

New determination of *Pediastrum orientale* in polar lake sediments and its palaeoecological implications – Reindeer Lake, Bellsund, Spitsbergen

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ABSTRACT. The main component of microfossils in the bottom sediments of Reindeer Lake from Spitsbergen, documenting the almost 8,000-year history of this water body, are algae representing colonies of a very rare species *Pediastrum orientale* (Skuja) Jankovská et Komárek 1995 with only a very small (lower than 1%) admixture of other green algae species. It has also been recorded in other lake sediments in Spitsbergen. The specimens belong to the morphotype “b” of the species, known previously from the Scandinavian lakes. Due to its unique nature and scarce information on ecological conditions, this study analysed the palaeoenvironmental factors favouring the occurrence of *Pediastrum orientale* together with an assessment of its bioindication value. The affinity of the species to oligotrophic lakes, where blooms of this alga are observed, was confirmed. The presence of numerous colonies of *Pediastrum orientale* in fossil lake sediments can provide a rationale for inferring palaeoecological conditions, including the trophic state of water bodies, thus expanding knowledge of their evolutionary directions and documenting key events in the geological history of the catchment. Further studies of lake gyttjas in Spitsbergen should pay more attention to the taxonomic composition of *Pediastrum* and other green algae, as well as to the determinants of sediment deposition in different lake catchment environments.

KEYWORDS: *Pediastrum orientale*, green alga, bioindicators, oligotrophy, Holocene, Svalbard lakes

INTRODUCTION

In palaeoecological investigations of lacustrine sediments colonial green algae of *Pediastrum* Meyen 1829 (Komárek and Fott, 1983) are frequently counted along with pollen. Due to algaenan content these green algae survive harsh treatment of palynological samples

(Cronberg, 1982, 1986; Blokker et al., 1998; Bennett and Willis, 2001; Komárek and Jankovská, 2001; Lenarczyk, 2015). However, only percentages of *Pediastrum* in relation to the pollen sum are typically recorded. In the last decades, several papers were published that help to identify the *Pediastrum* to species and varieties level, which seems relatively easy with the

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use of standard light microscope (Komárek and Jankovská, 2001; Lenarczyk, 2014). The genus belongs to the Hydrodictyaceae family (Chlorococcales, Chlorophyta) and has been the subject of intense research in the last years. Recently, detailed phylogenetic studies assigned species of the *Pediastrum* group into six genera (Buchheim et al., 2005; McManus and Lewis, 2011; Krienitz and Bock, 2012; McManus et al., 2018). These are: *Pediastrum* Meyen 1829, *Pseudopediastrum* E. Hegew 2005, *Lacunastrum* McManus et Lewis 2011, *Monactinus* Corda 1839, *Stauridium* Corda 1839. Among them *Pseudopediastrum boryanum* draws special attention (Lenarczyk, 2019; Lenarczyk et al., 2020). One of the most studied is also *Pediastrum duplex* (McManus and Lewis, 2005, 2011). Genomic studies across the green algae are uncovering new lineages, highlighting a wide diversity of genomes (Krienitz and Bock, 2012). Indicative value of several species has been stressed and palynologists have been encouraged to count not only *Pediastrum* sum, but each species separately to investigate changes of temperature and lake trophic state (Jankovská and Komárek, 2000). Numerous studies have shown that changes in the composition or abundance of *Pediastrum* species have great potential for studying palaeoenvironmental evolution. Recently, Huang et al. (2021) reconstructed temperature changes in north-western China using *Pediastrum* species data. They noticed a considerable decrease or absence of *Pediastrum simplex* during the cold events dated to 4.2–4.1 kyr and 3.6–3.5 kyr. On the other hand, a warm climatic interval at 4.7–4.3 kyr expressed by high abundance of this species in the lake deposits promoted human occupation of the Altai Mountains (Xiang et al., 2023). Turner et al. (2014) provided an overview of palaeoecological studies from Europe in which multiple *Pediastrum* taxa were determined in Late Glacial and early Holocene. Despite the accuracy of the determination to subspecies level, authors note methodological problems resulting, among other things, from the small sum of specimens. It makes impossible to track quantitative changes in relative abundance and/or calculation of *Pediastrum* percentages on the basis of the pollen sum. In such a case, changes in *Pediastrum* species composition were not visible. Lenarczyk (2014) in her detailed study shed light on all *Pediastrum* taxa determined in Poland. Among them, *P. orientale* is among the least numerous and

least recognised at a global scale. Earlier studies noted significant differences in the marginal cells of *P. orientale* coenobia, as well as differences in sculpture and cell shape, which made it possible to distinguish two morphotypes of this species (Jankovská and Komárek, 1995; Lenarczyk, 2014), which were labelled by Turner et al. (2014) as: “type a” (characterised by fine granulation in the cell wall) and “type b” with more wrinkled cell walls similar to *Pseudopediastrum kawraiskyi*. Lately Lenarczyk et al. (2020) have adapted the nomenclature of *Pediastrum* taxa to the results of new molecular studies on *Pseudopediastrum boryanum*.

The above review indicates the continued interest in the green algae group. Good taxonomic identification together with detailed information on the habitat preferences of individual species and morphotypes will help to increase their value as bioindicators. Turner et al. (2016) proved that the presence of *Pediastrum* assemblages on the Tibetan Plateau could be mainly determined by summer temperature and salinity. Xiang et al. (2021b) demonstrated that mean annual temperature is the most significant environmental variable influencing modern *Pediastrum* species composition and abundance in 26 natural lakes and 17 reservoirs, with varying hydro-chemical and climatic gradients, in China and western Mongolia. It also shows that these algae can yield extremely valuable information on palaeoenvironmental change (Nielsen and Sørensen, 1992; Weckström et al., 2010; Lütje, 2014; Huang et al., 2021; Xiang et al., 2021a). Recently, Huang et al. (2023) observed temperature sensitivity of the body size of *Pediastrum* and proposed that it is the body size of fossil *Pediastrum* in the sediments of mid-latitude lakes that can be treated as a reliable temperature proxy. Particular attention has been paid to changes in lake ecosystems in polar areas, including the likely high *Pediastrum* productivity under arctic conditions (Fredskild, 1983; Björck et al., 1993). Arctic lakes, as they are still among the least impacted water bodies by humans, provide an excellent setting for studies on long term climatic variability (Weckström et al., 2010). Low temperatures of polar lake waters along with algaenan content enable good preservation of algal remains in their deposits, such as *Pediastrum* and *Botryococcus* coenobia, which can be a potentially valuable source of information about the polar palaeoenvironment

