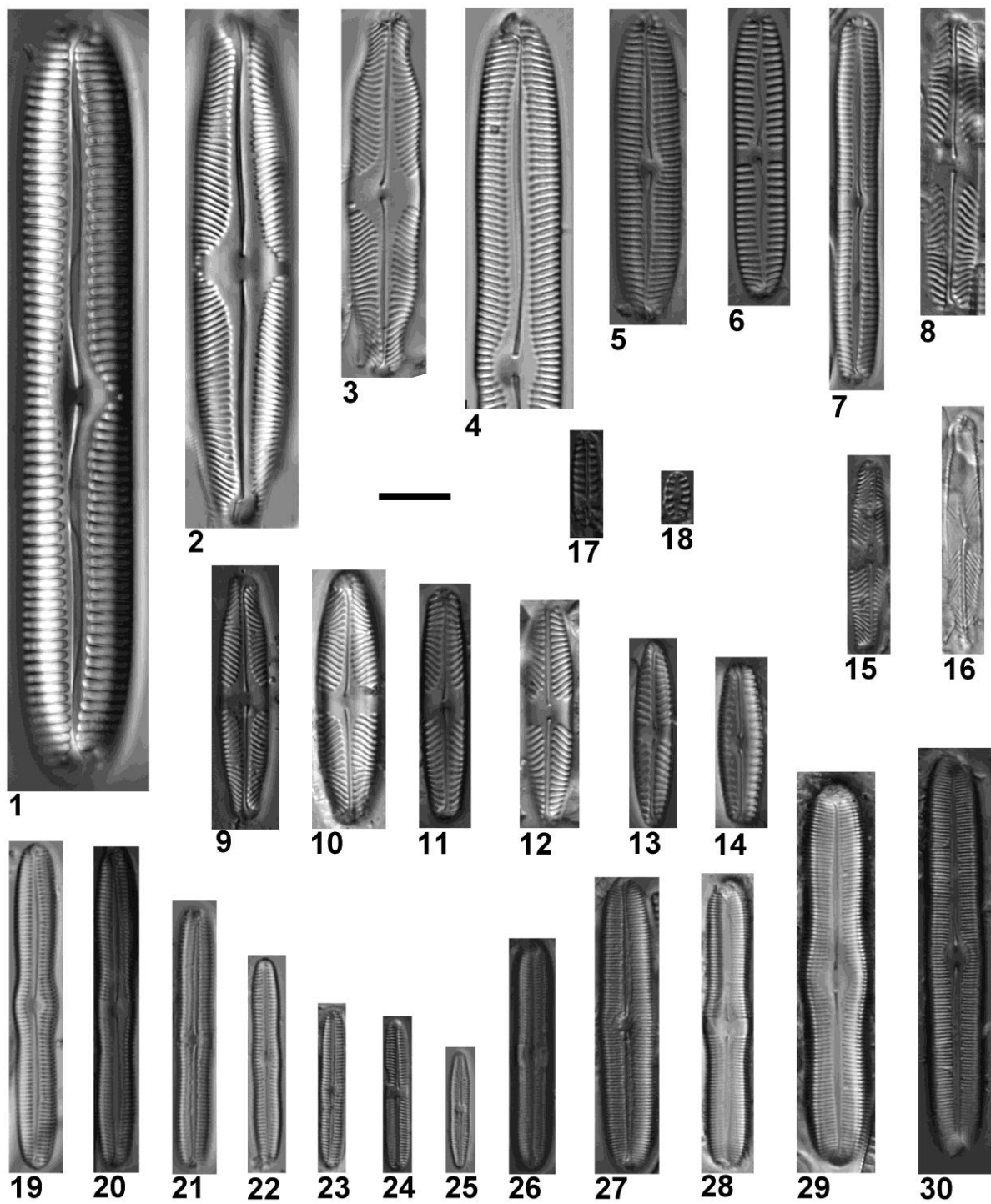


FIGURE C6. LM images. *Pinnularia* – *Alveovallum* – *Hygropetra* – *Caloneis*. 1) *Pinnularia ilkaschoenfelderae*, 2) *Pinnularia divergens*, 3) *Pinnularia biceps*, 4) *Pinnularia viridiformis*, 5) *Pinnularia frequentis*, 6) *Pinnularia isostauron*, 7) *Alveovallum beyensii*, 8) *Pinnularia krammeri*, 9) *Pinnularia* cf. *marctica*, 10) *Pinnularia* sp2, 11) *Pinnularia* cf. *perinterrupta*, 12) *Pinnularia brebisonii* var. *acuta*, 13) *Pinnularia obscura*, 14) *Pinnularia* sp1, 15) *Pinnularia pseudodivergentissima*, 16) *Pinnularia divergentissima*, 17) *Pinnularia* cf. *intermedia*, 18) *Hygropetra balfouriana*, 19) *Caloneis arctica*, 20) *Caloneis backmanii*, 21-22) *Caloneis tenuis*, 23) *Caloneis fusus*, 24) *Caloneis fasciata*, 25) *Caloneis sublinearis*, 26) *Caloneis falcifera*, 27) *Caloneis thermalis*, 28) *Caloneis silicula* var. *intermedia*, 29) *Caloneis silicula*, 30) *Caloneis alpestris*. Scale bar = 10 μ m.

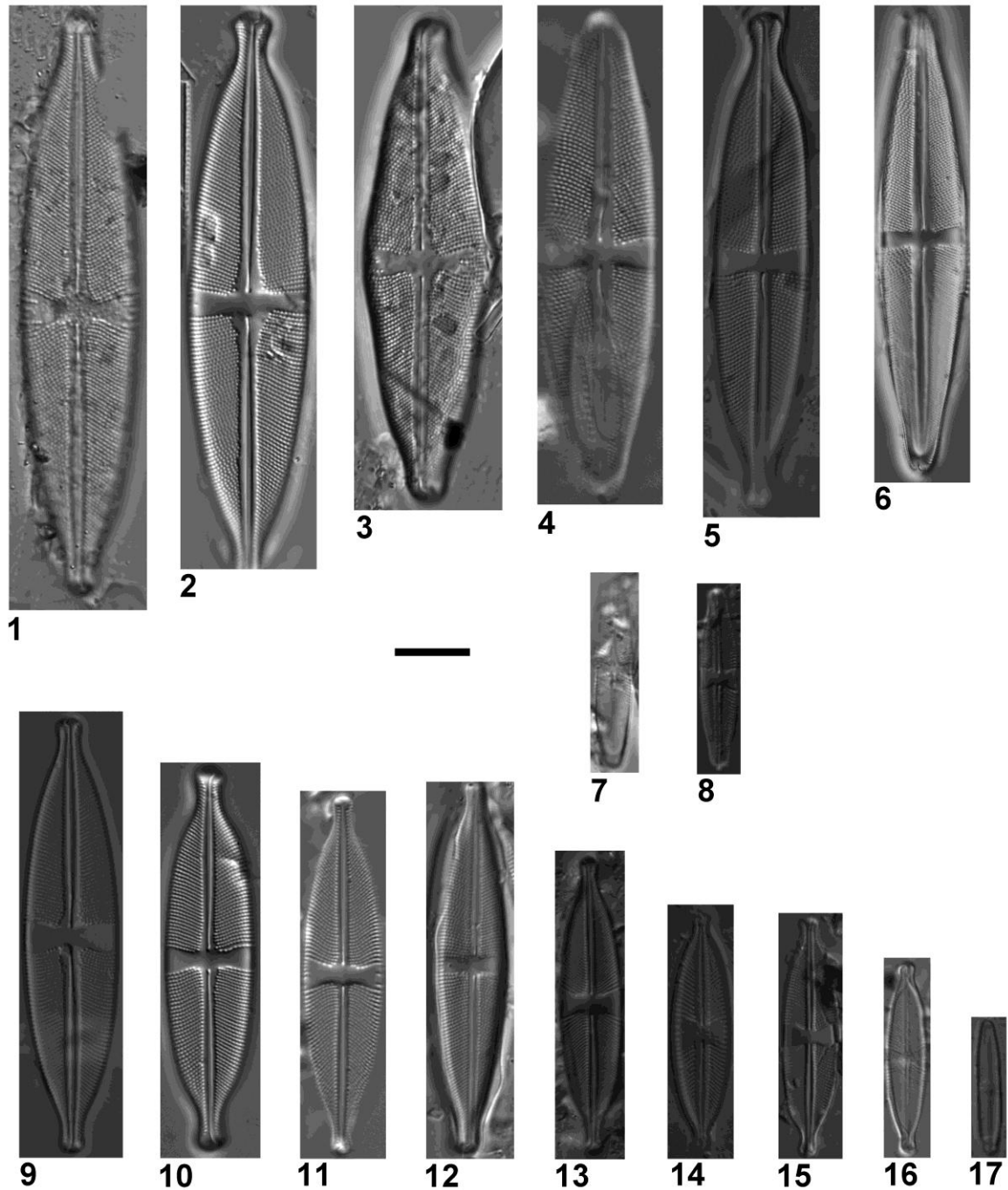


FIGURE C7. LM images. *Stauroneis*. 1) *Stauroneis circumborealoides*, 2) *Stauroneis clandestina*, 3) *Stauroneis* sp2, 4) *Stauroneis gelida*, 5) *Stauroneis amphicephala*, 6) *Stauroneis subhyperborea*, 7) *Stauroneis* aff. *obtusa*, 8) *Stauroneis lapponica*, 9) *Stauroneis svalbardensis*, 10) *Stauroneis reichardtii*, 11) *Stauroneis* sp1, 12) *Stauroneis* aff. *subgracilis*, 13) *Stauroneis fransisci-josephi*, 14) *Stauroneis* cf. *anceps* sensu Foged 1964, 15) *Stauroneis intricans*, 16) *Stauroneis agrestiformis*, 17) *Stauroneis* cf. *lundii*. Scale bar = 10 μ m, except Figure 6 (scale bar = 4 μ m).

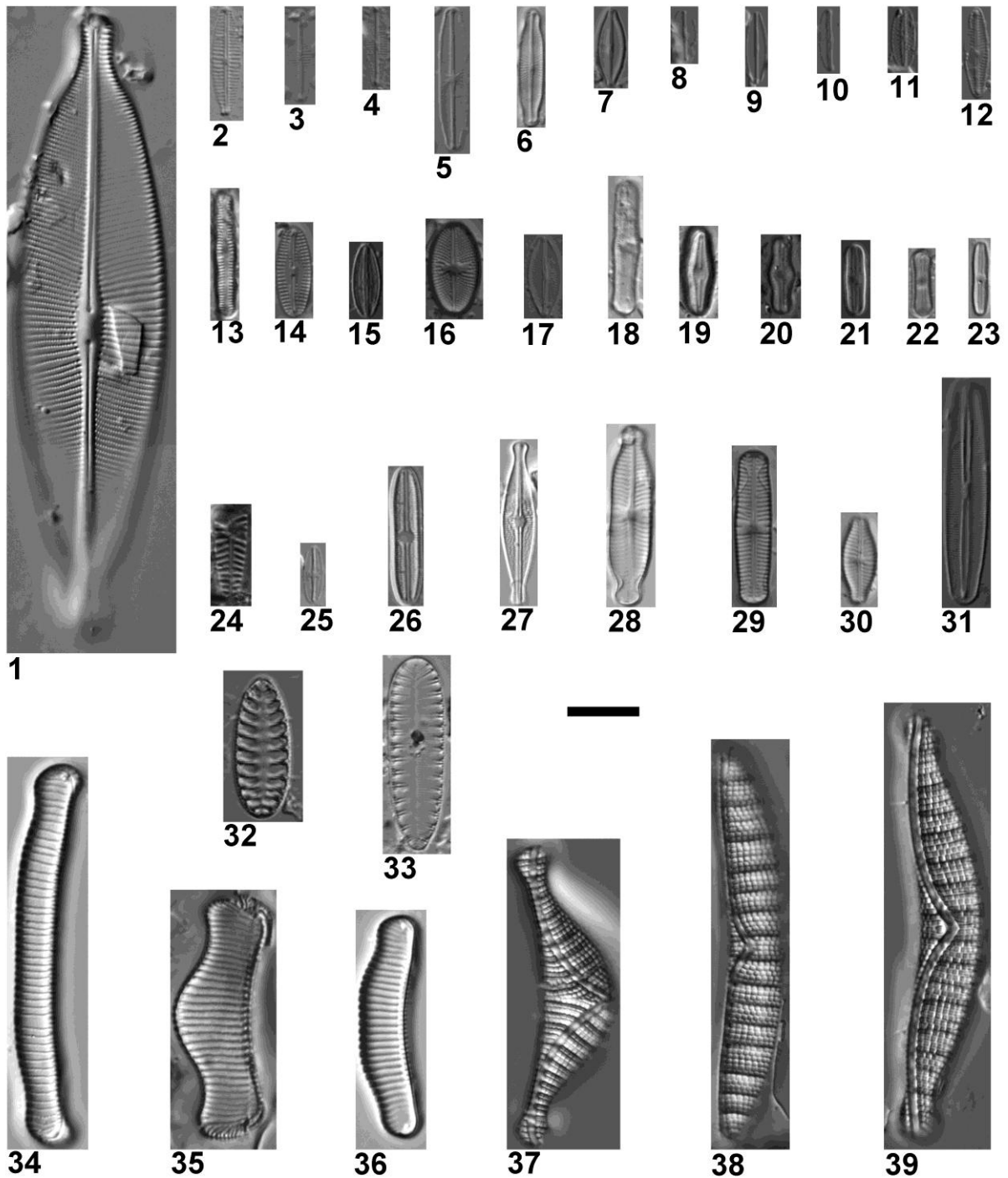


FIGURE C8. LM images *Craticula* – *Kobayasiella* – *Adlafia* – *Fistulifera* – *Mayamaea* – *Chamaepinnularia* – *Fallacia* – *Microcostatus* – *Cavinula* – *Humidophila* – *Hippodonta* – *Brachysira* – *Geissleria* – *Frustulia* – *Surirella* – *Eunotia* – *Epithemia*. 1) *Craticula ambigua*, 2) *Craticula submolesta*, 3) *Craticula minunsculoides*, *Craticula molestiformis*, 5) *Kobayasiella* sp. 6) *Adlafia bryophila*, 7) *Adlafia minuscula*, 8) *Fistulifera saprophila*, 9) *Mayamaea* cf. *aliena*, 10) *Mayamaea permitis*, 11) *Mayamaea atomus*, 12) *Chamaepinnularia* cf. *evanida*, 13) *Chamaepinnularia gandrupii*, 14) *Fallacia losevae*, 15) *Microcostatus krasskei*, 16) *Cavinula* sp, 17) *Cavinula cocconeiformis*, 18) *Humidophila* sp2, 19) *Humidophila perpusilla*, 20) *Humidophila ingeaeformis*, 21) *Humidophila brekkaensis*, 22) *Humidophila paracontenta*, 23) *Humidophila* sp1 sensu Antoniadou et al. 2008, 24) *Hippodonta hungarica*, 25) Unidentified diatom, 26) *Brachysira zellensis*, 27) *Brachysira neoexilis*, 28) *Geissleria* sp1, 29) *Geissleria paludosa*, 30) *Geissleria* sp2, 31) *Frustulia* sp, 32) *Surirella terricola*, 33) *Surirella minuta*, 34) *Eunotia* sp, 35) *Eunotia ewa*, 36) *Eunotia minor*, 37) *Epithemia sores*, 38) *Epithemia turgida*, 39) *Epithemia adnata*. Scale bar = 10 μ m.

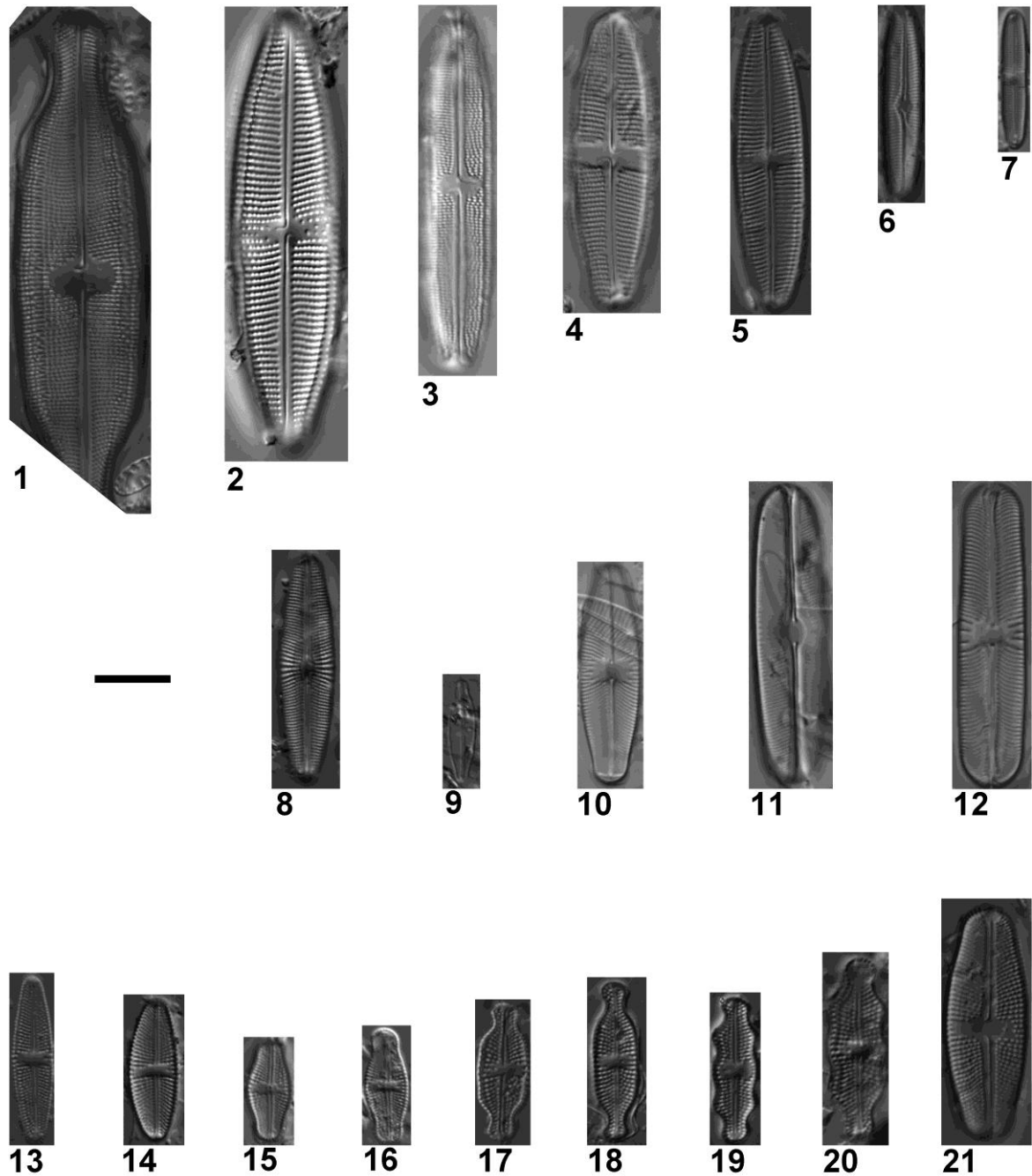


FIGURE C9. LM images. *Neidium* – *Muelleria* – *Sellaphora* – *Luticola*. 1) *Neidium productum*, 2) *Neidium distincte-punctatum*, 3) *Neidium decoratum*, 4) *Neidium kozlowii* var. *elliptica*, 5) *Neidium kozlowii* var. *densestriata*, 6) *Neidium bergii*, 7) *Neidium spitsbergense*, 8) *Muelleria gibbula*, 9) *Sellaphora nana*, 10) *Sellaphora pupula*, 11) *Sellaphora bacillum*, 12) *Sellaphora rectangularis*, 13) *Luticola similis*, 14) *Luticola frequentissima*, 15) *Luticola* sp1, 16) *Luticola* sp2, 17) *Luticola* sp3, 18) *Luticola bilyi*, 19) *Luticola triundulata*, 20) *Luticola quenquenodis*, 21) *Luticola cohnii*. Scale bar = 10 μ m.

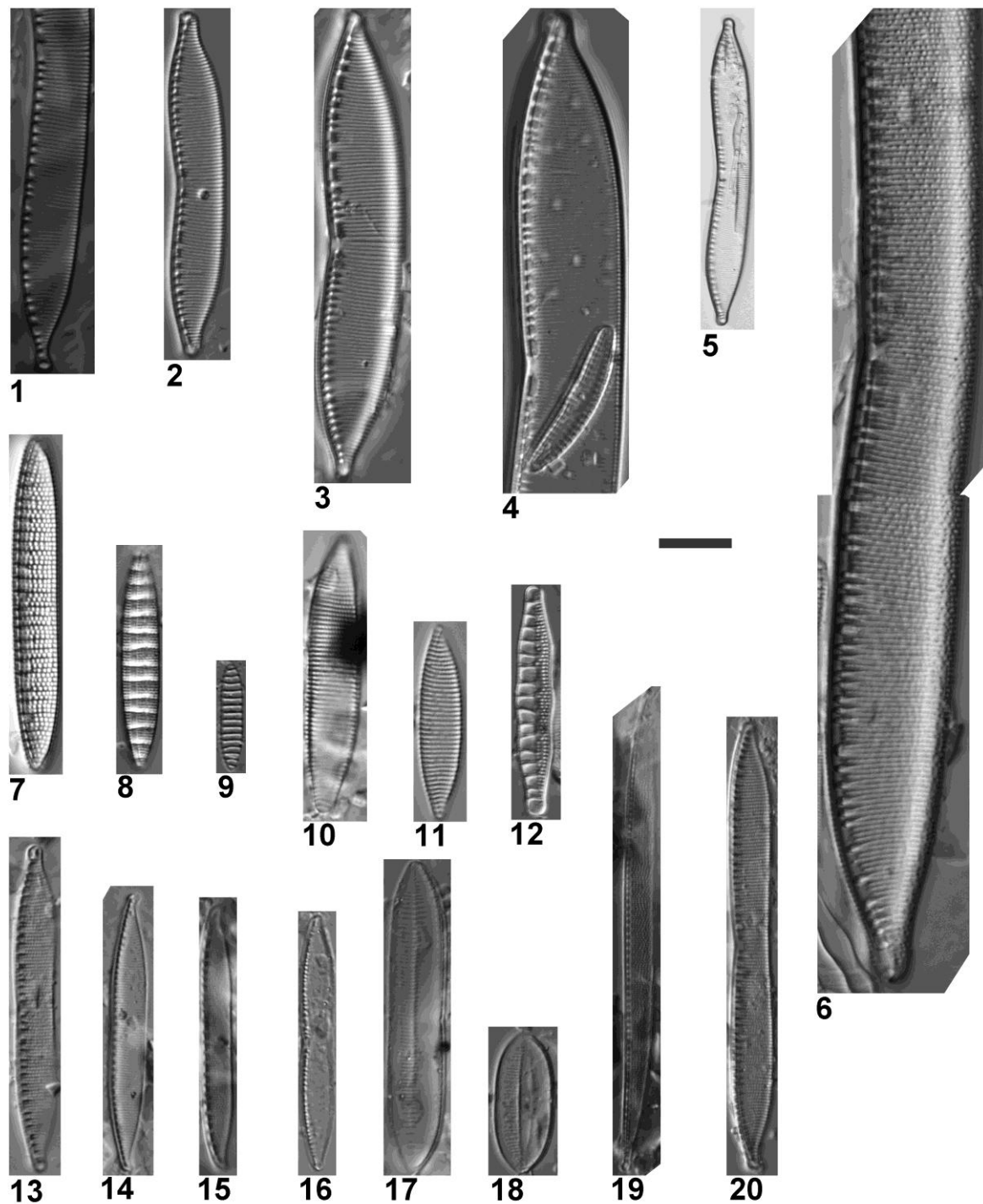


FIGURE C10. LM images. *Hantzschia* – *Denticula* – *Nitzschia* (part 1). 1) *Hantzschia vivacior*, 2) *Hantzschia amphioxys*, 3) *Hantzschia abundans*, 4-5) *Hantzschia hyperborea*, 6) *Hantzschia rhaetica*, 7) *Denticula kuetzingii* incl. var. *rumrichae*, 8) *Denticula tenuis*, 9) *Denticula subtilis*, 10) *Nitzschia angustata*, 11) *Nitzschia angustatula*, 12) *Nitzschia sinuata*, 13) *Nitzschia commutata*, 14) *Nitzschia* sp5, 15) *Nitzschia* sp3, 16) *Nitzschia hamburgiensis*, 17) *Nitzschia* cf. *levidensis* var. *salinarum*, 18) *Nitzschia debilis*, 19) *Nitzschia sigma*, 20) *Nitzschia subamphioxoides*. Scale bar = 10 μ m, except Figure 5 (scale bar = 4 μ m).

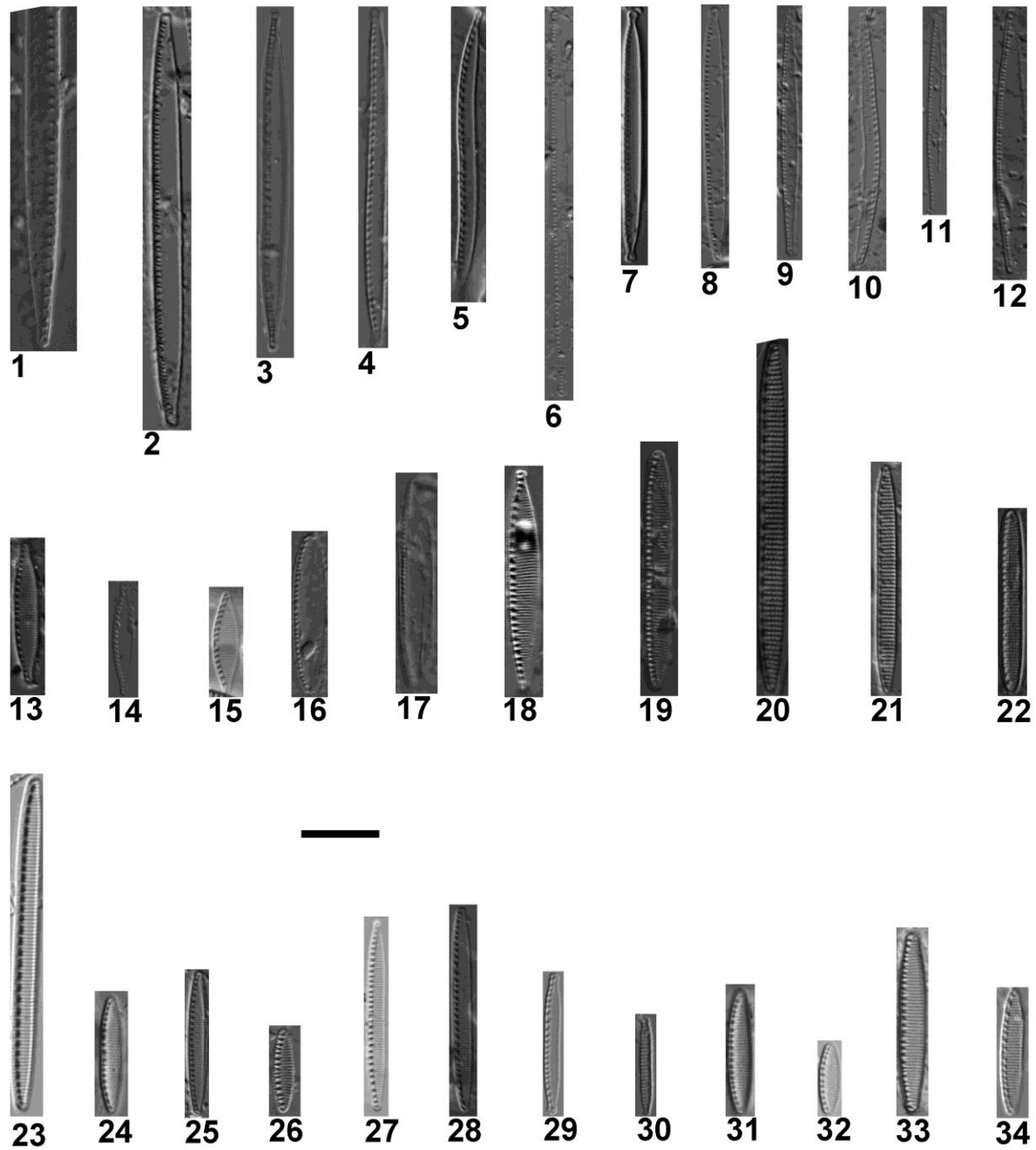


FIGURE C11. LM images. *Nitzschia* (part 2). 1) *Nitzschia recta*, 2) *Nitzschia sublinearis* var. *subtilis*, 3) *Nitzschia dissipata*, 4) *Nitzschia* cf. *graciliformis*, 5) *Nitzschia claussii*, 6) *Nitzschia graciliformis*, 7) *Nitzschia suchlandtii*, 8) *Nitzschia archibaldii*, 9) *Nitzschia paleacea*, 10) *Nitzschia* sp7, 11) *Nitzschia* sp1, 12) *Nitzschia palea*, 13) *Nitzschia bryophila*, 14) *Nitzschia lacuum*, 15) *Nitzschia fonticola*, 16) *Nitzschia communis*, 17) *Nitzschia thermaloides*, 18) *Nitzschia* sp4, 19) *Nitzschia* sp8, 20) *Nitzschia* sp2, 21) *Nitzschia modesta*, 22) *Nitzschia bacilliformis*, 23) *Nitzschia alpina*, 24) *Nitzschia perminuta* group 1, 25) *Nitzschia perminuta* group 2, 26) *Nitzschia perminuta* group 3, 27) *Nitzschia perminuta* group 4, 28) *Nitzschia perminuta* group 5, 29) *Nitzschia perminuta* group 6, 30) *Nitzschia* sp6, 31) *Nitzschia soratensis*, 32-33) *Nitzschia liebetruthii*, 34) *Nitzschia* sp9. Scale bar = 10 μ m.

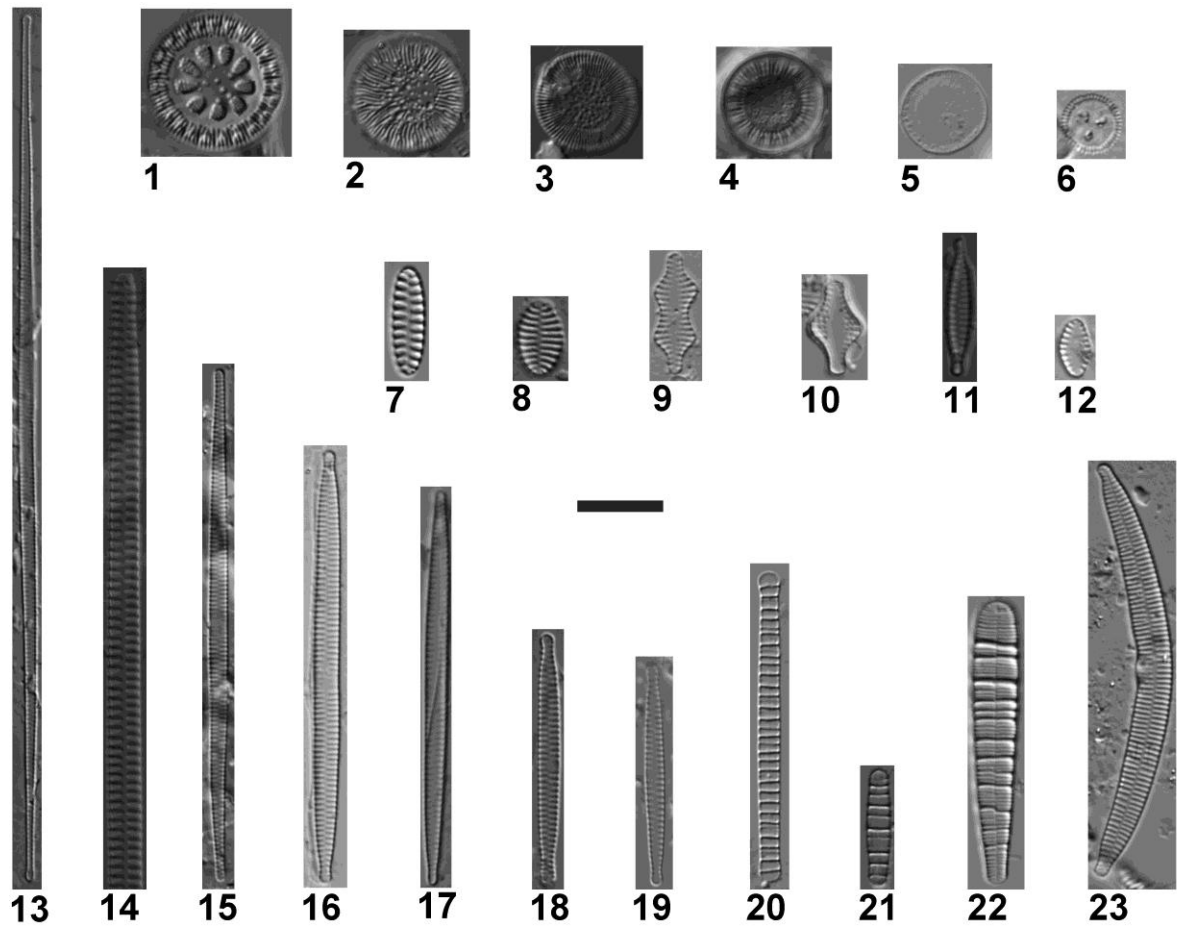


FIGURE C12. LM images. Araphidae. 1) *Cyclotella antiqua*, 2) *Cyclotella cf. comta*, 3) *Cyclotella pseudocomensis*, 4) *Cyclotella* sp1, 5) *Cyclotella* sp2, 6) *Cyclotella ocellata*, 7) *Staurosirella* aff. *lapponica*, 8) *Staurosira venter* 9) *Staurosira robusta*, 10) *Staurosira pseudoconstruens*, 11) *Staurosira oldenburgiana*, 12) *Pseudostaurosira brevistriata*, 13) *Ulnaria delicatissima*, 14) *Ulnaria danica*, 15) *Fragilaria tenera*, 16) *Fragilaria* sp1, 17) *Fragilaria gracilis*, 18) *Fragilaria* sp2, 19) *Fragilaria* sp3, 20) *Diatoma tenue*, 21) *Diatoma monoliformis*, 22) *Meridion circulare*, 23) *Hannaea arcus*. Scale bar = 10 μ m.

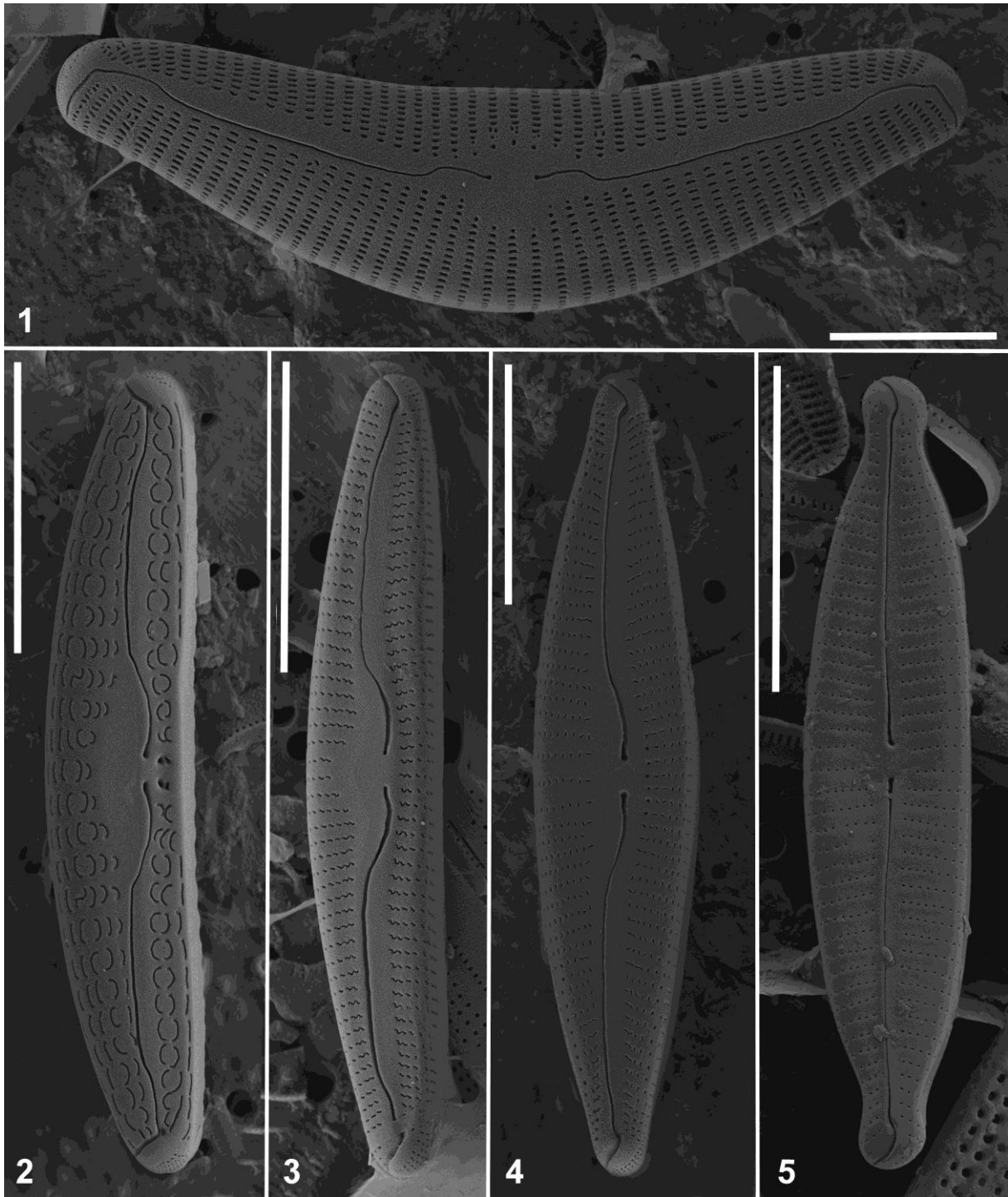


FIGURE C13. SEM images. 1) *Cymbella arctica*, 2) *Cymbella botellus*, 3) *Delicata spitsbergensis*, 4) *Cymbella* sp sensu Antoniadis et al. 2008, 5) *Cymbopleura angustata* var. *spitsbergensis*. Scale bar = 10 μ m.