(e.g. Fredskild, 1983). With very little direct anthropogenic pressure, these deposits are an excellent source of palaeoenvironment and palaeoclimate information, archiving the main events in the history of the lake catchment. The Svalbard Archipelago, due to its geographical location, is widely regarded as a natural testing area for the study of climate change (Isaakson et al., 2003), but the number of palaeoecological studies is still not sufficient. That is why, what is emphasized by Birks et al. (2004), it is so important to document the results of each new palaeoecological research from this region, which expands the database on the trends of changes in the natural environment of polar regions during the Holocene. Although several detailed palaeolimnological studies have been performed in Svalbard, but still Douglas et al. (2004) noted that the potential for palaeoenvironment reconstructions recorded in the microfossils of algal remains is not fully utilised here. Recently Woelders et al. (2018) showed evidence of sharp growth in freshwater green algae, as well as distinct diatom assemblage changes since ~1995, retrieved from a high-Arctic (80°N) lake sediment record on Barentsøya (Svalbard). The authors determined *Pediastrum* taxa to the species level, and apart from abundant *P. boryanum* var. *boryanum*, they pointed out the high proportion of *Pediastrum orientale* (Skuja) Jankovská et Komárek 1995 in samples of this lake. In 2016 we recovered a sediment core from the non-glacial Reindeer Lake, Spitsbergen with the aim to analyse it in terms of pollen and non-pollen palynomorphs and basic physicochemical parameters. The core turned out to be empty of pollen, but the abundance of *Pediastrum* algae encouraged us to trace their species diversity along the core section, providing a basis for considerations on the ecological stability of the water body in the climate changes in polar regions during the Holocene. Abundant occurrence of *Pediastrum orientale* in the examined lake sediments was surprising for us. Due to the rarity of the occurrence of this species in other areas, the differences in morphotypes “a” and “b” and the hitherto unrecognised palaeoenvironmental conditions for its occurrence, the present work undertakes a palaeoenvironmental study that may indicate bioindicative value of *P. orientale* and the type of lake reservoir which favours the mass occurrence of this alga.

STUDY SITE

Reindeer Lake (77°32'41"N, 14°47'06"E) is a small, non-glacial lake in the Reinodden Cape (1 km long headland dividing Bellsund, Recherchefjorden and Malbukta) in the NW part of Wedel Jarlsberg Land, western Spitsbergen. The lake (area 40 acres; 15 m a.s.l.; max. depth 1.6 m) is located on the raised marine terrace No III (Zagórski et al., 2013), called Reinsletta, uplifted 12–20 m a.s.l. and dated for the transition between Weichselian and Holocene. The study site is geologically located within the Reinodden Block composed of Upper Paleozoic and Lower Mesozoic rocks, represented by mudstones, claystones and sandstones (Dallmann et al., 1990; Birkenmajer, 2004; Fig. 1).

The climate of Wedel Jarlsberg Land is subarctic with a long winter of more than 7 months, summer of more than 2.5 months and short, 1 month long, transitional seasons: spring and autumn (Marsz and Styszyńska, 2013). Weather conditions in the NW part of the region are recorded by the station in Calypsobyen, located on the other side of Recherchefjorden (Fig. 1). However, it only operates during the summer expeditions of the Maria Curie-Skłodowska University in Lublin. In contrast, the year-round station of the Polish Academy of Sciences in Hornsund, located at the opposite end of the region, has a long-term observation series. For this reason, the characteristics of weather conditions for the Reindeer Lake area were based on meteorological data from the Hornsund Station, while for the summer periods averaged data from both stations were used. The values of cloudiness measurements (6.6 on a scale of 0–8), just like mean wind speeds (4.3 m·s⁻¹), show no significant differences between the stations in Calypsobyen and Hornsund. In contrast, the mean air temperature in summer, 5.1°C in Calypsobyen, was 0.6°C higher than in Hornsund. Conversely, the winter air temperature is lower in Calypsobyen. As a result, the average annual air temperature in the Reindeer Lake area is around -4.5°C. The annual total precipitation is 435 mm in Hornsund (Gluza and Siwek, 2013; Marsz and Styszyńska, 2013). Such conditions hinder the accumulation of snow cover, which is destroyed by wind and mid-winter thaws, causing icing of the tundra surface (Rodzik, 1988). The ice cover of Reindeer Lake

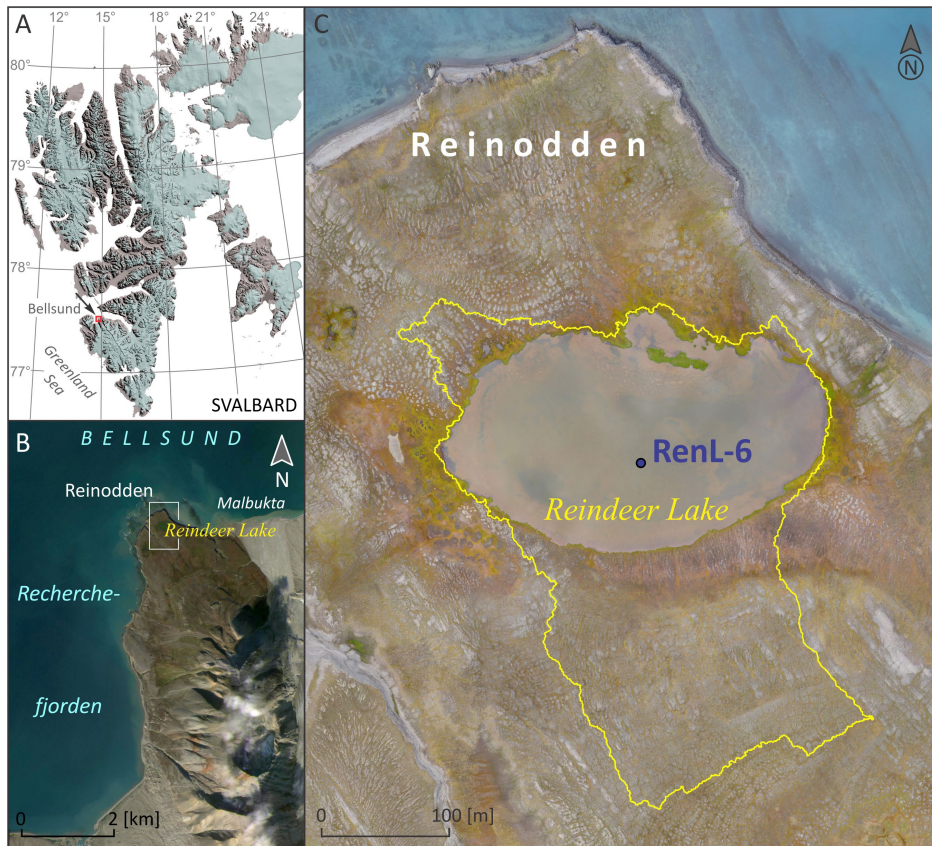


Figure 1. A, B. Localization of study area (B. Background: Satellite image, 25th August 2020, Planet Labs, Inc.); C. Sampling point location. Yellow continuous line – catchment boundaries designated in Global Mapper Pro v23 software. Orthophotomap made in 2022