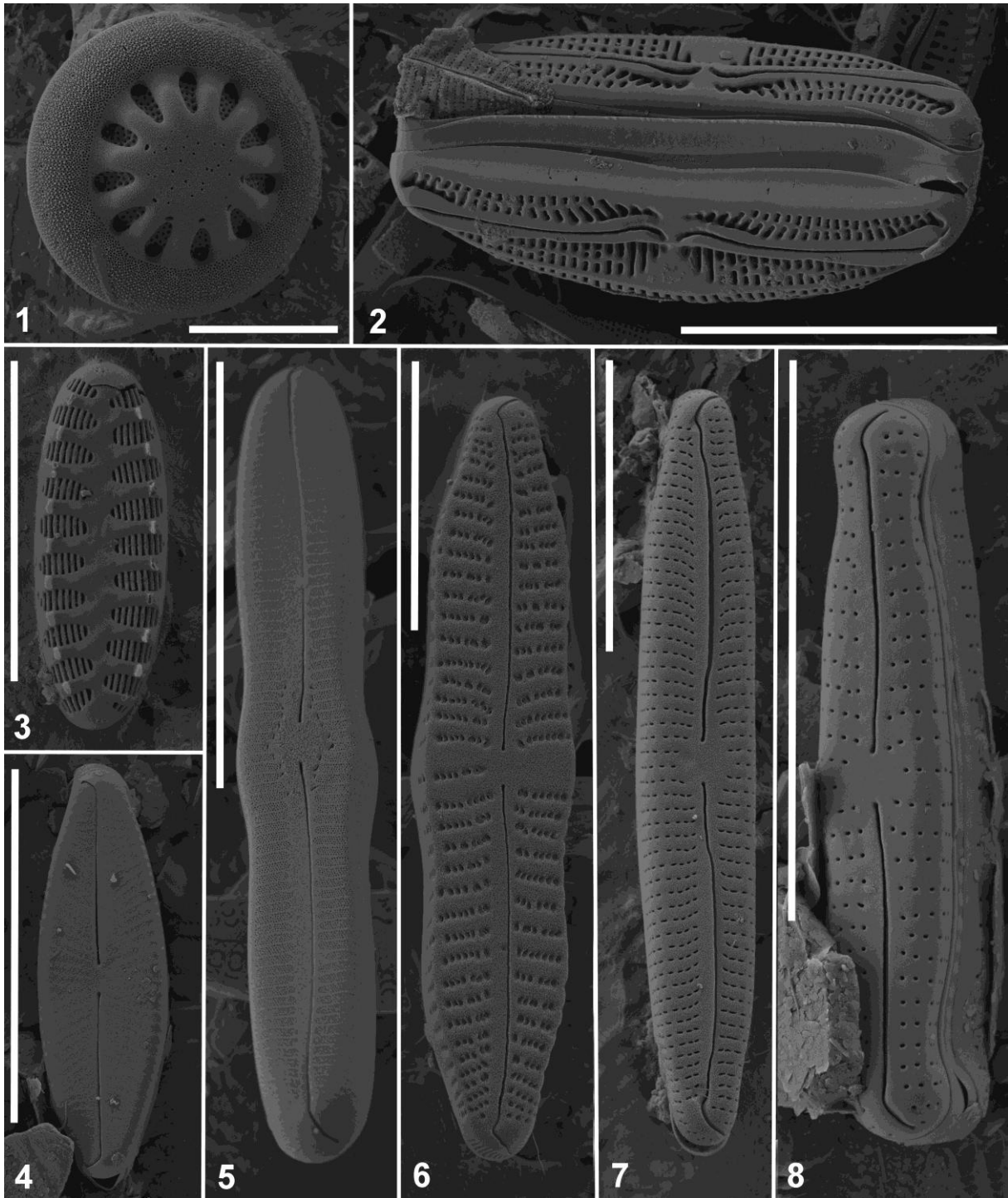


FIGURE C14. SEM images. 1) *Cyclotella antiqua*, 2) *Amphora affinis*, 3) *Staurosirella* aff. *lapponica*, 4) *Adlafia minuscula*, 5) *Caloneis alpestris*, 6) *Gomphonema svalbardense*, 7) *Encyonopsis* sp1, 8) *Encyonopsis* sp5. Scale bar = 10 μ m.

Appendix D. Figures



FIGURE D1. Different lake types in the study area: a) kettle lake nearby the Nordenskiöld glacier (picture: Kateřina Kopalová), b) proglacial lake nearby Ragnar glacier (picture: Kateřina Kopalová), c) tectonic determined lake on Oblik Peninsula (picture: Jan Kavan), d) snow depression related lake at Mimerdalen (picture: Jan Kavan), e) marine terrace lake at Brucebyen, f) marine terrace lake at Ebbadalen, g) marine terrace lake at Mathiessendalen, h) karst lake at Mathiessendalen (picture: Kateřina Kopalová).

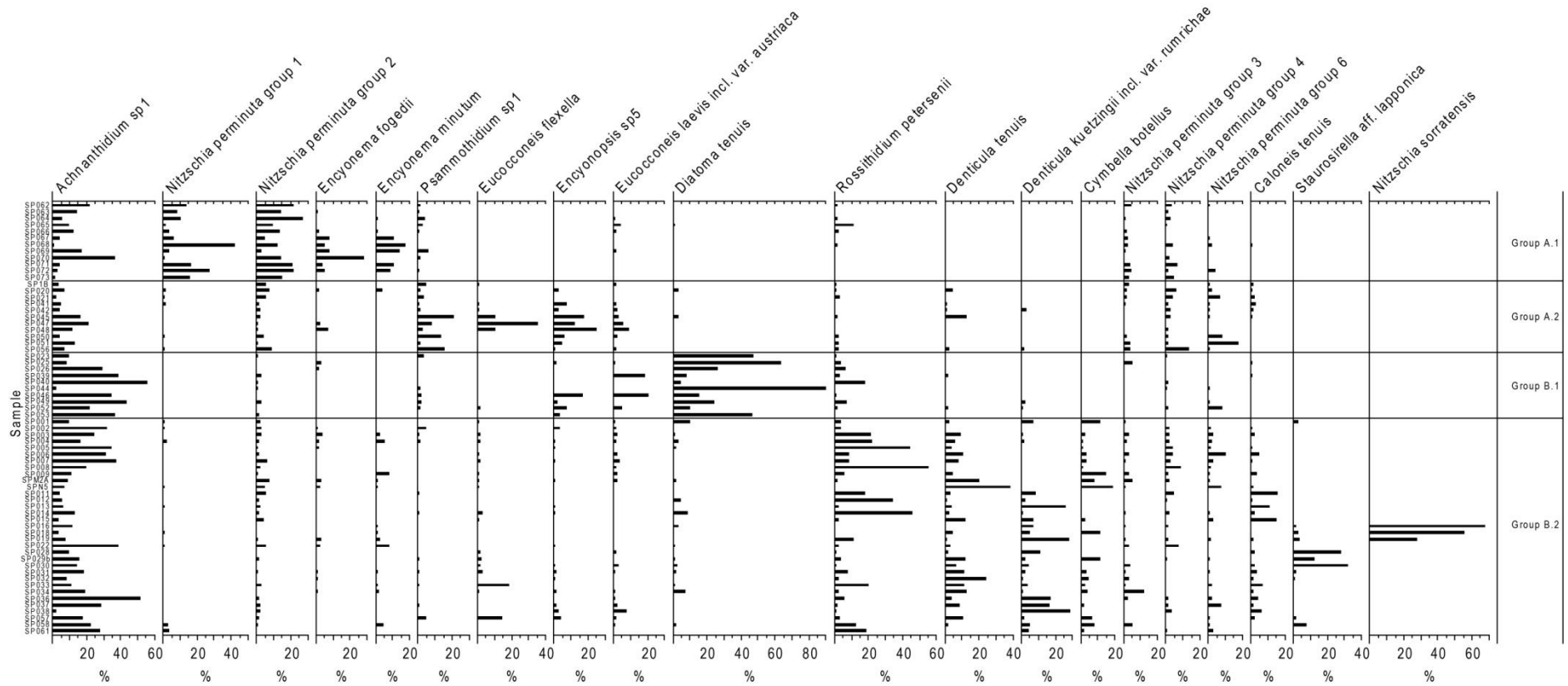


FIGURE D2. Most abundant taxa of the 4 different assemblages distinguished in the recent lake samples (part 1). The X-axis indicates the percentage of the total counted diatom valves. The sample numbers are explained in Appendix E (Table E2). The scale bar of the X-axis is identical for all graphs.

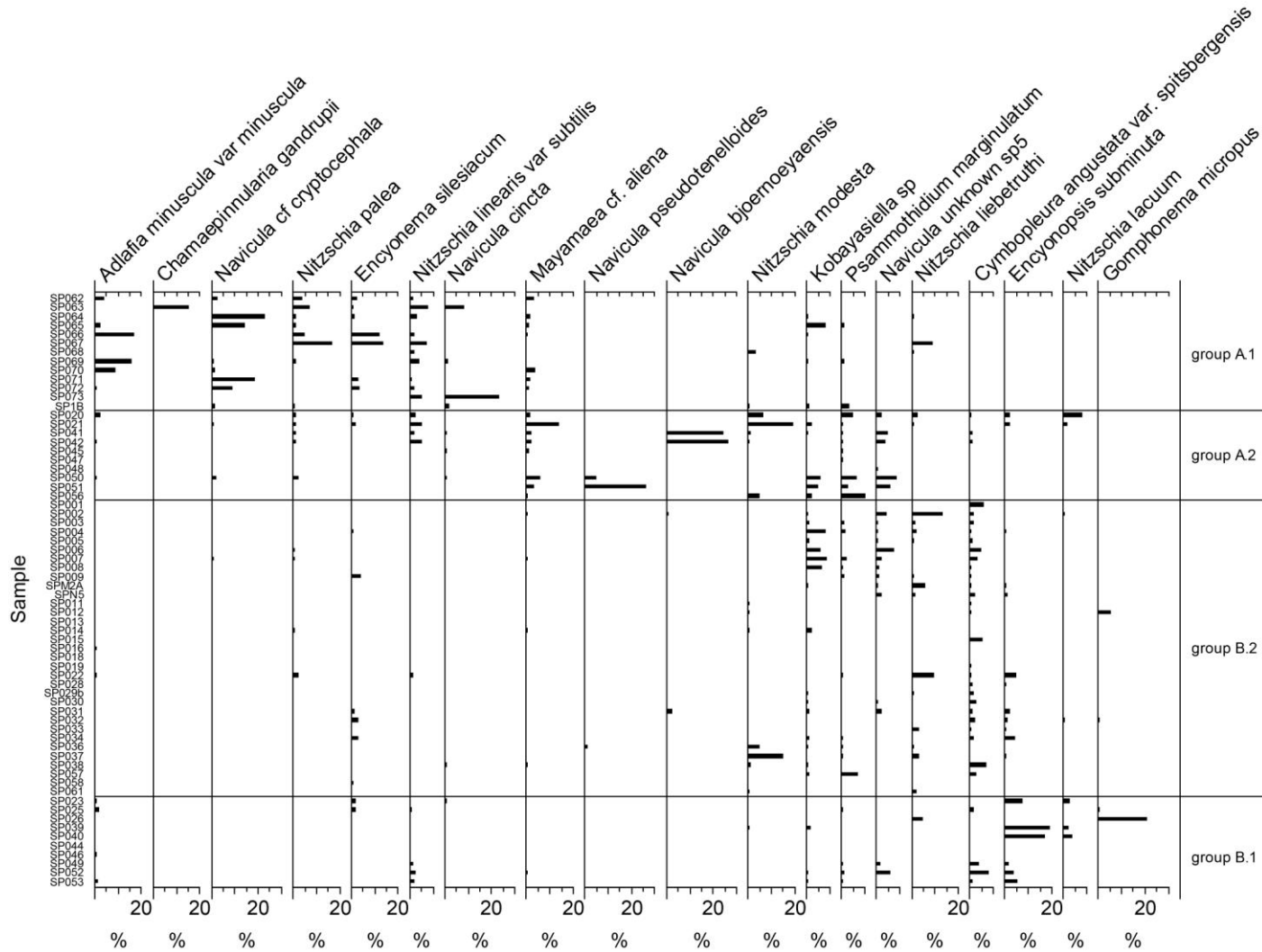


FIGURE D3. Most abundant taxa of the 4 different assemblages distinguished in the recent lake samples (part 2). The X-axis indicates the percentage of the total counted diatom valves. The sample numbers are explained in Appendix E (Table E2). The scale bar of the X-axis is identical for all graphs.

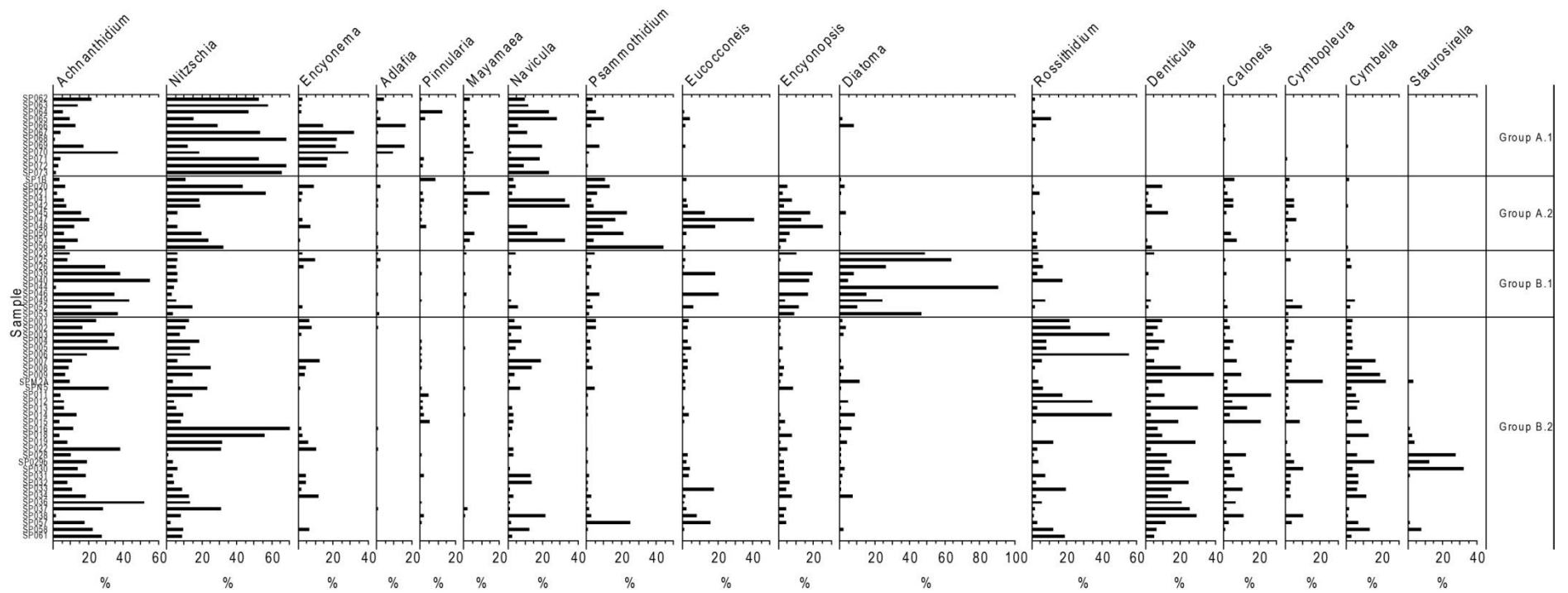


FIGURE D4. Most abundant genera of the 4 different assemblages distinguished in the recent lake samples. The X-axis indicates the percentage of the total counted diatom valves. The sample numbers are explained in Appendix E (Table E2). The scale bar of the X-axis is identical for all graphs.