reaches a considerable thickness of >1 m under these conditions, analogous to similar lakes in Hornsund, also covering the bottom sediments probably entirely (freezing to the lake bottom). However, the lake's shallow depth and exposure to solar radiation in spring means that the ice in such lakes usually disappears as early as June (Wojtasik, 2012). Thus, it can be assumed that the algae find good conditions for growth throughout the summer, from June even until early September. Reindeer Lake's supply is small and comes from snowmelt, rainfall and permafrost melt. The small catchment area of the lake is noteworthy. The limited water exchange in the absence of ice cover means that the water heats up quickly in summer. However, on cloudy days significant temperature drops may occur at the bottom due to energy consumption for heating and thawing of the substrate (Nowiński and Wiśniewska, 2006; Wojtasik, 2012).

The trophic state of the lakes with permafrost thawing supply in Hornsund is low. This is due to the peculiarities of the recharge and phase transformations of the water, affecting almost the entire volume of the basin. Based

on long-time observations in Hornsund, the waters of such lakes are characterised by low conductivity (30–100 $\mu\text{S}/\text{cm}$) and low salinity (20–70 mg/dm^3). The study of the lakes similar to Reinodden by Szumińska et al. (2018) in Bellsund in 2013 revealed that their pH ranged from 8.00 to 8.07, the values of conductivity ranged from 270–287 $\mu\text{S}/\text{cm}^{-1}$, ion sums remain within the low mineralisation range (<100 mgL^{-1}). Concentrations of Ca^{2+} varied between 27.22 and 49.62%, those of Cl⁻ between 17.45 and 23.54% and those of NO_3^- ranged from 12.93% to 15.70%. Moreover the concentration of SO_4^{2-} was found to range between 21.59 and 29.69%. Thus, the results showed a considerable contribution of elements of geogenic origin: Ca^{2+} , Mg^{2+} , SO_4^{2-} , Sr, which is in line with the findings of other authors, who have indicated that these elements tend to prevail in the tundra lakes of Svalbard. Szumińska et al. (2018) identified the main sources of the chemical composition of tundra lake water including influence of permafrost degradation processes, atmospheric transport of contamination and to smaller extent marine aerosol effect as well.

MATERIAL AND METHODS

CORING AND SAMPLING

The bottom sediments of the lake were identified by geological drilling (7 boreholes) along two orthogonal transects defining the longer and shorter axes of the lake (Fig. 1). Simplified piston corer (1.5 m long PVC tubes with 50 mm in diameter), was used for coring. All boreholes were positioned precisely using GNSS receivers (Leica system 500). All of the sediment cores were sampled at every 1 cm for detailed laboratory analysis.

LABORATORY TREATMENT

Pollen and Pediastrum analysis

One core (coded RenL-6, location shown in Fig. 1) was selected for palynological analyses. This core showed the greatest thickness of gyttja (22 cm). Seven samples of gyttja, taken in 3–4 cm intervals, were subjected to laboratory processing typical for palynological analyses (Berglund and Ralska-Jasiewiczowa, 1986). Samples were analysed under a light microscope NIKON Eclipse E600 with a magnification of 400×. *Pediastrum* species were identified following Jankovská and Komárek (1995), Komárek and Jankovská (2001) and Lenarczyk (2014). Taxonomy considered the revisions of Buchheim et al. (2005), McManus and Lewis (2011) and Krienitz and Bock (2012). During counting *Pediastrum* coenobia, the method of Woelders et al. (2018) was followed who counted coenobia only if it was estimated that >50% of the coenobium was complete. The proportions of *Pediastrum* species are based on the total sum of identified coenobia of this genus. *Pediastrum orientale* was counted until a sum of ~400 coenobia was reached. Additionally, the whole slide was searched for different other species of *Pediastrum* and/ or pollen and Musci spores. They were counted until 400 of *Pediastrum orientale* coenobia were reached on one microscopic slide. Percentages of Musci spores and pollen grains were counted based on the total sum (*Pediastrum* coenobia + Musci spores /or pollen grains/ = 100%). Results are presented in Fig. 2.

Chronology

Chronology was based on artificial radionuclide ^{137}Cs and AMS radiocarbon dating (^{14}C).

Caesium-137 dating. Samples were dried overnight at 105°C and packed into 100 ml polypropylene cylindrical containers. The dry mass of these samples varied between 0.69 g and 2.11 g. Caesium-137 was determined using high-resolution gamma-spectrometry with a planar HPGe (high-purity germanium) detector; the $^{137\text{m}}\text{Ba}$ emission peak at 662 keV was measured. Six samples from RenL-6 profile were measured. The laboratory performing the analyses (Department of Nuclear Physical Chemistry at the Institute of Nuclear Physics, Polish Academy of Sciences in Cracow, Poland) has ISO 17025 accreditation for gamma spectrometric measurements.

AMS Radiocarbon dating. Due to the measurement limitations of the caesium method (assumed

older age of the sediments throughout the study profile), a bottom sediment sample from the RenL-6 core was analysed using AMS. Radiocarbon dating was performed at the Laboratory of Ion Beam Physics, ETH Zurich, Switzerland (RenL-6/22). Assay of a bulk sediment (algae gyttja) from 22 cm depth was carried out. The results, performed for the total organic carbon (TOC) of fine fraction (<125 μm), were expressed as radiocarbon ages BP with associated uncertainty. The results were calibrated using IntCal20 (Reimer et al., 2020) calibration curves and OxCal (Bronk Ramsey, 2009) software.

Physical properties

The relative content of organic matter (OM) in lacustrine sediments (10 samples) was determined by loss on ignition (LOI) after heating the samples to 500 and 1000°C following the method of Heiri et al. (2001). Samples were taken from every 2 cm in the 22 cm long core RenL-6.

This method, widely recognized as an exceptionally good summary of the many changes in the lake ecosystem and giving basic information on sediment lithology, provides one of the most widely used simple physical lines of proxy evidence in palaeolimnology (Dean, 1974; Boyle, 2004).