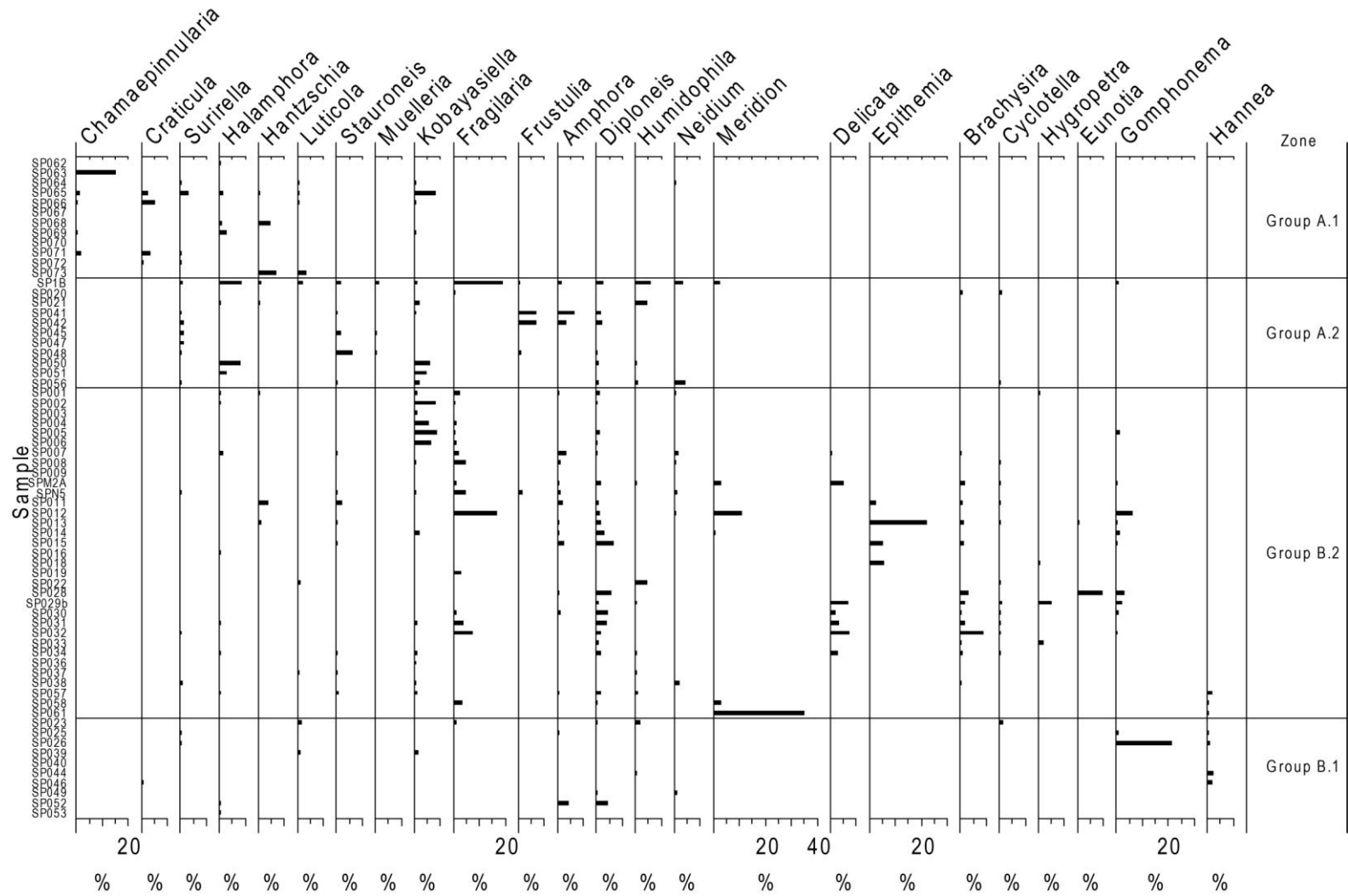


FIGURE D5. Several of the less abundant genera of the 4 different assemblages distinguished in the recent lake samples. The X-axis indicates the percentage of the total counted diatom valves. The sample numbers are explained in Appendix E (Table E2). The scale bar of the X-axis is identical for all graphs.

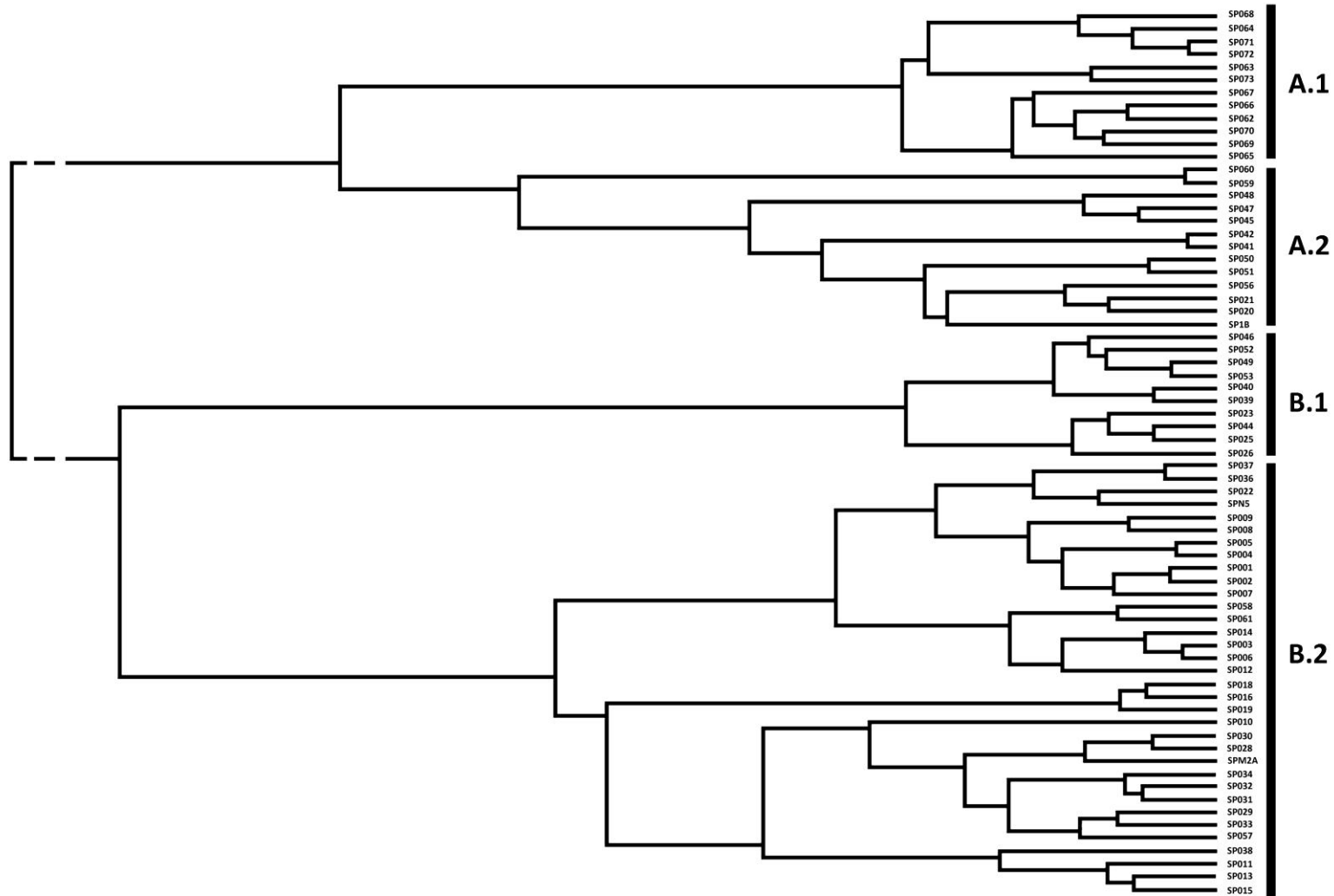


FIGURE D6. Cluster diagram for the recent lake samples. The 3 samples indicated as outliers in the DCA are shown, i.e. samples SP059 and SP060 in group A.2 and sample SP010 in group B.2.

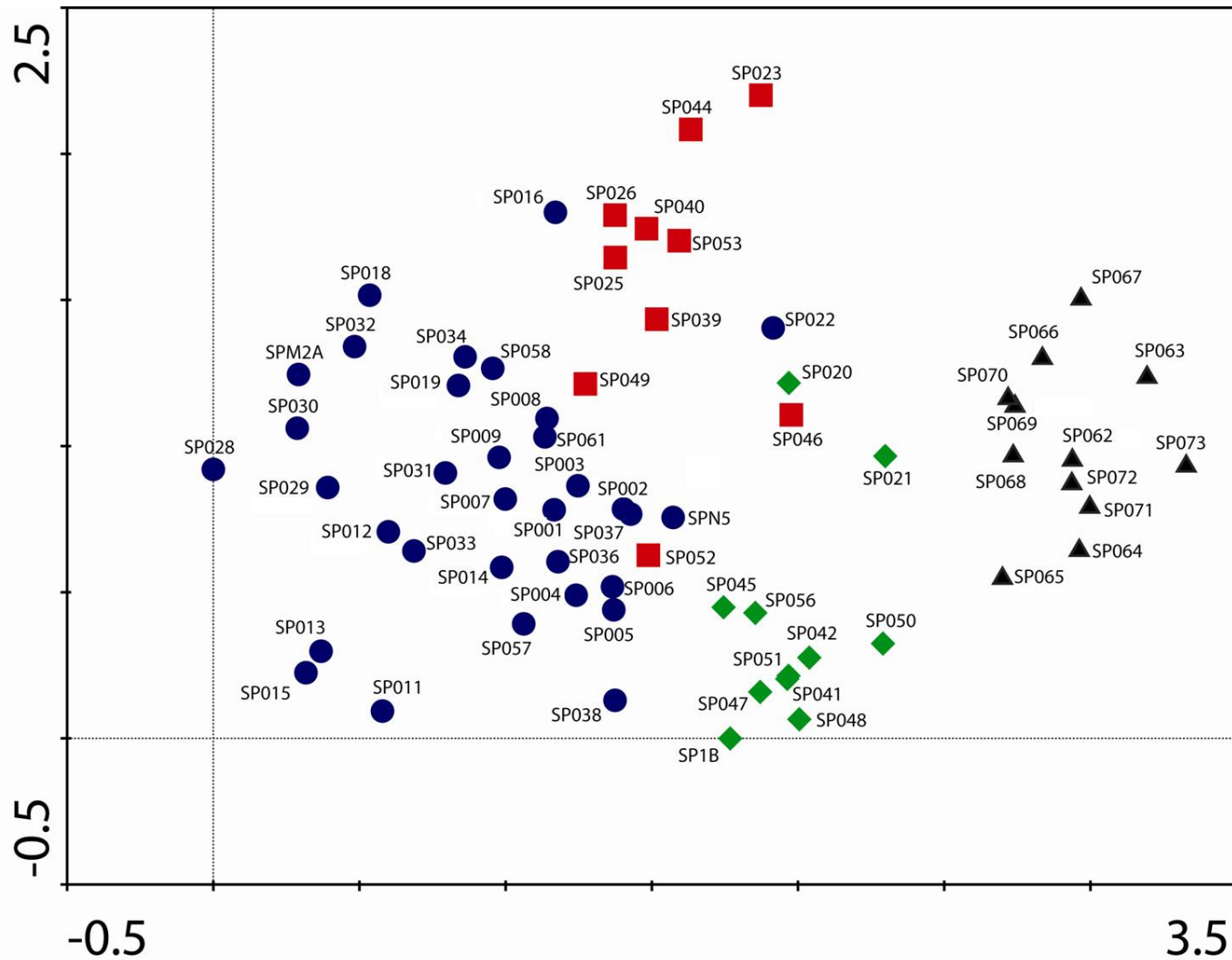


FIGURE D7. Detrended correspondence analysis (DCA) showing the position of the recent lake samples plotted on the first 2 axes of the DCA. The 3 outliers were removed. The separation of the different assemblages was based on the cluster analysis in MVSP. Black triangles = *Nitzschia perminuta* assemblage (group A.1), green diamonds = *Psammothidium* assemblage (group A.2), red squares = *Diatoma tenuis* assemblage (group B.1) and blue dots = *Denticula – Rossithidium* assemblage (group B.2). The explanation of the different sample numbers is given in Appendix E (Table E2). A DCA biplot with indication of the most important taxa is given in Appendix D (Figure D8).

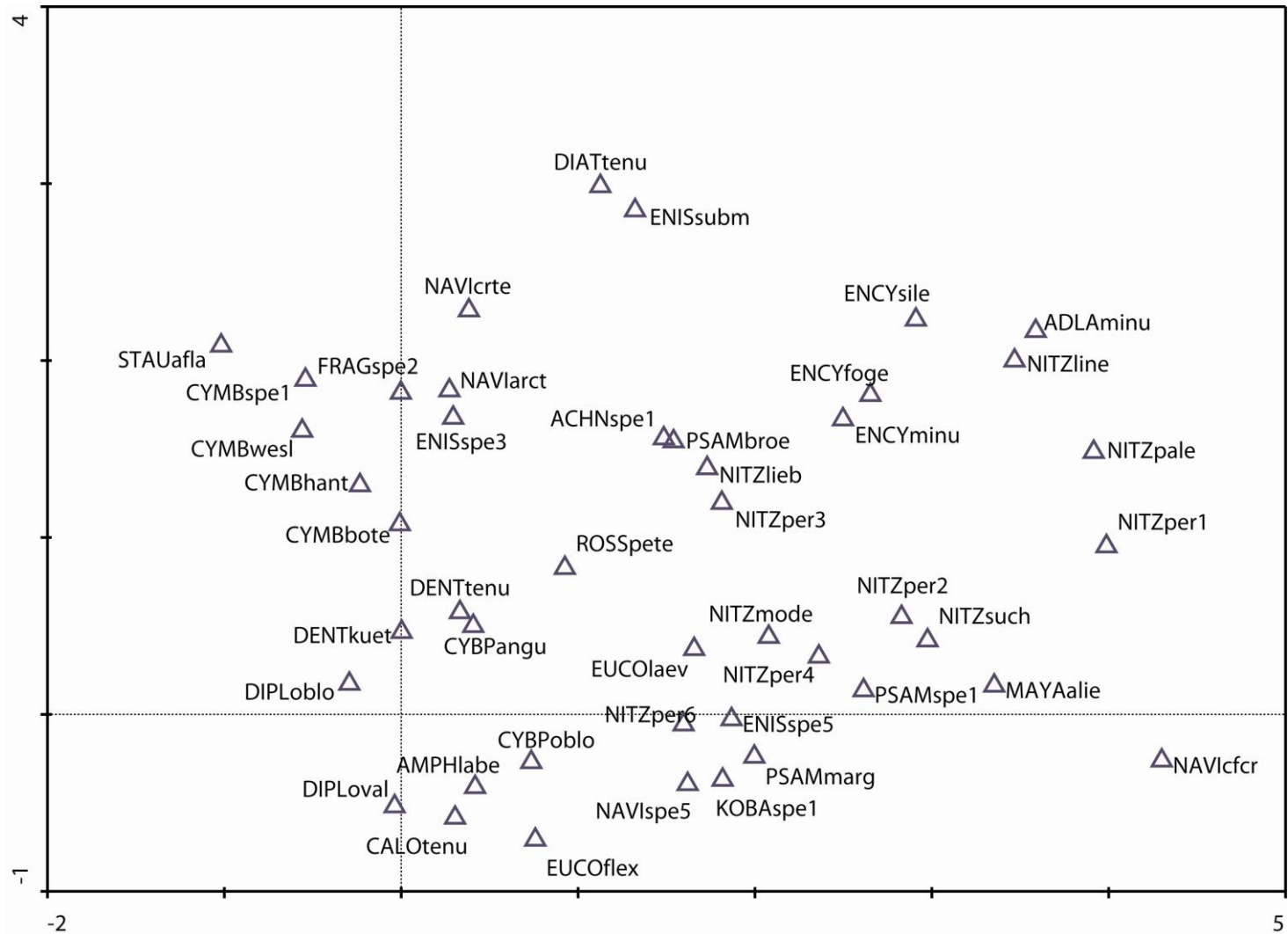


FIGURE D8. Detrended correspondence analysis (DCA) showing the position of the most important taxa plotted on the first 2 axes of the DCA. The abbreviations of the taxon names are clarified in Appendix B (Table B1).

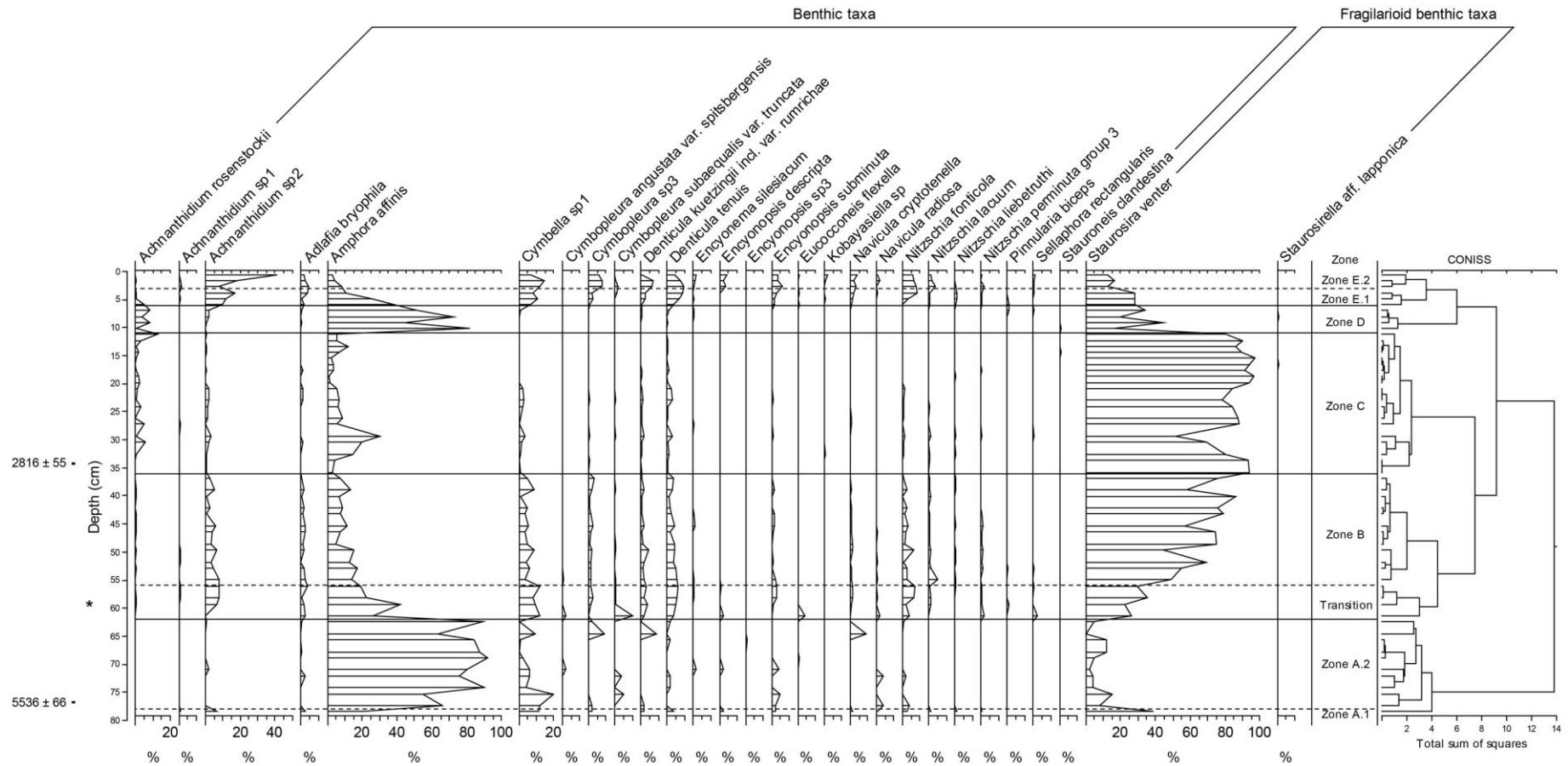


FIGURE D9. Diatom stratigraphy of the sediment core (master core). The X-axis indicates the percentage of the total counted diatom valves. The zonation is based on the CONISS constrained cluster analysis and the broken stick significance test. In the layers below the asterisk (*) less than 400 diatom valves were counted in all samples except one (i.e. 67.8 cm depth). The lines in the stratigraphy indicate the position of the examined samples. The scale bar of the X-axis is identical for all graphs. The indicated ages are expressed in 'cal. yr BP'.