In addition, pH of water and lacustrine sediments in the whole analysed core were marked. All heating and weighing procedures followed the protocols by Nelson et al. (1996) and Hoogsteen et al. (2015). The analyses were performed at the laboratory of the Institute of Earth and Environmental Sciences, Maria Curie-Skłodowska University in Lublin, Poland.

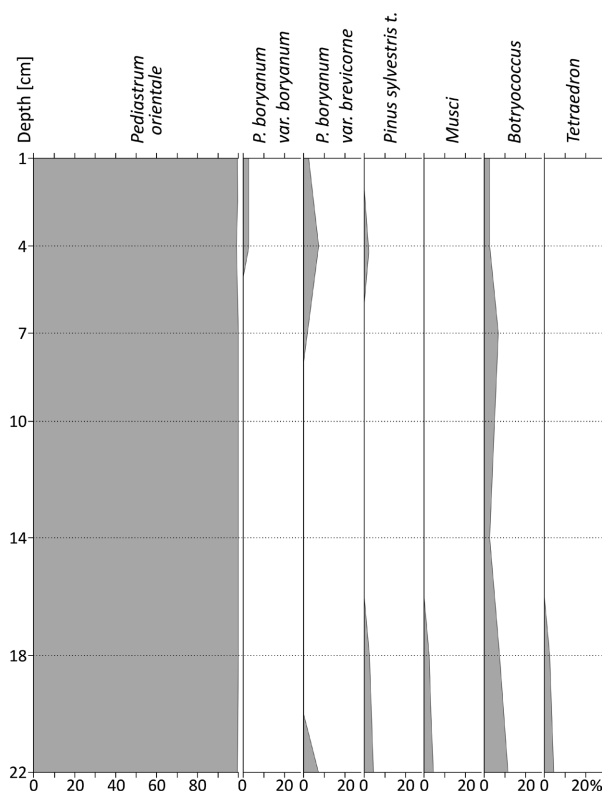


Figure 2. Percentage diagram of algae species, Musci spores and *Pinus* pollen in total assemblages of palynological samples of RenL-6 core

RESULTS

POLLEN AND *PEDIASTRUM* ANALYSIS

Microscopic analyses of 7 gyttja samples from the RenL-6 core (from the 1–22 cm section) showed a complete absence of pollen and plant spores, with the exception of occasional moss spores and a single *Pinus* pollen grain. In

contrast, all organic matter in each sample was colonies of the alga *Pediastrum*. The species composition of the algal assemblage showed very few changes (Fig. 2). Approximately 99–100% of each sample was *Pediastrum orientale* (Skuja) Jankovská et Komárek 1995 (Figs 3A–D, 5A–C), with the remaining few coenobia being identified as *Pseudopediastrum boryanum* var. *boryanum* with a single occurrence of

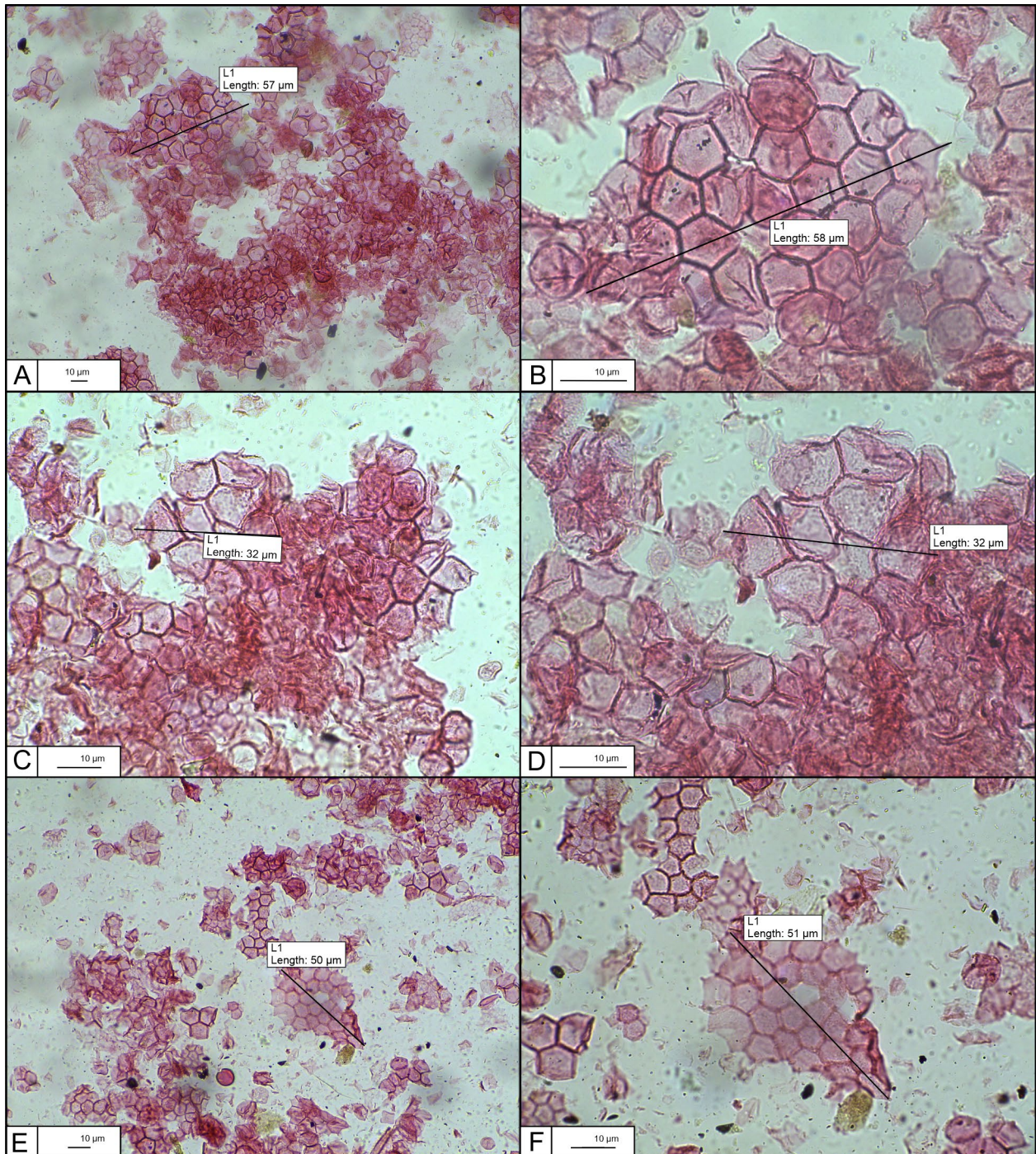


Figure 3. A–D. Mass occurrence of *Pediastrum orientale* in the sample RenL-6 depth 7 cm, A. *P. orientale* coenobium at magnification 200×, B. the same coenobium as in A, at magnification 600×, C. another *P. orientale* coenobium at magnification 400×, D. the same coenobium as in C, at magnification 600×; E, F. Single occurrence of *P. boryanum* var. *brevicorne*; E. magnification 200×, F. the same coenobium at magnification 400×