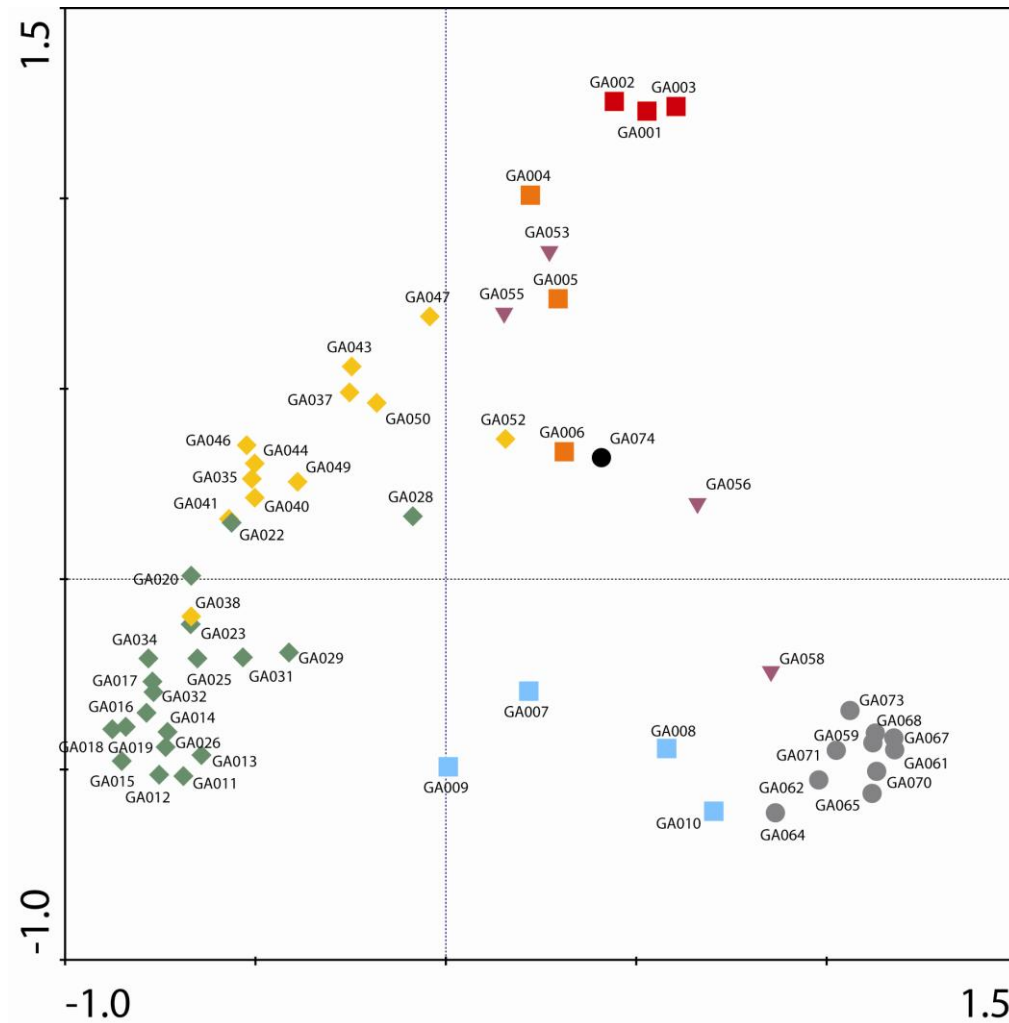


FIGURE D10. Principal Component Analysis (PCA) of the sediment core samples plotted on the first 2 axes of the PCA. The separation of the different groups is based on the CONISS constrained cluster analysis. Black = zone A.1, Grey = zone A.2, Purple = transition zone, yellow = zone B, green = zone C, blue = zone D, orange = zone E.1, red = zone E.2. Explanation of the sample numbers is given in Appendix E (Table E7).

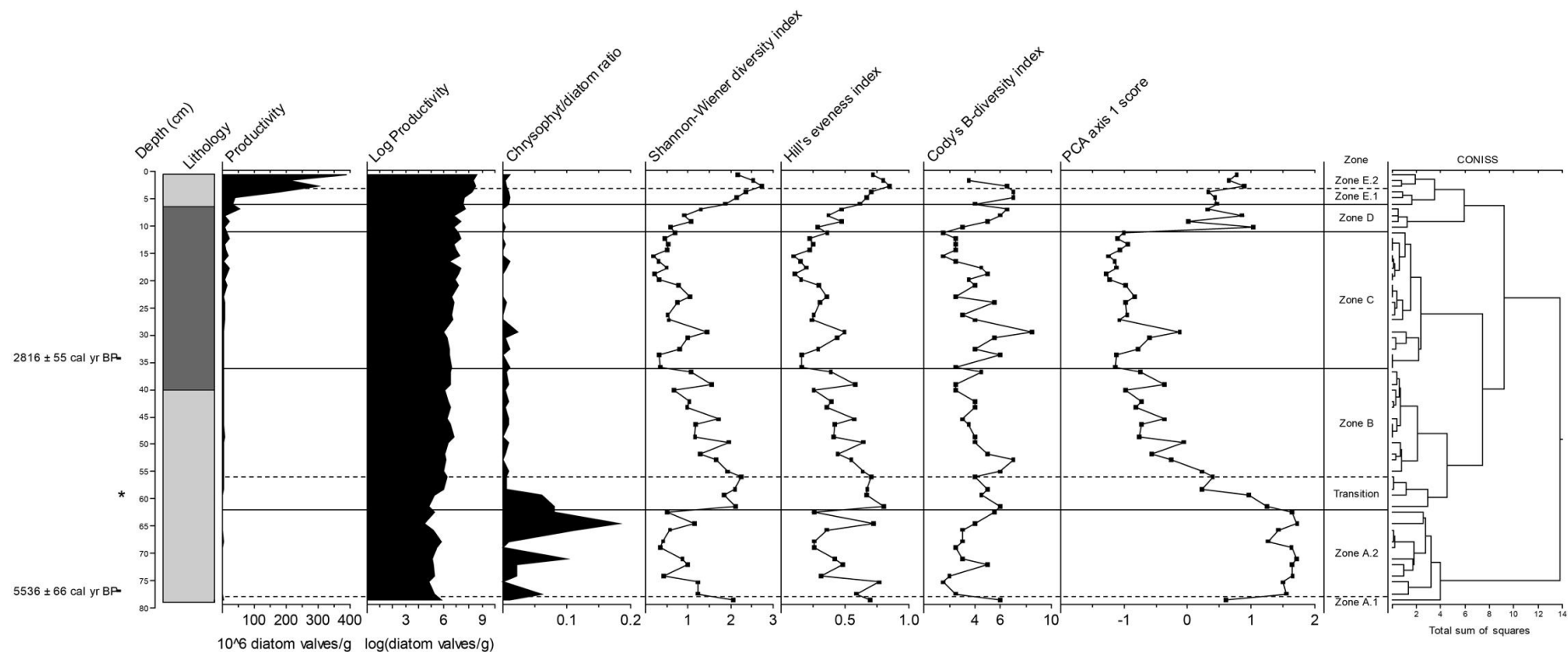


FIGURE D11. Lithology (light gray zones = homogeneous sediment, dark gray zone = varved sediment), productivity, chrysophyte diatom ratio, Shannon-Wiener diversity index, Hill's evenness index, Cody's β -diversity index and the score of the first PCA axis as a function of the depth of the sediment core (master core). In the layers below the asterisk (*) less than 400 diatom valves were counted in all samples except one (i.e. 67.8 cm depth). A more detailed graph of the logarithm of the productivity is given in Appendix D (Figure D12).

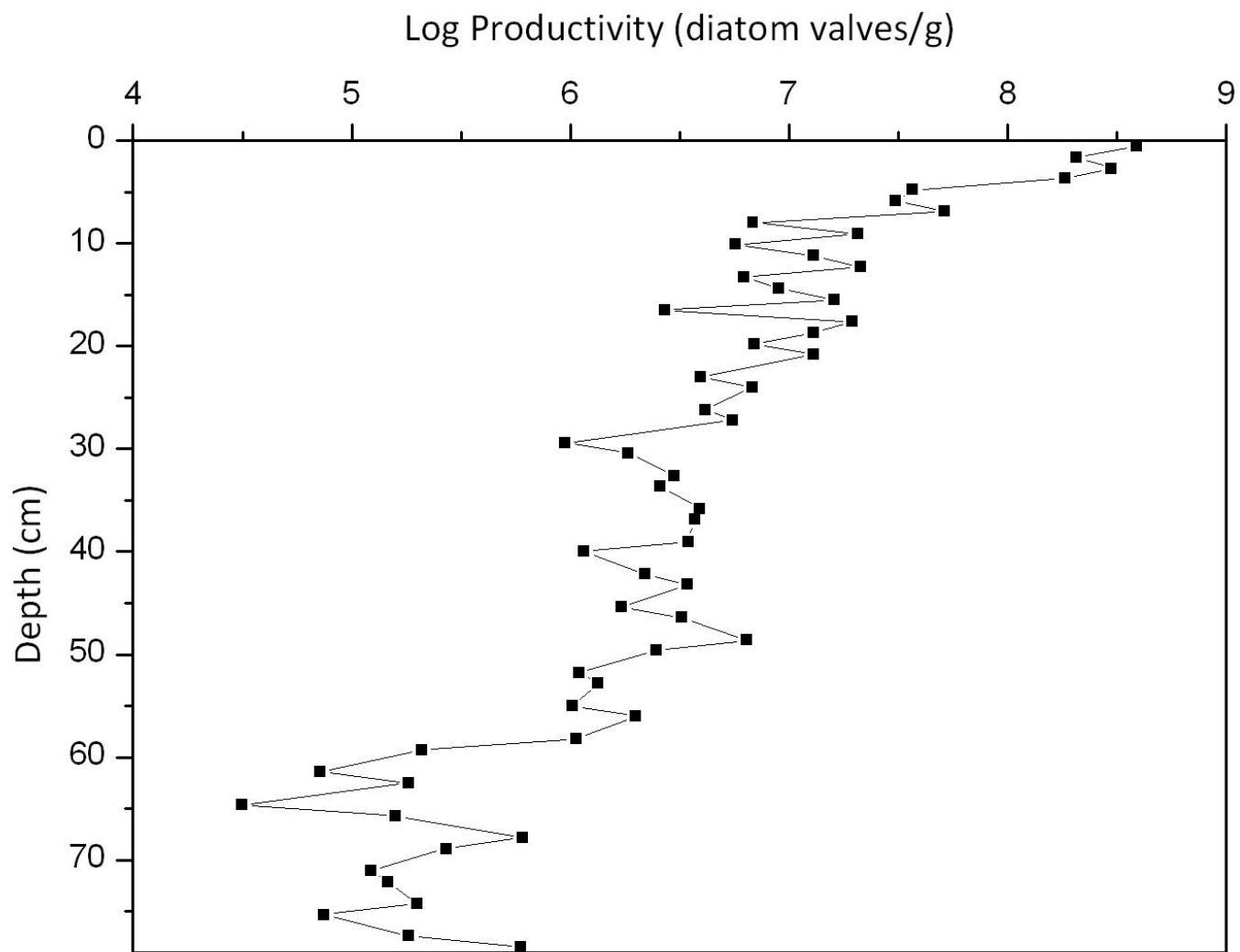


FIGURE D12. *Logarithm of the diatom productivity as a function of the depth of the sediment core (master core).*

Appendix E. Tables

TABLE E1. Overview of previous diatom studies on Svalbard. NS = not specified, UN = unknown by the author of this thesis. Recent changes in genus boundaries have been implemented. The studies that focused on Spitsbergen are indicated with an asterisk.

Study	Locality	# Genera	# Taxa	# New taxa	Habitat	Examined material	Type of the study
Cleve (1867) *	Kobbefjorden	UN	71	UN	freshwater	recent	biodiversity
Lagerstedt (1873) *	Spitsbergen & Bjørnøya	UN	84	UN	freshwater	recent	biodiversity
Zanon (1929) *	Kongsfjord	UN	56+	UN	freshwater, marine	recent	biodiversity
Hustedt (1937) *	Kongsfjord	UN	30	UN	freshwater, moss	recent	biodiversity
Krasske (1938) *	West Spitsbergen	34	208	15	freshwater, moss	recent	biodiversity
Thomasson (1958)	Nordautlandet	6	11	0	freshwater	recent	biodiversity
Foged (1964) *	Spitsbergen	52	572	43	freshwater, moss, soil	recent	biodiversity
Willén (1980) *	Spitsbergen	11	19	0	freshwater	recent	biodiversity & ecology
Picińska-Fałtynowicz (1988) *	Horsund fjord	35	157	0	freshwater	recent	biodiversity & ecology
Beyens & De Bock (1989)	Edgeøya	30	119	0	moss	recent	biodiversity & ecology
Wohlfart <i>et al.</i> (1995)	Bjørnøya	NS	NS	0	sediment core	fossil	paleoecology
Metzeltin & Witkowski (1996)	Bjørnøya	95	625	22	freshwater, marine	recent	biodiversity
Van de Vijver <i>et al.</i> (1999) *	Brøgger peninsula	36	131	0	freshwater	recent	biodiversity & ecology
Beyens & Van de Vijver (2000)	Hopen Island	30	116	0	freshwater, moss	recent	biodiversity & ecology
Jones & Birks (2004) *	West Spitsbergen	NS	182	0	freshwater, sediment core	fossil, recent	(paleo)ecology
Guilizzoni <i>et al.</i> (2006) *	Kongressvatnet	NS	140	0	sediment core	fossil	paleoecology
Holmgren <i>et al.</i> (2010) *	West Spitsbergen	NS	NS	0	sediment core	fossil	paleoecology
Jiang <i>et al.</i> (2011) *	Ny-Ålesund	NS	NS	0	sediment core	fossil	paleoecology
Luoto <i>et al.</i> (2011)	Nordautlandet	NS	NS	0	sediment core	fossil	paleoecology

TABLE E2. Codes of the different recent lake samples as used in the DCA. The samples that were removed from the data set due to too low diatom abundances are underlined and indicated in italic. The samples that were outliers in the DCA are indicated in bold. The last 3 samples are additional examined material collected in 2011. Note that samples SP54 and SP55 are not included in the table. These constitute samples of terrestrial mosses and were not examined in this study.

Code	Lake	Sample type
SP01-03 & 06	Garmaksla	epiphyton
SP04-05	Garmaksla	epipelon
SP07-09	Garmaksla	epilithon
SP10	Garmaksla	top trial sediment core (epipelon)
SP11-13	Ebbadalen 1	epiphyton
SP14-15	Ebbadalen 2	epiphyton
SP16	Brucebyen 1	epilithon
<u>SP17</u>	<u>Brucebyen 1</u>	<u>epiphyton</u>
SP18	Brucebyen 2	epilithon
SP19	Brucebyen 2	epiphyton
SP20	Nordenskiöld 1	epilithon
SP21	Nordenskiöld 2	epilithon + epiphyton
SP22	Nordenskiöld 3	epilithon + epiphyton
SP23	Nordenskiöld 4	epilithon
<u>SP24</u>	<u>Nordenskiöld 5</u>	<u>epilithon</u>
SP25-26	Mathiessendalen 1	epilithon
<u>SP27</u>	<u>Mathiessendalen 1</u>	<u>epiphyton</u>
SP28-29	Mathiessendalen 2	epiphyton
SP30	Mathiessendalen 2	epilithon
SP31	Mathiessendalen 3	epiphyton
SP32	Mathiessendalen 3	epilithon
SP33	Mathiessendalen 4	epiphyton
SP34	Mathiessendalen 4	epilithon
<u>SP35</u>	<u>Mathiessendalen 5</u>	<u>epiphyton</u>
SP36	Sven 1	epiphyton
SP37	Sven 1	epilithon
SP38	Sven 2	epipelon
SP39	Sven 3	epilithon
SP40	Sven 3	epiphyton
SP41	Horbye 1	epilithon
SP42	Horbye 1	epipelon
<u>SP43</u>	<u>Horbye 1</u>	<u>epiphyton</u>
SP44	Horbye 2	epilithon
SP45	Horbye 3	epilithon
SP46	Horbye 4	epilithon
SP47	Horbye 5	epilithon
SP48	Horbye 5	epiphyton + epipelon
SP49	Ragnar 1	epiphyton
SP50	Ragnar 1	epilithon
SP51	Ragnar 2	epiphyton

TABLE E2 – continued.

Code	Lake	Sample type
SP52	Ragnar 2	epipelon
SP53	Ragnar 2	epilithon
SP56	Mimerdalen 1	epiphyton
SP57	Mimerdalen 1	epilithon
SP58	Mimerdalen 2	epiphyton
SP59	Mimerdalen 3	epiphyton
SP60	Mimerdalen 3	epilithon
SP61	Mimerdalen 2	epilithon + epiphyton
SP62	Oblik 1	epilithon
SP63	Oblik 2	epilithon
SP64	Oblik 3	epilithon
SP65	Oblik 4	epiphyton + epilithon
SP66	Oblik 5	epilithon
SP67	Oblik 6	epilithon
SP68	Oblik 7	epiphyton
SP69	Oblik 8	epiphyton + epilithon
SP70	Oblik 9	epilithon
SP71-72	Oblik 10	epiphyton + epilithon
SP73	Oblik 11	epilithon
SPB1	Pyramiden 1	epilithon
SPM2A	Mathiessendalen 2	epilithon
SPN5	Nordenskiöld 5	epilithon

TABLE E3. Overview of the samples taken during the 2013 field campaign. The date gives the day on which the lakes were sampled. The last 3 columns indicate the number of samples taken from the different habitat types. The epilithon/epipelon samples indicated with an asterisk are mixed samples of epilithon/epipelon and epiphyton.

Lake name	Date of sampling	N	E	Epi-lithon	Epi-phyton	Epi-pelon
Ebbadalen 1	23/07/2013	78° 42' 9.8"	16° 36' 57.2"	0	3	0
Ebbadalen 2	23/07/2013	78° 42' 10.2"	16° 36' 56.7"	0	2	0
Brucebyen 1	24/07/2013	78° 63' 78.0"	16° 73' 65.0"	1	1	0
Brucebyen 2	24/07/2013	78° 63' 65.0"	16° 73' 01.0"	1	1	0
Nordenskiöld 1	24/07/2013	78° 38' 19.2"	16° 49' 35.8"	1	0	0
Nordenskiöld 2	24/07/2013	78° 38' 19.4"	16° 49' 41.1"	1 *	0	0
Nordenskiöld 3	24/07/2013	78° 38' 17.6"	16° 50' 1.5"	1 *	0	0
Nordenskiöld 4	24/07/2013	78° 38' 17.6"	16° 50' 5.1"	1	0	0
Nordenskiöld 5	24/07/2013	78° 38' 15.3"	16° 50' 24.9"	1	0	0
Mathiessendalen 1	26/07/2013	78° 34' 52.2"	16° 33' 00.0"	2	1	0
Mathiessendalen 2	26/07/2013	78° 33' 47.4"	16° 35' 14.1"	1	2	1
Mathiessendalen 3	26/07/2013	78° 33' 33.4"	16° 36' 54.2"	1	1	0
Mathiessendalen 4	26/07/2013	78° 33' 55.9"	16° 35' 44.1"	1	1	0
Mathiessendalen 5	26/07/2013	78° 33' 51.3"	16° 35' 34.5"	0	1	0
Garmaksla	27/07/2013	78° 36' 16.0"	16° 20' 14.7"	3	4	3
Sven 1	30/07/2013	78° 43' 30.7"	16° 24' 55.4"	1	0	0
Sven 2	30/07/2013	78° 43' 36.8"	16° 24' 52.4"	0	0	1
Sven 3	30/07/2013	78° 43' 47.9"	16° 24' 40.4"	1	1	0
Horbye 1	30/07/2013	78° 44' 5.0"	16° 26' 34.1"	1	1	1
Horbye 2	30/07/2013	78° 44' 13.0"	16° 26' 14.1"	1	0	0
Horbye 3	30/07/2013	78° 44' 35.4"	16° 24' 44.9"	1	0	0
Horbye 4	30/07/2013	78° 45' 14.0"	16° 21' 46.2"	1	0	0
Horbye 5	30/07/2013	78° 45' 24.5"	16° 22' 0.8"	1	0	1 *
Ragnar 1	31/07/2013	78° 44' 20.3"	16° 38' 42.5"	1	1	0
Ragnar 2	31/07/2013	78° 44' 21.4"	16° 38' 53.5"	1	1	1
Mimerdalen 1	24/08/2013	78° 37' 27.8"	15° 58' 5' 2.7"	1	1	0
Mimerdalen 2	24/08/2013	78° 36' 7.2"	15° 54' 9.7"	1 *	1	0
Mimerdalen 3	24/08/2013	78° 35' 31.9"	15° 55' 21.4"	1	1	0
Oblik 1	26/08/2013	78° 39' 24.9"	16° 54' 46.5"	1	0	0
Oblik 2	26/08/2013	78° 39' 27.8"	16° 54' 34.3"	1	0	0
Oblik 3	26/08/2013	78° 39' 23.0"	16° 54' 44.4"	1	0	0
Oblik 4	26/08/2013	78° 39' 19.3"	16° 54' 37.8"	1 *	0	0
Oblik 5	26/08/2013	78° 39' 21.4"	16° 54' 39.9"	1	0	0
Oblik 6	26/08/2013	78° 39' 18.6"	16° 54' 38.5"	1	0	0
Oblik 7	26/08/2013	78° 39' 16.3"	16° 54' 21.9"	0	1	0
Oblik 8	26/08/2013	78° 39' 8.5"	16° 54' 51.4"	1 *	0	0
Oblik 9	26/08/2013	78° 39' 14.6"	16° 55' 28.5"	1	0	0
Oblik 10	26/08/2013	78° 39' 14.1"	16° 55' 16.4"	2 *	0	0
Oblik 11	26/08/2013	78° 39' 9.0"	16° 55' 8.7"	1	0	0

TABLE E4. Overview of several parameters of the during the 2013 field campaign sampled lakes. The date gives the day on which the parameters (temperature, conductivity, pH) were measured.

Lake name	Date	Temperature (°C)	Conductivity (µS/cm)	pH	Altitude a.s.l. (m)	Distance to the sea (m)	Surface area (ha)	Estimated age (years)
Ebbadalen 1	23/07/2013	7.4	336	8.94	4	249	< 0.1	500 – 1000
Ebbadalen 2	23/07/2013	8.3	313	8.94	5	236	< 0.1	500 – 1000
Brucebyen 1	28/07/2013	10.1	1222	8.45	7	131	2.1	500 – 1000
Brucebyen 2	28/07/2013	10.1	420	8.72	11	184	0.9	500 – 1000
Nordenskiöld 1	26/08/2013	8.3	443	8.52	28	663	0.1	± 100
Nordenskiöld 2	26/08/2013	8.6	329	8.55	24	611	0.2	± 100
Nordenskiöld 3	26/08/2013	8.4	658	8.33	29	588	0.6	± 100
Nordenskiöld 4	26/08/2013	8.7	566	8.60	26	569	< 0.1	± 100
Nordenskiöld 5	26/08/2013	8.8	326	8.60	28	469	< 0.1	± 100
Mathiessendalen 1	26/07/2013	3.2	1391	7.40	5	434	4	500 – 1000
Mathiessendalen 2	26/07/2013	8.8	761	8.14	30	951	0.5	> 1000
Mathiessendalen 3	26/07/2013	9.2	234	8.29	72	1550	1.2	> 1000
Mathiessendalen 4	26/07/2013	8.3	184	8.63	49	1190	< 0.1	50 - 200
Mathiessendalen 5	26/07/2013	9.2	190	8.69	34	1090	< 0.1	50 – 200
Garmaksla	27/07/2013	8.5	167	8.48	308	633	3.2	> 1000
Sven 1	30/07/2013	9.8	403	8.52	62	2060	< 0.1	50 – 60
Sven 2	30/07/2013	10.6	662	8.39	53	2020	< 0.1	50 – 60
Sven 3	30/07/2013	10.1	290	8.62	52	2480	0.1	50 – 60
Horbye 1	30/07/2013	11.6	1325	8.18	35	2310	< 0.1	30 – 60
Horbye 2	30/07/2013	12.7	180	8.45	40	2600	0.8	30 – 60
Horbye 3	30/07/2013	12.2	218	8.54	50	3470	< 0.1	30 – 60
Horbye 4	30/07/2013	9.2	198	9.20	106	4990	< 0.1	< 10
Horbye 5	30/07/2013	8.7	182	8.39	107	5230	< 0.1	< 10
Ragnar 1	25/08/2013	7.6	227	8.70	102	2650	< 0.1	50 – 60
Ragnar 2	25/08/2013	7.0	1948	8.15	92	2730	0.4	50 – 60
Mimerdalen 1	24/08/2013	9.2	232	8.73	275	8820	0.7 – 3	> 1000
Mimerdalen 2	24/08/2013	8.9	149	8.78	332	9470	7.1	> 1000
Mimerdalen 3	24/08/2013	4.9	67	8.87	434	8300	0.1 – 0.2	> 1000
Oblik 1	26/08/2013	8.2	592	8.80	20	38	< 0.1	30 – 40
Oblik 2	26/08/2013	8.1	256	9.60	7	19	< 0.1	30 – 40
Oblik 3	26/08/2013	8.5	377	8.90	24	72	< 0.1	30 – 40
Oblik 4	26/08/2013	8.1	281	9.30	18	103	< 0.1	30 – 40
Oblik 5	26/08/2013	7.4	510	8.70	20	63	< 0.1	30 – 40
Oblik 6	26/08/2013	8.0	319	8.70	28	117	< 0.1	30 – 40
Oblik 7	26/08/2013	8.4	174	9.80	24	27	< 0.1	30 – 40
Oblik 8	26/08/2013	9.0	347	9.20	7	21	< 0.1	30 – 40
Oblik 9	26/08/2013	9.0	450	9.40	11	53	< 0.1	30 – 40
Oblik 10	26/08/2013	9.1	147	9.60	26	46	< 0.1	30 – 40
Oblik 11	26/08/2013	9.7	133	10.90	17	19	< 0.1	30 – 40

TABLE E5. Overview of the lake types and environmental characteristics of the during the 2013 field campaign sampled lakes. Legend: 1) **Biotic influence** (influence of animals, e.g., birds and reindeer): 0 – no animal traces are found, 1 – limited amounts of animal traces are found, 2 – high amounts of animal traces are found, 3 – bird colony nearby. 2) **Glacier nearby**: Yes – lakes/pools are located in the terminal moraines of a glacier, Yes * – lakes/pools are located on a peninsula in front of a glacier, No – lakes/pools are not located in the terminal moraines of a glacier nor on an peninsula in front of a glacier 3) **Vegetation in the lake** (moss vegetation and/or cyanobacterial crust on the lake bottom excluding the shores): Yes – vegetation is present, No – no or very limited vegetation coverage, e.g., maximally a few individual plants. 4) **Vegetation on the shores** (moss and higher plant vegetation and/or cyanobacterial crust on the shores): 0 – no vegetation, 1 - limited amount of vegetation, e.g., a few individual plants, 2 – medium amount of vegetation, e.g., ca. half of the shore is vegetated, 3 – high amount of vegetation, e.g., the complete shore is surrounded by vegetation. 5) **Catchment vegetation** (vegetation in the large vicinity, e.g., 100 m around the lake): 0 – no or very limited vegetation coverage, e.g., maximally a few individual plants, 1 – intermediate vegetation coverage, e.g., patches of vegetation in the surroundings, 2 – high vegetation coverage, e.g., almost the entire ground surface is covered 6) **Streams draining in/out the lake**: 0 – no streams, 1 – small stream(s) with low discharge probably representing temporary surface runoff, 2 – big stream(s) with high discharge.

Lake name	Lake type	Biotic influence	Glacier nearby	Vegetation in the lake	Vegetation on the shores	Surrounding vegetation	Streams draining in/out the lake
Ebbadalen 1	Sea terraces lake	2	No	Yes	3	2	1
Ebbadalen 2	Sea terraces lake	2	No	Yes	3	2	0
Brucebyen 1	Sea terraces lake	2	No	No	3	1	0
Brucebyen 2	Sea terraces lake	2	No	No	3	1	0
Nordenskiöld 1	Kettle lake	0	Yes	No	0	0	0
Nordenskiöld 2	Kettle lake	0	Yes	No	0	0	0
Nordenskiöld 3	Kettle lake	0	Yes	No	0	0	0
Nordenskiöld 4	Kettle lake	0	Yes	No	0	0	0
Nordenskiöld 5	Kettle lake	0	Yes	No	0	0	0
Mathiessendalen 1	Sea terraces lake	2	No	No	1	0	2
Mathiessendalen 2	Karst lake	1	No	No	2	1	1
Mathiessendalen 3	Karst lake	1	No	No	1	1	1
Mathiessendalen 4	Karst lake	0	No	No	2	1	0
Mathiessendalen 5	Karst lake	0	No	No	2	1	0
Garmaksla	Landslide related lake	1	No	No	1	0	1
Sven 1	Kettle lake	0	Yes	No	0	0	0
Sven 2	Kettle lake	0	Yes	No	0	0	0
Sven 3	Kettle lake	0	Yes	No	0	0	1
Horbye 1	Kettle lake	1	Yes	No	2	0	0
Horbye 2	Kettle lake	0	Yes	No	0	0	2
Horbye 3	Kettle lake	0	Yes	No	0	0	0
Horbye 4	Kettle lake	0	Yes	No	0	0	1
Horbye 5	Kettle lake	0	Yes	No	0	0	0
Ragnar 1	Proglacial lake	0	Yes	No	0	0	0

TABLE E5- continued.

Lake name	Lake type	Biotic influence	Glacier nearby	Vegetation in the lake	Vegetation on the shores	Surrounding vegetation	Streams draining in/out the lake
Ragnar 2	Proglacial lake	1	Yes	No	0	0	1
Mimerdalen 1	Snow related depressions	0	No	No	0	0	1
Mimerdalen 2	Snow related depressions	0	No	No	2	0	2
Mimerdalen 3	Snow related depressions	0	No	No	0	0	0
Oblik 1	Tectonic determined	3	Yes *	No	1	1	0
Oblik 2	Tectonic determined	3	Yes *	No	1	1	0
Oblik 3	Tectonic determined	3	Yes *	No	1	0	0
Oblik 4	Tectonic determined	3	Yes *	No	1	0	0
Oblik 5	Tectonic determined	3	Yes *	No	1	0	0
Oblik 6	Tectonic determined	3	Yes *	No	2	1	0
Oblik 7	Tectonic determined	3	Yes *	No	2	1	0
Oblik 8	Tectonic determined	3	Yes *	No	1	0	0
Oblik 9	Tectonic determined	3	Yes *	No	1	0	0
Oblik 10	Tectonic determined	3	Yes *	No	1	0	0
Oblik 11	Tectonic determined	3	Yes *	No	1	0	0

TABLE E6. Additional samples analysed in this study. The numbers of the lakes correspond with the numbers given at the lakes during the 2013 field campaign. All 3 samples are epilithon. Legend: * = not available.

Lake name	Date	N	E	Temperature (°C)	Conductivity (µS/cm)	pH
Pyramiden 1	12/07/2011	78° 39' 52.2"	16° 16' 57.6"	*	*	*
Mathiessendalen 2	20/07/2011	78° 33' 47.4"	16° 35' 14.1"	10.2	550	8.4
Nordenskiöld 5	13/07/2011	78° 38' 15.3"	16° 50' 24.9"	9.6	194	8.7

TABLE E7. Codes of the different sediment core samples as used in the PCA with indication of the corrected mean depths of each sample, the number of counted diatom valves, the number of added and counted *Lycopodium* spores/tablets and the number of counted *Chrysophyte* cysts.

Code	Depth (cm)	Number of counted diatom valves	Number of counted <i>Lycopodium</i> spores	Number of added <i>Lycopodium</i> tablets	Number of counted <i>Chrysophytes</i> cysts
GA001	0.5	400	11	20	4
GA002	1.6	400	16	20	1
GA003	2.7	400	3	20	2
GA004	3.7	400	6	20	3
GA005	4.8	400	20	20	4
GA006	5.9	400	26	20	3
GA007	6.9	400	46	20	0
GA008	8.0	400	298	20	0
GA009	9.1	400	62	20	0
GA010	10.1	400	368	10	1
GA011	11.2	400	58	10	0
GA012	12.3	400	55	10	0
GA013	13.3	400	247	10	1
GA014	14.4	400	47	10	0
GA015	15.5	400	60	10	0
GA016	16.5	400	289	10	4
GA017	17.6	400	32	10	2
GA018	18.7	400	47	10	0
GA019	19.8	400	56	10	0
GA020	20.8	400	57	10	0
GA022	23.0	400	76	10	0
GA023	24.0	400	87	10	2
GA025	26.2	400	116	10	0
GA026	27.2	400	102	10	0
GA028	29.4	400	755	10	9
GA029	30.4	400	435	10	1
GA031	32.6	400	258	10	4
GA032	33.6	400	206	10	0
GA034	35.8	400	231	10	4
GA035	36.8	400	89	10	2
GA037	39.0	400	54	10	3
GA038	40.0	400	201	10	1
GA040	42.2	400	402	10	3
GA041	43.2	400	104	10	1
GA043	45.4	400	127	10	3
GA044	46.4	400	69	10	3
GA046	48.6	400	61	10	0
GA047	49.6	400	174	10	3
GA049	51.8	400	301	10	1
GA050	52.8	400	308	10	0

TABLE E7- continued.

Code	Depth (cm)	Number of counted diatom valves	Number of counted <i>Lycopodium</i> spores	Number of added <i>Lycopodium</i> tablets	Number of counted Chrysophytes cysts
GA052	55.0	250	368	10	3
GA053	56.0	400	265	10	2
GA055	58.2	400	228	10	2
GA056	59.3	200	559	10	12
GA058	61.4	50	585	10	4
GA059	62.5	150	454	10	12
GA061	64.6	11	190	10	2
GA062	65.7	100	391	10	11
GA064	67.8	400	724	10	3
GA065	68.9	100	388	10	0
GA067	71.0	50	155	10	5
GA068	72.1	50	285	10	1
GA070	74.2	50	247	10	1
GA071	75.3	20	239	10	0
GA073	77.4	50	347	10	3
GA074	78.5	200	613	10	2

TABLE E8. Summary of the ordination results of the DCA analysis (recent samples) and PCA analysis (sediment core).

	Axis 1	Axis 2	Axis 3	Axis 4
DCA recent samples				
Eigenvalues	0.413	0.201	0.157	0.122
Lengths of gradient (SD units)	3.328	2.201	2.555	2.196
Cumulative % variance of species	11.7	17.4	21.8	25.3
PCA sediment core				
Eigenvalues	0.473	0.265	0.146	0.028
Cumulative % variance of species	47.3	73.8	88.4	91.2

TABLE F1 - continued. Frequences (%) of the diatom taxa of the recent lake samples (part 1). * = taxon present in the sample but not observed during the counts. The sample numbers correspond with those given in Appendix E (Table E2) with 'SP' omitted.