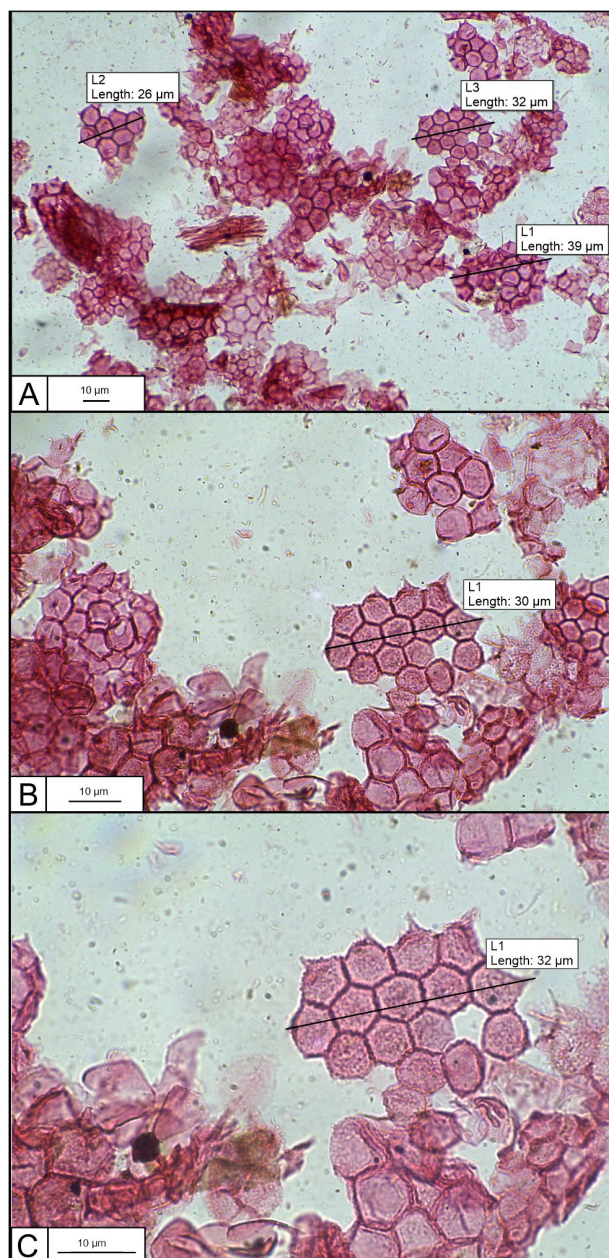


Figure 4. A–C. Mass occurrence of *Pediastrum orientale* in the sample RenL-6 depth 22 cm, **A**, magnification 200×, **B**, coenobium L3 from the right upper corner of **A** at magnification 400×, **C**, the same coenobium as in **B**, with diameter measured and characteristic sculpture and processes of the outer cells (magnification 600×)

colonies of *Pseudopediastrum boryanum* var. *brevicorne* (Figs 3E, F, 6A, B). Considering the characteristics of *P. orientale* in our core, it can be seen that it represents morphotype “b” of this species (Lenarczyk, 2014), which, unlike morphotype “a”, is characterised by short processes well visible under the magnification of 600× (see examples Figs 3B, D, 5C).

RADIOMETRIC MEASUREMENTS

All samples from profile RenL-6 contained undetectable amounts of ^{137}Cs (Table 1). The

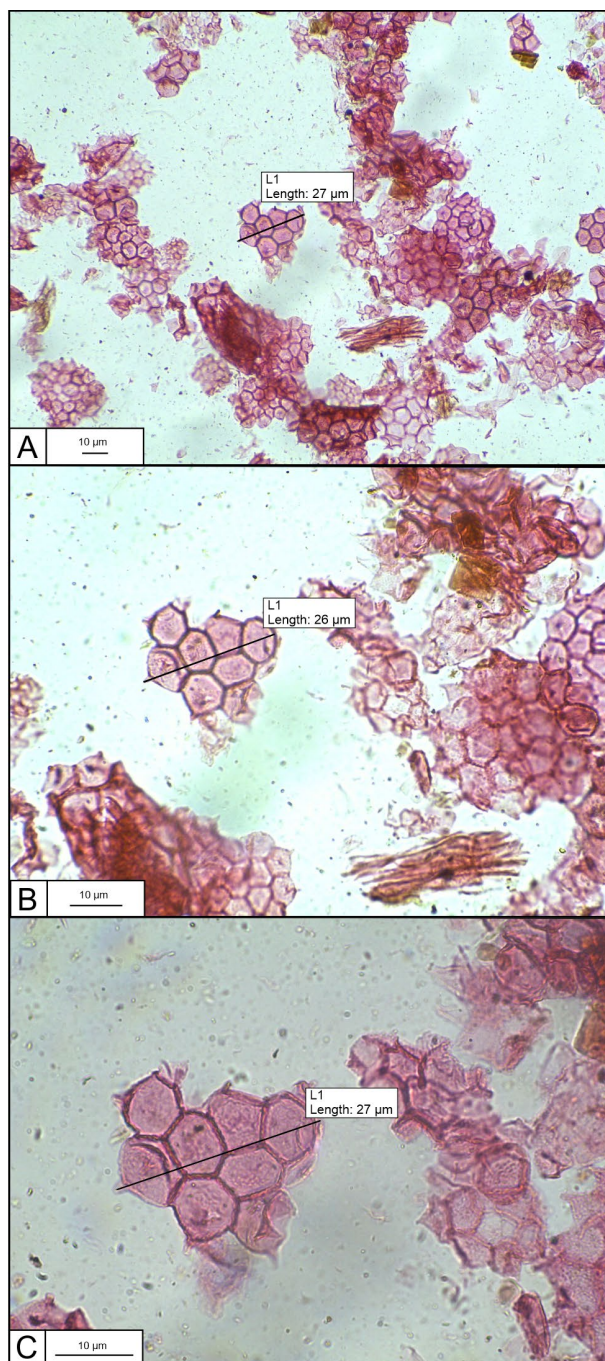


Figure 5. A–C. Mass occurrence of *P. orientale* in the sample RenL-6 depth 22 cm, **A**, coenobium measured at magnification 200×, **B**, the same coenobium measured diameter and visible short processes of the outer cells (magnification 400×), **C**, the same coenobium with visible sculpture and shape of processes of the outer cells (magnification 600×)