	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73
<i>Achnantheidium minutissimum</i> var. <i>Jackii</i>															
<i>Achnantheidium rosenstockii</i>															
<i>Achnantheidium</i> sp1	0.3	2.3	27.5	21.8	13.8	5.0	9.3	12.3	4.0	0.5	16.8	36.8	3.8	2.5	1.0
<i>Achnantheidium</i> sp2															
<i>Achnantheidium</i> sp3															
<i>Adulfia bryophila</i>															
<i>Adulfia minuscula</i>				3.5	*	0.3	2.0	16.5	0.3		15.5	8.8		0.8	
<i>Alveollum beyensii</i>															
<i>Amphora affinis</i>															
<i>Amphora inariensis</i>															
<i>Amphora lange-bertalotii</i> var. <i>tenuis</i>															
<i>Aneomastus tusculus</i>															
<i>Brachysira neoexilis</i>															
<i>Brachysira zellensis</i>															
<i>Caloneis alpestris</i>															
<i>Caloneis arctica</i>				*											
<i>Caloneis backmanii</i>															
<i>Caloneis falcifera</i>															
<i>Caloneis fasciata</i>								*	0.5						
<i>Caloneis fusus</i>															
<i>Caloneis silicula</i>															
<i>Caloneis silicula</i> var. <i>intermedia</i>															
<i>Caloneis sublinearis</i>															
<i>Caloneis tenuis</i>				*	*					0.5					
<i>Caloneis thermalis</i>															
<i>Cavinula cocconeiformis</i>				*											
<i>Cavinula</i> sp	0.3														
<i>Chamaepinnularia</i> cf. <i>evanida</i>								1.3	0.3					1.5	
<i>Chamaepinnularia gandrupii</i>					15.0						0.3				
<i>Craticula ambigua</i>															
<i>Craticula minusculoides</i>								2.5					3.3	0.5	
<i>Craticula molestiformis</i>								5.0							
<i>Craticula submolesta</i>						0.3									
<i>Cyclotella antiqua</i>															
<i>Cyclotella</i> cf. <i>camta</i>															
<i>Cyclotella ocellata</i>															
<i>Cyclotella pseudocomensis</i>															
<i>Cyclotella</i> sp1															
<i>Cyclotella</i> sp2															
<i>Cymbella arctica</i>		1.5	0.3												
<i>Cymbella botellus</i>			1.5												
<i>Cymbella cleve-eulerae</i>															
<i>Cymbella designata</i>															
<i>Cymbella hantzschiana</i> var. <i>borealis</i>			0.3	0.3							0.3				
<i>Cymbella neocistula</i>	0.3	6.0	0.3												
<i>Cymbella neoleptoceras</i> var. <i>tenuistriata</i>															
<i>Cymbella</i> sp sensu Antoniadis et al. 2008															
<i>Cymbella</i> sp1															
<i>Cymbella</i> sp2															
<i>Cymbella weslowski</i>				*											
<i>Cymbopleura amphicephala</i>															
<i>Cymbopleura anglica</i>															
<i>Cymbopleura angustata</i> var. <i>spitsbergensis</i>															
<i>Cymbopleura broenlundensis</i>															
<i>Cymbopleura incerta</i> var. <i>incerta</i>															
<i>Cymbopleura incerta</i> var. <i>spitsbergensis</i>															
<i>Cymbopleura incertiformis</i>															
<i>Cymbopleura oblongata</i> var. <i>parva</i>				*									0.5		
<i>Cymbopleura subaequalis</i> s.l.															
<i>Cymbopleura subaequalis</i> var. <i>truncata</i>															
<i>Cymbopleura tynni</i>															
<i>Cymbopleura</i> sp1															
<i>Cymbopleura</i> sp2															
<i>Cymbopleura</i> sp3															
<i>Cymbopleura venetaeformis</i>															
<i>Delicata delicatula</i>															
<i>Delicata spitsbergensis</i>															
<i>Denticula kuetzingii</i> incl. var. <i>rumrichae</i>				4.3											
<i>Denticula subtilis</i>															
<i>Denticula tenuis</i>				0.5											
<i>Diatoma moniliformis</i>									7.0						
<i>Diatoma tenuis</i>								1.0	0.5						
<i>Diatomella balfoeriana</i>	0.3														
<i>Diadmosphenia geminata</i>															
<i>Diploneis oblongella</i>															
<i>Diploneis oculata</i>															
<i>Diploneis ovalis</i> ssp. <i>arctica</i>															
<i>Diploneis parva</i>															
<i>Encyonema</i> aff. <i>aueri</i>															
<i>Encyonema</i> aff. <i>ventricosum</i>															
<i>Encyonema elginense</i>															
<i>Encyonema fagedii</i>				*	1.0			1.5	7.5	4.8	7.3	28.0	3.3	4.5	
<i>Encyonema hebridicum</i>															
<i>Encyonema lange-bertalotii</i>															

TABLE F1 - continued. Frequences (%) of the diatom taxa of the recent lake samples (part 2). * = taxon present in the sample but not observed during the counts. The sample numbers correspond with those given in Appendix E (Table E2) with 'SP' omitted.

	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73
<i>Encyonema minutum</i>				*	0.3	0.8		0.8	10.8	17.3	13.8	0.5	10.5	8.3	
<i>Encyonema obscurum</i>															
<i>Encyonema perminutum</i>															
<i>Encyonema silesiacum</i>				2.3	0.5	1.0		11.5	13.3		0.3		2.8	3.3	
<i>Encyonema silesiacum</i> var. <i>lata</i>															
<i>Encyonema</i> sp1															
<i>Encyonema</i> sp2															
<i>Encyonema</i> sp3															
<i>Encyonema</i> sp4															
<i>Encyonema</i> sp5															
<i>Encyonema</i> sp6															
<i>Encyonema</i> sp7															
<i>Encyonopsis cesatii</i>															
<i>Encyonopsis cesatii</i>															
<i>Encyonopsis</i> cf. <i>sp1</i> sensu Antoniadis et al. 2008															
<i>Encyonopsis descripta</i>															
<i>Encyonopsis krammeri</i>															
<i>Encyonopsis subminuta</i>															
<i>Encyonopsis</i> sp1															
<i>Encyonopsis</i> sp2															
<i>Encyonopsis</i> sp3															
<i>Encyonopsis</i> sp4															
<i>Encyonopsis</i> sp5															
<i>Epithemia adnata</i>															
<i>Epithemia sorex</i>															
<i>Epithemia turgida</i>															
<i>Eucocconeis flexella</i>															
<i>Eucocconeis laevis</i> incl. var. <i>austriaca</i>	1.3	3.0				0.8	4.3	1.0			1.5				
<i>Eunotia ewa</i>															
<i>Eunotia minor</i>															
<i>Eunotia</i> sp															
<i>Fallacia losevae</i>					1.5			0.5							
<i>Fistulifera saprophila</i>				0.3	0.3										
<i>Fragilaria gracilis</i>															
<i>Fragilaria tenera</i>															
<i>Fragilaria</i> sp1															
<i>Fragilaria</i> sp2															
<i>Fragilaria</i> sp3															
<i>Frustulia</i> sp															
<i>Geissleria paludosa</i>	0.5			*											
<i>Geissleria</i> sp1															
<i>Geissleria</i> sp2															
<i>Gomphonema distans</i>															
<i>Gomphonema kaweckanum</i>					*										
<i>Gomphonema lagerheimii</i>															
<i>Gomphonema micropus</i>															
<i>Gomphonema nathorstii</i>	3.3	11.8													
<i>Gomphonema productum</i>															
<i>Gomphonema svalbardense</i>															
<i>Gyrosigma acuminatum</i>															
<i>Halamphora dusenii</i>					0.3			*		0.8	2.8				
<i>Halamphora obscura</i>								1.3							
<i>Halamphora oligotrophenta</i>															
<i>Hannea arcus</i>				0.3											
<i>Hantzschia abundans</i>										1.8	0.3				
<i>Hantzschia amphioxys</i>								0.5	*	2.8					6.8
<i>Hantzschia hyperborea</i>															
<i>Hantzschia rhaetica</i>	*		*												
<i>Hantzschia vivacioides</i>															
<i>Hippodonta hungarica</i>															
<i>Humidophila brekkaensis</i>															
<i>Humidophila inaeformis</i>															
<i>Humidophila paracontenta</i>	38.5	37.0													
<i>Humidophila perpusilla</i>	45.3	34.5													
<i>Humidophila</i> sp1 (sensu Diademsis sp1 Antoniadis et al. 2008)															
<i>Hygropetra balfouriana</i>															
<i>Kobayasiella</i> sp			*			0.5	8.0	0.5			0.5				
<i>Luticola bilyi</i>															
<i>Luticola cohnii</i>	*														
<i>Luticola frequentissima</i>	*			*							0.3		0.3	*	3.3
<i>Luticola quinquenaoides</i>															
<i>Luticola similis</i>															
<i>Luticola triundulata</i>															
<i>Luticola</i> sp1	*					0.5	0.3	0.5							
<i>Luticola</i> sp2							0.3								
<i>Luticola</i> sp3															
<i>Mayamaea atomus</i>								0.3							
<i>Mayamaea</i> cf. <i>aliena</i>				3.0		1.3	0.8	0.3				3.5	1.3	1.0	
<i>Mayamaea permutis</i>				0.3			0.3	2.5	0.3	1.3	2.8	1.3			0.3
<i>Meridion circulare</i>			35.0												
<i>Microcostatus krasskei</i>															
<i>Muelleria gibbula</i>															
<i>Navicula arctatenelloides</i>	*		2.0												
<i>Navicula bjaerneaensis</i>											0.3				

TABLE F1 - continued. Frequences (%) of the diatom taxa of the recent lake samples (part 4). * = taxon present in the sample but not observed during the counts. The sample numbers correspond with those given in Appendix E (Table E2) with 'SP' omitted.

	59	60	61	62	63	64	65	66	67	68	69	70	71	72	73
<i>Pinnularia cf. marchica</i>															
<i>Pinnularia divergens</i>															
<i>Pinnularia divergentissima</i>			*												
<i>Pinnularia frequentis</i>															
<i>Pinnularia ikaschoenfelderæ</i>															
<i>Pinnularia isostauron</i>															
<i>Pinnularia krammeri</i>															
<i>Pinnularia obscura</i>				0.5											
<i>Pinnularia pseudodivergentissima</i>															
<i>Pinnularia sp1</i>			*												
<i>Pinnularia sp2</i>															
<i>Pinnularia viridiformis</i>															
<i>Placoneis amphibola</i>															
<i>Placoneis amphibola f. rectangularis</i>															
<i>Placoneis elginensis</i>			*												
<i>Planothidium fragilaroides</i>				1.5											
<i>Platessa rupestris</i>		*													
<i>Psammothidium bioretii</i>															
<i>Psammothidium broenlundense</i>															
<i>Psammothidium daonense</i>					0.5										
<i>Psammothidium grischunum</i>					0.8										
<i>Psammothidium helveticum</i>			*				0.3								
<i>Psammothidium kryophilum</i>	4.5														
<i>Psammothidium marginulatum</i>								0.8			0.8				
<i>Psammothidium rossii</i>															
<i>Psammothidium scoticum</i>															
<i>Psammothidium sp1</i>		0.3		1.3	0.5	3.5	2.5	0.5			5.8	1.3		0.3	
<i>Psammothidium sp2</i>				0.5		1.5	6.3	1.8			0.8				
<i>Psammothidium sp3</i>															
<i>Psammothidium ventralis</i>															
<i>Rossthidium petersenii</i>	5.8	2.3	18.5	1.8	0.3	1.5	10.8	2.0		1.8	0.3	0.3		0.3	
<i>Rossthidium pusillum</i>															
<i>Sellaphora bacillum</i>															
<i>Sellaphora nana</i>															
<i>Sellaphora pupula</i>															
<i>Sellaphora rectangularis</i>															
<i>Stauroneis aff. obtusa</i>															
<i>Stauroneis aff. subgracilis</i>															
<i>Stauroneis agrestiformis</i>															
<i>Stauroneis amphicephala</i>															
<i>Stauroneis cf. lundii</i>															
<i>Stauroneis circumborealoides</i>															
<i>Stauroneis clandestina</i>															
<i>Stauroneis francisci-josephi</i>															
<i>Stauroneis gelida</i>															
<i>Stauroneis intricans</i>															
<i>Stauroneis lapponica</i>															
<i>Stauroneis reichardtii</i>															
<i>Stauroneis anceps</i> sensu Foged 1964															
<i>Stauroneis subhyperborea</i>															
<i>Stauroneis svalbardensis</i>															
<i>Stauroneis sp1</i>															
<i>Stauroneis sp2</i>															
<i>Staurosira pseudoconstruens</i>			*												
<i>Staurosira robusta</i>															
<i>Staurosira venter</i>															
<i>Staurosirella aff. lapponica</i>															
<i>Staurosirella oldenburgiana</i>															
<i>Surirella minuta</i>							0.5	2.8	*				0.5	0.5	
<i>Surirella terricola</i>															
<i>Ulnaria danica</i>															
<i>Ulnaria delicatissima</i>															
Unidentified valve															

Appendix G. “*Gomphonema svalbardense* sp. nov., a new freshwater diatom species (Bacillariophyta) from the Arctic Region”



Gomphonema svalbardense sp. nov., a new freshwater diatom species (Bacillariophyta) from the Arctic Region

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Abstract

During a survey of freshwater diatoms from lakes in the region of Petuniabukta on Spitsbergen (Svalbard Archipelago) a new *Gomphonema* species, *G. svalbardense* sp. nov., has been recorded. The new taxon was previously cited in the literature as *G. angustatum* var. *undulatum* but this identification proved to be erroneous. Detailed morphology description of *G. svalbardense* based on light and scanning electron microscopy is presented in this paper and the morphological features of the taxon have been compared with similar species. *Gomphonema svalbardense* is characterized by its typical linear, almost naviculoid outline with undulating margins, with clearly inflated central part, asymmetric central area, lateral raphe with simple straight proximal endings and the weakly radiate striae. History, ecology and biogeography of the species, mainly based on literature data, have been included.

Key words: Svalbard, Arctic Region, *Gomphonema*, diatoms, taxonomy, morphology, new species

Introduction

In the middle of the twentieth century, the diatom flora of the Arctic Svalbard Archipelago (74°–81°N, 10°–35°E) was the focus of several large morphological and taxonomic studies, published by among others Hustedt (1937), Krasske (1938) and Foged (1964), the latter listing more than 572 taxa in 207 samples. During more recent years, diatom studies on Svalbard were restricted to a few sparse floristic and (paleo-)ecological accounts (e.g., Picińska-Fałtynowicz 1988, Beyens 1989, Van de Vijver *et al.* 1999, Guilizzoni *et al.* 2006, Luoto *et al.* 2011) and only a few new taxa were described from the archipelago. Van de Vijver *et al.* (2004) described three new *Stauroneis* taxa from Svalbard in their revision of this genus in the Arctic and Antarctic Regions.

Since 2011 the interest in diatom research on Svalbard has revived with the Czech education program of polar ecology undertaken by the Centrum for Polar Ecology (University of South Bohemia). During the regular field expeditions, several lakes in the surroundings of the Petuniabukta fjord area have been studied (Reports of Czech research activities in Petuniabukta, http://polar.prf.jcu.cz/docs_cz.htm). The Petuniabukta fjord area is located in the northern part of Billefjorden, the inner branch of Isfjorden in the central part of Spitsbergen, the main island of the Svalbard Archipelago. The area is situated in the maritime High Arctic climate zone, with a mean annual temperature of about -7.5 °C and low precipitation rates of about 200 mm a year, mainly in the form of snow (Rachlewicz *et al.* 2007, Komárek *et al.* 2012, Láska *et al.* 2012). The geology of the study area is strongly correlated to the north-south facing Billefjorden Fault zone which resulted in a complex of different rock formations belonging to four structural entities differing in age and origin (Dallmann *et al.* 1999, Szczuciński & Rachlewicz 2007). The entire fjord is surrounded by steep mountains ranging between 265 and 935 m a. s. l. (Komárek *et al.* 2012). During the early Holocene, the entire area rose due to glacioisostatical uplift which resulted in the development of several good-preserved marine terraces (Szczuciński & Rachlewicz 2007). About ten glaciers, of which the tide-water glacier Nordenskiöld is the biggest, are located in the area. Since the beginning of the 20th century, the glaciers are retreating with speeds ranging from a few meters to 50 meters a year (Szczuciński

& Rachlewicz 2007). Several lakes and pools, differing in origin, type and age, are located in the area, often situated in recent deglaciated zones or on raised marine terraces. The shores of some of these lakes are characterized by a dense moss vegetation. Due to erosion, extreme climatic conditions on exposed sites and recently deglaciated, not yet colonized, areas, large parts of Petuniabukta are not or sparsely vegetated. Vegetated parts show a rather high plant diversity, mainly with *Carex*, *Dryas* and *Silene* taxa (Prach *et al.* 2012). Due to recent deglaciation, erosion and extreme climatic conditions, large parts of Petuniabukta are not or only sparsely vegetated, although the vegetated parts show a rather high plant diversity, mainly with *Carex*, *Dryas* and *Silene* taxa (Prach *et al.* 2012). Several large bird colonies, e.g. of *Sterna paradisaea* Pontoppidan and *Rissa* sp., occur along the shores.

During the summers of 2011, 2012 and 2013 a large number of samples were collected from more than 30 different lakes, offering the opportunity for a more thorough taxonomic and ecological survey of the non-marine diatom communities of this Arctic site. Recently, analysis of the diatom flora revealed the presence of more than 300 taxa including several unknown taxa that could not be identified using the currently available (Arctic) diatom literature. In the past, most of these taxa would have been force-fitted (Tyler 1996) into Western-European or North-American diatom taxa (mainly based on Krammer & Lange-Bertalot 1986–1991), but following our current concept of diatom taxonomy (Mann 1999), this practice has been abandoned and new species need to be described as new for science.

The present paper describes a new species: *Gomphonema svalbardense* sp. nov., which was previously reported several times from the Arctic as *G. angustatum* var. *undulata* ms. Grunow (in Cleve 1894: 181).

Material & Methods

During a limnological survey in the area of Petuniabukta, epilithon, epiphyton and moss samples were taken from several ponds and lakes for further diatom analysis. During an initial screening of the samples, only four samples could be found in which the new *Gomphonema* taxon was present. Table 1 lists all samples and slides used in the present study are listed in table 1 together with their GPS positions and measured ecological parameters. Diatom samples were fixed with 96 % ethanol for preservation. The pH and specific conductance of the water were measured using a HANNA Combo pH/EC Tester.

Small sub-samples were prepared for LM observation following the method described in Van der Werff (1955). Small parts of the samples were cleaned by adding 37% H₂O₂ and heating to 80°C for about 1h. The reaction was completed by addition of KMnO₄. Following digestion and centrifugation (three times 10 minutes at 3700 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[®]. For scanning electron microscopy (SEM), 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 in a ZEISS Ultra SEM microscope at 3 kV (Natural History Museum London, UK). As the new taxon proved to be very rare in the samples, only a few SEM observations could be made of the valves. The girdle structure was not observed. Samples and slides are stored at the BR-collection, property of the Belgian federal government and given in permanent loan to the Botanic Garden Meise (Belgium). Diatom terminology on valve outline and raphe structure follows Ross *et al.* (1979) and Round *et al.* (1990) whereas for typical gomphonemoid structures, Reichardt (1999) and Thomas *et al.* (2009) have been used. The term ‘isolated pore’ is used instead of the more commonly used ‘stigma’ as the latter term can only be used for the genus *Cymbella* (and some related genera) (Cleve 1894, p. 157) as current research showed important morphological differences in these structures in the different genera (Van de Vijver & Cox, unpubl. res.). Comparisons with other northern Hemisphere *Gomphonema* taxa, are based on Cleve-Euler (1955), Reichardt (1999), Lange-Bertalot & Genkal (1999) and Antoniadou *et al.* (2008).