Table 1. Results of ^{137}Cs determinations in the core RenL-6

Sample number	Depth [cm]	MDC ^{137}Cs (Bq/kg)
RenL-6/02	2.0	<104
RenL-6/05	5.0	<58
RenL-6/10	10.0	<38
RenL-6/14	14.0	<41
RenL-6/18	18.0	<26
RenL-6/22	22.0	<41

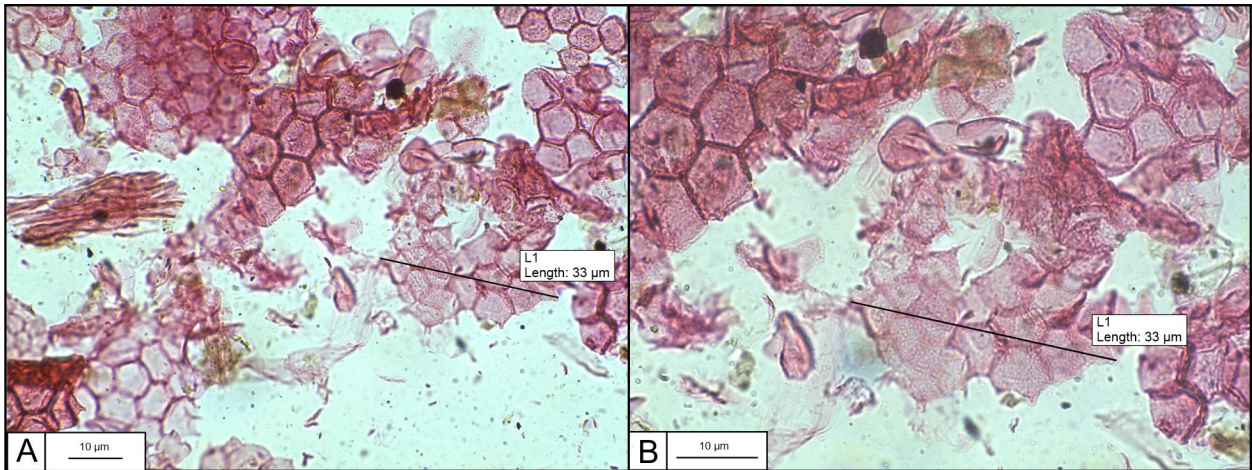


Figure 6. A, B. Single occurrence of *P. boryanum* var. *brevicorne* (diameter measured of two neighbouring coenobia. On the left *Pediastrum orientale*, on the right – *P. boryanum* var. *brevicorne*), **A.** at magnification 400×, **B.** at magnification 600×

minimum detectable concentrations are very high due to the small mass of samples.

Determination of the radiocarbon age of a bottom sediment sample from Reindeer Lake (RenL-6/22) indicates that the onset of organic accumulation in the reservoir is the time interval 7940–7784 cal BP (95.4%).

PHYSICAL PROPERTIES OF GYTTJA

Organic matter (OM) values in the whole profile are on average 44% of the dry mass. The maximum OM is recorded in the bottom lake sediments (61.7%). OM values gradually decrease upwards in the profile, reaching the minimum in the core top (35%). Dried gyttja pH measurements show relatively little variation in the profile. The pH values vary from 7.4–7.5 in the lower and middle parts of the core to 6.7 in the top part of the sediments, with an average value of 7.3.

DISCUSSION AND CONCLUSIONS

METHODOLOGICAL CONCLUSIONS/ SUGGESTIONS

Although the samples examined were prepared according to the procedure for pollen analysis, the absence of pollen (except for a single occurrence of *Pinus* pollen grain at the depth of 4 cm) and only the occasional presence of moss spores should not have been surprising. An explanation for the absence of pollen in the case of Reindeer Lake could be the fact that the profile was taken in the middle of a lake surrounded by bryophyte tundra communities of its small catchment. Such

vegetation produces low amounts of pollen and, due to its short height, also has a poor ability to disperse it and get it into the lake sediment. The problem of the very poor pollen representation of the local vegetation in the lake sediments of Spitsbergen had been pointed out previously by other authors (Wohlfarth et al., 1995; Birks et al., 2004; Woelders et al., 2018) indicating the presence of only a few pollen grains on the surface of the coverslip, including the dominance of long-distance transport elements (mainly pine pollen) and the impossibility of reliable interpretation. This results in a discouraging lack of effect of this analysis in relation to the effort made (Birks et al., 2004) for further palynological studies.

PALAEOECOLOGICAL IMPLICATIONS

In our study, the surprisingly high proportion of *Pediastrum orientale* in the gyttja from the Reindeer Lake and the virtually unchanged composition of the green algae may indicate extremely stable conditions in the lake over a very long period of time. Taking into account the radiocarbon dating of the bottom sample, falling in the Atlantic phase of the Holocene, and the fact that the youngest dated samples are older than the range of the radioactive ^{137}Cs method, we are dealing with a sedimentary section representing several thousand years in a 22 cm long core. Unfortunately, the studied sediments do not record the youngest period of several hundred years. It can be assumed that our shallow lake was formed during the Atlantic phase of the Holocene, fed by waters from a small catchment located on the slope of terraces III and IV (Fig. 1). This was the period

after intensive thawing of the permafrost in this area (Wohlfarth et al., 1995).

The very high dominance of *P. orientale* was not found in any previous studies in the Arctics. According to studies by Jankovská and Komárek (2000), *P. orientale* was listed among several taxa occurring only in clear water accompanied by *P. kawraiskyi* and *P. boryanum* var. *perforatum* (in the light of new data renamed to *Pseudopediastrium perforatum* and *Pseudopediastrium kawraiskyi*). The assemblage of *P. kawraiskyi* and

P. orientale and their occurrence under cool climatic conditions is also reported in several other localities (Table 2). *Botryococcus* specimens determined sporadically in our material belonged most probably to *B. pila* that occurs in peaty waters. The dominant occurrence of *Pediastrum boryanum* var. *longicorne*, *P. integrum* and *Botryococcus pila* is assumed to indicate past existence of smaller waterbodies with cool and dystrophic but otherwise clean water (Jankovská and Komárek, 2000). Rare occurrence of *Pediastrum orientale* in several

Table 2. Overview of the published data on the occurrence of *Pediastrum orientale*