Results

Division Bacillariophyta

Class Bacillariophyceae Haeckel emend. Medlin & Kaczmarska 2004

Subclass Bacillariophycidae D.G.Mann in Round *et al.* 1990

Order Cymbellales D.G.Mann in Round *et al.* 1990

Family Gomphonemataceae Kütz. 1844

Genus *Gomphonema* Ehrenb. 1832

Gomphonema svalbardense sp. nov. (Figs 1–18)

Type:—Mathiessendalen, Petuniabukta (Central Spitsbergen—Svalbard), sample SPITS 2013/029 (78°33'47.4"N, 16°35'14.1"E), leg. E. Pinseel, coll. date 26/07/2013 (holotype, slide no. BR–4368; isotype, slide PLP–257, University of Antwerp, Belgium).

Synonym:—*Gomphonema angustatum* var. *undulatum* (Greg.) Grunow sensu Foged 1981 (p.97, plate LIII, figs 10, 11, non plate LIII, figs 9, 12, 13, 14).

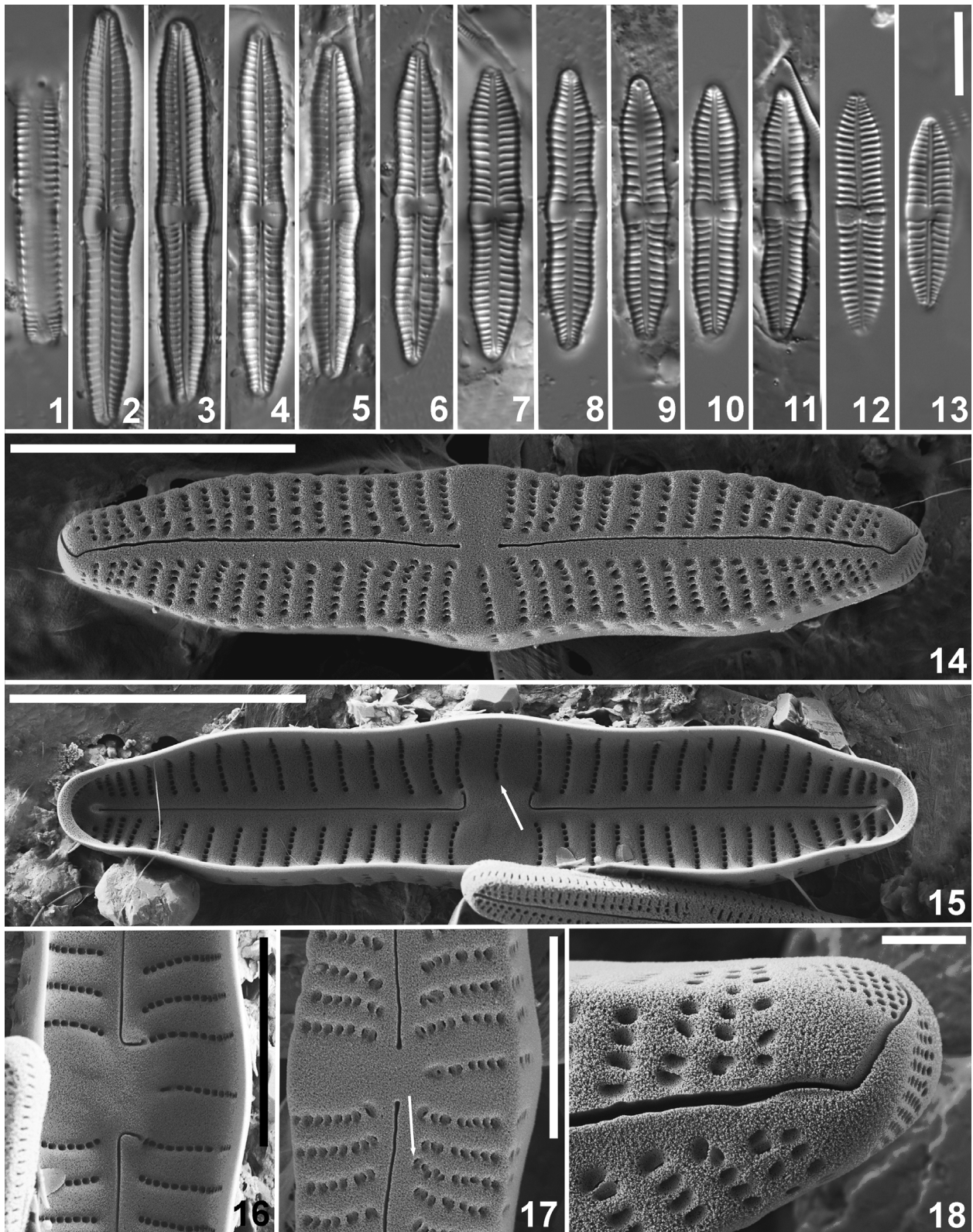
LM (Figs 1–13): Valves linear, asymmetric, only weakly clavate to even naviculoid, with undulating margins and a clearly inflated central part. Headpole and footpole protracted, rostrate, narrowly rounded, the latter only slightly broader than the headpole. Valve dimension (n=30): length 23–51 µm, width 5.7–7.2 µm. Axial area narrow, linear to weakly lanceolate, almost not widening towards the central area. Central area forming a rectangular to weakly wedge-shaped, asymmetric fascia. One striae present along one margin with a terminal isolated pore. The opposite margin always lacking any striae. Raphe weakly curved and undulating, clearly lateral with straight proximal raphe endings. Distal raphe endings not discernible in LM. Striae weakly radiate near the central area, becoming more radiate towards the apices, 9–13 in 10 µm, up to 14–19 near the apices. Areolae occasionally visible but usually difficult to resolve in LM.

SEM (Figs 14–18): Striae uniseriate, occasionally biseriate near the axial area (Figs 14, 17 see arrow), composed of more or less rounded areolae that are located at the bottom of rather deep, irregularly shaped depressions. External raphe branches curved, undulating (Fig. 14). Proximal raphe endings straight, simple (Fig. 17). Distal raphe fissures hooked, curving down on the mantle, separating the apical porefield into two fields (Fig. 18). Apical porefield on the footpole composed of several (5–6) rows of small, rounded porelli, physically removed and structurally differentiated from the areolae. Internally, small pseudosepta present on both apices (Fig. 15). Internal distal raphe endings terminating on small helictoglossae (Fig. 15). Internal proximal endings terminating on a raised central nodule, hooked and even recurved towards the isolated pore (Fig. 15). Areolar openings rounded, not lying in foraminal rows. Isolated pore opening slightly transapically elongated, not very differentiated from the areolae (Fig. 15, arrow). Apical porefield details not visible due to pseudoseptum (Fig. 15). No observations on the girdle structure could be made.

Ecology and Distribution:—*Gomphonema svalbardense* is described from a small lake (Petuniabukta, Central Spitsbergen – Svalbard). The lake is characterized by an alkaline pH (8.1) and a moderately high conductance value (761 µS/cm). At the type locality, this taxon was primarily found in moss samples taken from the lake's shore. Additional populations were found in various epilithon and epiphyton samples from three other localities (Table 1) with similar pH (8.6–8.9) but lower conductance value (184–336 µS/cm). The accompanying diatom flora included *Denticula kuetzingii* Grunow (1862: 546), *D. tenuis* Kütz. (1844: 43), *Meridion circulare* (Grev. 1823: 35) C.Agardh (1831: 40), *Rossithidium petersenii* (Hust. 1937: 179–180) Aboal (in Aboal *et al.* 2003: 178), *Epithemia adnata* (Kütz. 1833: 544) Bréb. (1838: 16), *Staurosirella* aff. *lapponica* (Grunow in Van Heurck 1881: 45) D.M. Williams & Round (1987: 274) and an at present unidentified *Achnanthisidium* Kützing (1844: 75) taxon.

The new taxon has already been reported in the past from Alaska (Foged 1981), Bear Island (Metzeltin & Witkowski 1996) and Siberia (Lange-Bertalot & Genkal 1999) showing that this taxon probably has a circumpolar, Arctic distribution. Due to confusion with other taxa previously identified as *G. angustatum* var. *undulata*, its correct biogeography is unclear.

Etymology:—The specific epithet *svalbardense* refers to the Arctic Svalbard Archipelago where the new taxon was found.



Figures 1–18. *Gomphonema svalbardense* sp. nov. Light and scanning electron micrographs. All pictures taken from the type population (BR-4368). **Figs 1–13.** Light microscopy views showing variation in size and valve outline. **Fig. 14.** SEM external view of an entire valve showing the raphe and striae structure. **Fig. 15.** SEM internal view of an entire valve. The arrow indicated the opening of the isolated pore. **Fig. 16.** SEM internal detail of the central area. **Fig. 17.** SEM external detail of the central area. The arrow indicates the occasional doubling of the areolae. **Fig. 18.** SEM external detail of the apical pore field. LM scale bar = 10 µm. SEM scale bar = 10 µm except for Figs 16–17 where scale bar = 5 µm and Fig 18, where scale bar = 1 µm.

TABLE 1. List of samples used in this study with their geographic position and measured ecological parameters.

Sample(s)	Collection date	Location	Lake type	N	E	pH	Cond. (µS/cm)	Sample type
SPITS 2013/028-030	26/07/2013	Mathiessendalen	Karst lake	78°33'47.4"	16°35'14.1"	8.1	761	Epiphyton & epilithon
SPITS 2013/033	26/07/2013	Mathiessendalen	Karst lake	78°33'55.9"	16°35'44.1"	8.6	184	Epilithon
SPITS 2013/012-013	23/07/2013	Ebbadalen	Marine terraces pond	78°42'9.8"	16°36'57.2"	8.9	336	Epiphyton
SPITS 2013/014-015	23/07/2013	Ebbadalen	Marine terraces pond	78°42'10.2"	16°36'56.7"	8.9	313	Epiphyton

Discussion

Gomphonema svalbardense has been known for a long time under the name of *Gomphonema angustatum* var. *undulata*. Apart from a very brief description ('*V. triundulate*. L. 0,02 to 0,028; B. 0,006 mm. Striae 10 in 0,01 mm.') without any illustration, nothing was known about the original morphology of this taxon (Cleve 1894). Unfortunately, the original type material of this taxon could not be retrieved. Later, several authors commented on the taxonomy of the variety *undulata*, connecting this taxon to *G. parvulum* (Kütz. 1844: 83) Kütz. (1849: 65), *G. angustatum* (Kütz. 1844: 83) Rabenh. (1864: 283) and even *G. lagerheimii* A.Cleve (1895: 22). Hustedt (1942), in his overview on the freshwater diatoms from Abisko (Sweden), illustrated a whole series of *G. angustatum* f. (not var.!) *undulata* Grunow sensu Hustedt (1942: 145, Figs 67–77) and combined the taxon with two taxa previously described by Cleve-Euler: *G. parvulum* var. *undulata* A.Cleve (1895: 21) and *G. lagerheimii* var. *distans* Cleve-Euler (1934: 72). However, careful analysis of these two taxa by Lange-Bertalot & Genkal (1999) and Reichardt (1999) resulted in a renewed separation and the description of *G. distans* Lange-Bertalot & Reichardt (in Lange-Bertalot & Genkal 1999: 54) (for *G. lagerheimii* var. *distans*) and *G. astridae* Reichardt & Lange-Bertalot 1999 (in Reichardt 1999: 29) (for *G. parvulum* var. *undulata*). In addition to both taxa, a third taxon, *G. subarcticum* Lange-Bertalot & Reichardt (in Lange-Bertalot & Genkal 1999: 59), was described for some valves that could be separated from *G. angustatum* f. *undulata* (Lange-Bertalot & Genkal 1999). All three taxa can easily be separated from each other (see Table 2). Additionally, in his discussion of one of the taxa, Reichardt (1999) mentioned the presence of several other, morphologically related, taxa that have not yet been described. One of these has been illustrated in Foged (1981), Metzeltin & Witkowski (1996) and Lange-Bertalot & Genkal (1999). These three records illustrate valves belonging to the same taxon that however could not be attributed to any of the three previously mentioned taxa. Careful analysis of the illustrations showed conspecificity with the unknown taxon from Spitsbergen, justifying partly the description of the latter as the new taxon *G. svalbardense*.

All authors agreed that a combination of these taxa with either *G. parvulum*, *G. angustatum* nor *G. lagerheimii* should be excluded based on major differences in the structure of areolae and raphe and valve outline.

Although most of above mentioned *Gomphonema* taxa occur in the Arctic Region, *G. svalbardense* can easily be separated from all of them. Table 2 gives an overview of the morphological features of all more or less linear taxa with undulating margins. For comparison, several other taxa such as *G. nathorstii* Foged (1964: 138) and *G. lapponicum* (A.Cleve 1895: 21) Cleve-Euler (1934: 72) have been added. Both the latter taxa show a more typical gomphonemoid (i.e. clavate) outline with a clear head- and footpole with a higher stria density (up to 15 in 10 µm) and more parallel striation pattern, contrary to *G. svalbardense* that has less dense and more radiate striae. *Gomphonema subarcticum* has a less tumid central part, broader apices and a more clavate outline. Most valves have a lower valve width (max. 6.5 µm) and are comparably smaller (max. length up to 40 µm). Additionally, differences in the structure of the central area (with a shortened stria on both sides), the less lateral raphe, the more expanded proximal raphe endings and the typical deep internal foraminal rows (absent in the new taxon), exclude all conspecificity with *G. svalbardense*. *Gomphonema astridae* shows more similarities in valve outline although the much lower valve dimensions exclude all confusion. Moreover, *G. astridae* lacks the typical inflation of the central part, lacks a complete fascia due to the presence of a shortened striae on both sides of the central area and has an almost filiform raphe. The most similar seems to be *G. distans*, although showing somewhat lower valve

length (up to 46 µm). *G. distans* has a comparable, even higher valve width (6.5–9.0 µm). The latter can also be separated by its lower stria density (max. 9 in 10 µm), a more clavate valve outline with a less inflated central part, a larger headpole, a more prominently visible isolated pore and a different central area with a shortened striae on both sides.

Table 2. Overview of the main morphological features of closely related *Gomphonema* taxa that can be confused with *G. svalbardense*.

	<i>G. svalbardense</i>	<i>G. distans</i>	<i>G. astridae</i>	<i>G. subarcticum</i>	<i>G. nathorstii</i>	<i>G. lapponicum</i>
	this study	Lange-Bertalot & Genkal 1999	Reichardt 1999	Lange-Bertalot & Genkal 1999	Foged 1964	Cleve-Euler, A. (Cleve) 1934
Valve length (µm)	23–51	38–46	24–30.5	22–40	27–57	22–46
valve width (µm)	5.7–7.2	6.5–8	3.8–4.5	5–6.5	9–10	7.5–9.8
valve outline	almost naviculoid, linear with parallel, undulating margins, central part inflated	rather clavate, with undulating margins, central part slightly inflated	rather clavate, linear with parallel undulating margins, central part almost not inflated	rather clavate, linear with parallel, undulating margins	clavate, undulating margins, central part slightly inflated	clavate, undulating margins
apices	headpole and footpole protracted, rostrate, narrowly rounded, the foodpole slightly broader than the headpole	headpole and footpole slightly protracted, narrowly rounded, the headpole slightly broader than the footpole	headpole and footpole protracted, rostrate, narrowly rounded	headpole and footpole slightly protracted, narrowly rounded, the headpole slightly broader than the footpole	headpole and footpole protracted, broadly rounded, headpole slightly broader than footpole	headpole and footpole protracted, broadly rounded, headpole clearly broader than footpole
axial area	narrow, linear to weakly lanceolate, almost not widening towards the central area	narrow, linear to weakly lanceolate, not widening towards the central area	narrow, linear to weakly lanceolate, not widening towards the central area	narrow, linear to weakly lanceolate not widening towards the central area	narrow, linear, not widening towards the central area	narrow, linear to weakly lanceolate not widening towards the central area
central area	rectangular to weakly wedge-shaped, asymmetric fascia, one stria present along one margin with a terminal isolated pore	rectangular to weakly wedge-shaped, asymmetric fascia, one stria present on both sides with a terminal isolated pore on one side	rectangular, asymmetric fascia, one stria present along both margins with a terminal isolated pore on one side	rectangular to weakly wedge-shaped, asymmetric fascia, one shortened stria present at each side with a terminal isolated pore	rectangular to weakly wedge-shaped, asymmetric fascia with varying numbers of striae, each with a terminal isolated pore	wedge-shaped, asymmetric fascia, variable numbers of short striae present
raphe	weakly curved, undulating, lateral with straight proximal raphe endings	weakly curved, undulating, lateral with straight proximal raphe endings and curved distal raphe endings	weakly curved, undulating, lateral with straight proximal raphe endings	weakly curved, undulating, lateral with straight proximal raphe endings	filiform, lateral with straight proximal raphe endings and curved distal raphe endings	curved, undulating lateral with straight proximal raphe endings and curved distal raphe endings
striae	weakly radiate near the central area, becoming more radiate towards the apices	weakly radiate near the central area, becoming parallel towards the apices	weakly radiate near the central area, becoming only slightly more radiate towards the apices	weakly radiate near the central area, becoming parallel towards the apices	weakly radiate near the central area, becoming parallel towards the apices	strongly radiate near the central area becoming parallel towards the apices
number of striae (in 10 µm)	9–13 up to 14–19 towards the apices	5–9	13.5–16	9–11	13–14	12–15

Gomphonema svalbardense shows some interesting features that seem to be unique within the genus *Gomphonema*, such as the structure of the areolae and the structure of the internal isolated pore. Hardly any known *Gomphonema* taxon shows similar areolar openings. In most taxa and complexes, the areolae are either rounded poroids [e.g., *G. micropus* Kützing (1844: 84) or *G. drutelungense* Reichardt (1999: 38)] (Reichardt 1999) or c-, e-

or s-shaped with or without central flaps [e.g., *G. acuminatum* Ehrenberg (1832: 88)-complex and the *G. truncatum* Ehrenberg (1832:88)-complex] (Reichardt 1999, 2001). Occasionally species show depressed areolae such as in *G. vibrioides* (Reichardt 1991: 524) or *G. latipes* Reichardt (2001: 196), but never as deep as in *G. svalbardense* where the areolae are small rounded poroids each positioned eccentrically at the bottom of a deep, irregularly shaped depression. Reichardt (1999) showed one picture of *G. lapponicum* (Plate 46, fig. 10) where rounded areolae are visible at the bottom of shallow, rounded depressions but this structure is entirely different from the areolae in *G. svalbardense*. The internal opening of the isolated pore is hardly separated from the areola series in the central area. In most *Gomphonema* taxa, the internal opening is usually a slit-like, elongated opening, positioned between the internal proximal raphe endings (see for instance *G. acuminatum* in Reichardt 1999, plate 55, Fig. 4) or located at the end of a (shortened) series of areolae (*G. angustatum* in Reichardt 1999, plate 23, Figs 15–16) but then the opening can always be distinguished as an elongated, thin slit contrary to the short slit in *G. svalbardense*.

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