A. Rare occurrence of <i>Pediastrum orientale</i> in contemporary lakes in Poland			
Locality	Accompanying <i>Pediastrum</i> taxa	References	
Lakes and pond of the Southern Baltic Coast (Poland): Bukowo, Gardno, Łebsko, Jamno, Sarbsko, unnamed pond east of Święta	Low frequency of each of four <i>Pediastrum</i> species: <i>P. boryanum</i> , <i>P. kawraiskyi</i> , <i>P. duplex</i> Rare: <i>P. tetras</i> , <i>P. alternans</i> , <i>P. biradiatum</i>	Lenarczyk (2014) Kowalska and Wołowski (2010)	
Polesie region (E Poland): Kościuszkó pond near Libiszów, unnamed pond near Giewont Pond near Libiszów, Hetman pond near Sosnowica	Frequent: <i>P. simplex</i> , <i>P. boryanum</i> , <i>P. tetras</i> Rare: <i>P. patagonicum</i> , <i>P. biradiatum</i>	Lenarczyk (2014)	
Sumin lake	High frequency: <i>Pediastrum boryanum</i> , <i>P. duplex</i> , <i>P. tetras</i> , <i>P. simplex</i> Rare: <i>P. kawraiskyi</i>	Pasztaleniec and Poniewozik, 2004	
B. Occurrence of <i>Pediastrum orientale</i> in fossil lake sediments			
Locality	Accompanying <i>Pediastrum</i> taxa	Frequency of <i>P. orientale</i>	References
Żabie Oko peat bog in the Tatra Mts (Poland)	<i>P. boryanum</i> var. <i>boryanum</i> , var. <i>longicorne</i> , var. <i>brevicorne</i> , <i>P. integrum</i> , <i>P. duplex</i> var. <i>rugulosum</i>	Sporadic occurrence in the Atlantic and Subboreal periods of the Holocene	Wołowski et al., 2002
Fossil lake at Švarcenberk (Czech Republic)	<i>P. boryanum</i> group	Small proportion in <i>Pediastrum</i> assemblages in the deposits covering the Late Glacial-Preboreal	Pokorný and Jankovská, 2000
Jeetzel River valley (Germany)	Dominant: <i>P. kawraiskyi</i> Accompanying: <i>P. boryanum</i> var. <i>boryanum</i> , <i>P. boryanum</i> var. <i>longicorne</i> , var. <i>brevicorne</i> , <i>P. duplex</i> var. <i>rugulosum</i>	Frequent in the period covering Late Pleniglacial-Preboreal	Turner et al., 2014
Zdany (Siedlce Upland, Central-Eastern Poland)	Dominant: <i>P. kawraiskyi</i> , Frequent: <i>P. boryanum</i> var. <i>boryanum</i>	Very frequent in sediments of stadial periods of the Cromerian Complex, (misnamed <i>P. cf. kawraiskyi</i>)	Pidek, 2003
Lysmosen (Denmark)	Accompanying: <i>P. boryanum</i> var. <i>boryanum</i> , <i>P. kawraiskyi</i>	Frequent in fossil lake deposits	Nielsen and Sørensen, 1992
Seven subarctic lakes in Finnish Lapland	<i>P. boryanum</i> var. <i>brevicorne</i> , <i>P. integrum</i> , <i>P. boryanum</i> var. <i>forcipatum</i> , <i>P. boryanum</i> var. <i>boryanum</i> , <i>P. boryanum</i> var. <i>longicorne</i>	Frequent, maximum abundance 24%	Weckström et al., 2010
Lake Sundneset on the Barentsøya Island (Eastern Spitsbergen)	Dominant: <i>P. boryanum</i> var. <i>boryanum</i> Accompanying: <i>P. boryanum</i> var. <i>brevicorne</i> , <i>P. integrum</i>	Frequent in subfossil lake deposits covering the period 1985–2015	Woelders et al., 2018
Lake Tso Moriri (Tibetan Plateau, Trans-Himalayan region, north-western India)	Co-domination of <i>P. boryanum</i>	Co-dominant	Leipe et al., 2014
25 large lakes (area >100 ha) and 26 ponds (area, 1 ha) in Tibetan Plateau	<i>P. boryanum</i> var. <i>longicorne</i> , var. <i>brevicorne</i> , var. <i>boryanum</i> , <i>P. integrum</i>	Frequent	Turner et al., 2016
Lake Lielais Svētīnu (Eastern Latvia)	<i>P. boryanum</i> var. <i>boryanum</i> , <i>P. kawraiskyi</i> , <i>P. integrum</i> , <i>P. simplex</i> , <i>P. angulosum</i>	Sporadic in the Younger Dryas	Stivrins et al., 2015
Surface lake sediments in China and western Mongolia	<i>P. boryanum</i> var. <i>boryanum</i> , <i>P. boryanum</i> var. <i>longicorne</i> , <i>P. boryanum</i> var. <i>brevicorne</i> , <i>P. integrum</i>	Sporadic occurrence in two samples	Xiang et al., 2021b

coastal lakes of the Southern Baltic coast was reported by Kowalska and Wołowski (2010) and Lenarczyk (2014), while Wołowski et al. (2002) found it in the Żabie Oko peatbog in the Tatra Mts. Turner et al. (2014) found a maximum of *Pediastrum orientale* (32%) in the Pre-boreal period, during which the proportions of *P. kawraiskyi* gradually declined and several new *Pediastrum* species started to grow. In the lake deposits with the record of cold periods, *Pediastrum orientale* was found in lake Švarcenberk (Czech Republic) accompanied by a significant number of representatives of the widely defined *Pediastrum boryanum* group (Pokorný and Jankovská, 2000) and in the Zdany site (central Poland) where *P. orientale* was accompanied by abundant *P. kawraiskyi* in stadial periods of glacial sediments of the Cromerian complex (Pidek, 2003).

In our data from Reindeer Lake deposits only slight morphological differences were observed between the outer cells of *Pediastrum orientale* colonies (Figs 3A–D, 5A–C). Indeed, as noted by Kowalska and Wołowski (2010), *P. orientale* shows morphological differences under different environmental conditions. The very small differences in external cells may further suggest the stability of environmental conditions over a long time. In the Polish water bodies, it occurred only sporadically (less than 0.2% of the algae assemblage) in waters differing in terms of pH, conductivity, hardness, nitrate contents, etc. (Table 2). The intraspecific variability allowed Lenarczyk (2014) to distinguish two morphotypes: first (labelled as morphotype “a” by Turner et al., 2014) is characterized by longer processes of the marginal cells and was found only in fish ponds and coastal lakes. Specimens of this morphotype exhibited similarities to *Pediastrum boryanum* var. *brevicorne*. The second morphotype (labelled as morphotype “b” by Turner et al., 2014) has been illustrated in fig. 9A–F of Lenarczyk (2014: 41) and resembled *Pediastrum kawraiskyi*, but has short processes of the marginal cells, maximally ca. one fourth of cell length. Several authors pointed to the need for further study on the morphological variability of the species as *P. orientale* belonged to the most variable *Pediastrum* species in their assemblage (Wołowski et al., 2002; Kowalska and Wołowski, 2010; Lenarczyk, 2014).

Nielsen and Sørensen (1992) reported this species in the sediments of Lake Lysmosen

in Denmark, which they initially considered a morphotype of *Pediastrum kawraiskyi* due to the similarity of the sculpture and the nature of the processes of the outer cells. However, the paper by Jankovská and Komárek (1995) already suggested that the photograph taken by Nielsen represents morphotype “b” of *Pediastrum orientale*. The differences with morphotype “a” determined by Jankovská and Komárek in the Švarcenberk fossil lake of the Czech Republic were also given. It was precisely the sculpture not resembling *P. kawraiskyi*, as well as the long processes of the outer cells. Jankovská and Komárek (op.cit.) therefore suggested the necessity of long-term studies on the influence of temperature on *Pediastrum* growth in different climate zones. This opinion is strongly supported by the results of Huang et al. (2023). Their investigation in five lakes in northern China shows that regional temperature conditions significantly impacted the body size of *Pediastrum* as temperature affects the physiological processes of algae.

It can be assumed that the external differences in the two morphotypes recognised so far also reflect deeper genotypic differences and thus defines the habitat preferences of individuals belonging to one or the other morphotype.

Genetic studies on morphotypes indicate how slight morphological differences can translate into more significant differences in DNA and thus into different habitat preferences. Perhaps future genetic studies will resolve this issue and may identify a morphotype specific to Arctic lakes. Perhaps *P. orientale* morphotype “b” observed in the Reindeer Lake finds excellent living conditions particularly in polar areas and therefore occurs abundantly and forms a dominant or co-dominant component of the gyttja.

Due to the lack of sediments representing the youngest decades, we cannot fully compare our data from western Spitsbergen with those developed in the lake from Barentsøya Island in eastern Spitsbergen (Woelders et al., 2018). The aforementioned work clearly shows a moment of significant change in the high-Arctic lake after 1995. A very important aspect is the abundant presence of *P. orientale*, which, together with *P. boryanum* var. *boryanum*, accounts for 85–100% of the *Pediastrum* sum. The other two species *P. boryanum* var. *brevicorne* and *P. integrum* occur sporadically. At the same time, it is important to emphasize

the quantitative predominance of *P. boryanum* var. *boryanum* over *P. orientale*, the opposite of what is the case in the Reindeer Lake samples, in which only *P. orientale* strongly dominates and reaches up to 100%, while *P. boryanum* var. *boryanum* is considered to be a taxon associated with a wide range of eutrophic but unpolluted freshwater habitats, *P. orientale* strongly prefers oligotrophic conditions. Hence its rare occurrence today.

To date, most algal determinations from Arctic lakes involve diatoms (e.g. Jones and Birks, 2004; Holmgren et al., 2010; Gjerde et al., 2018). Holmgren et al. (2010), in their study of lake sediments from four small lakes on western Spitsbergen, report a marked diatom floristic change coupled with increased diatom concentrations beginning in ~1920. Not just Holmgren et al. (2010) but other authors also highlight the pronounced environmental changes in lake sediments from many regions of the Arctic in the late nineteenth and twentieth centuries (see also Douglas et al., 1994; Gajewski et al., 1997; Wolfe and Perren, 2001; Sorvari et al., 2002; Birks et al., 2004; Smol et al., 2005). In general, the changes in microorganism species composition reported in these studies are considered an ecological response to recent climate warming, including longer growing seasons. Furthermore, Holmgren et al. (2010) consider the sensitivity of Arctic lakes to nitrogen deposition, based on the studied responses observed in other low-nutrient lake systems (Sickman et al., 2003; Bergström and Jansson, 2006), and conclude that it has been predicted to be high. Lutyńska (2011) drew similar conclusions when studying diatoms in lakes on the tundra in Petuniabukta. She noted the low thickness of gyttja sediments (33 cm), but nevertheless the variability of diatom assemblages in the upper part of the sediment profile indicated eutrophication most likely related to anthropogenic pressure.

Given that the species composition and biomass of phytoplankton in lakes is variable over time and dependent on many factors, both biotic and abiotic, the high frequency of the same species (*Pediastrum orientale*) in the lake sediments of Reindeer Lake is noteworthy. Changes in *Pediastrum* assemblage could be expected due to increased anthropogenic pressure and nitrogen content. However, the observed changes in our data are negligible.

Understanding how the adaptation of planktonic organisms, characterized by a very short life cycle, to the extreme, and time-varying, environmental conditions of Spitsbergen takes place requires an in-depth analysis of their ecology.

FINAL REMARKS

Several factors can be considered potential reasons for the preservation of the species *Pediastrum orientale* throughout the limnic core from Reindeer Lake, representing the last few thousand years. These include: (i) the specific location of the lake, including the small catchment area, limited supply of allochthonous material throughout the lifetime of the reservoir; (ii) the period of biological activity in the lake, limited to a few months per year, consequently translating into a survival effect whereby the best adapted algal species with a preference for oligotrophic conditions survives; (iii) the extent of climatic change throughout the Holocene (with the exception of the last centuries) was relatively small, providing an opportunity for long-term species adaptation of *Pediastrum orientale*; (iv) further studies on two morphotypes of *Pediastrum orientale* are needed, similar to recent phylogenetic and morphometric analyses of *Pseudopediastrum boryanum* (Lenarczyk et al., 2020). These may help to answer the question whether morphotype “b” prefers arctic oligotrophic lakes. Krienitz and Bock (2012) stressed that different phylogenetic species can be hidden under one morphotype and the morphology of green algae does not adequately reflect their phylogenetic position. In the case of *P. orientale*, its mass occurrence in Reindeer Lake provides a unique opportunity to further trace its relationship with environmental conditions using modern molecular methods.

The geographical distribution of morphotype “a” and “b” also requires further study. Perhaps morphotype “b”, which seems to prefer cold waters of the northern and mountain lakes and is found in small numbers in coastal Baltic lakes, can be regarded as a post-glacial relict in the Baltic. *Pediastrum orientale* has also been found in lakes in the Netherlands, Argentina and Turkey (Luka Sato in Guiry, M.D., Guiry, G.M., 2023). Considering the hypothesis of a possible postglacial origin of *Pediastrum orientale* in the Baltic Sea, variants of this species from the Netherlands and

the other locations given by www.algaebase.com should also be examined more closely.

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