

Morphology and indicator value of non-pollen palynomorphs in Arctic ice-wedge polygon mires in NE Siberia[☆]

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ABSTRACT

Non-pollen palynomorphs (NPPs) are important ecological indicators and are increasingly used in the study of Arctic ice-wedge polygon mires in Siberia. This paper provides an overview of NPPs found in high-spatial-resolution (1 m sample distance) surface samples along transects crossing various polygon microtopographical elements, and in high-temporal-resolution (sample distance 0.5 cm) contiguous samples in peat profiles. Whereas algal palynomorphs - of e.g. *Botryococcus*, *Pediastrum*, and various Zygnemataceae - show a distinct presence in open water settings, testate amoebae tests - of *Arcella*, *Assulina*, and *Amphitrema flavum* - are typical for dry peatland settings such as polygon rims. Various other NPPs were encountered including types not yet described. The latter have been denominated using morphological terms to facilitate future identification. These types are often typical for distinct polygon microhabitats and thus have indicator values that allow the reconstruction of past ecological settings without knowing the taxa that produce them.

1. Introduction

The Arctic is subject to rising temperatures at a faster rate than the global average (Meredith et al., 2019; Rantanen et al., 2022). It contains around 50% of the estimated global belowground organic carbon pool, which is twice the current atmospheric content (Tarnocai et al., 2009; Kuhry et al., 2013; Schuur et al., 2013; Hugelius et al., 2014). The thawing of permafrost (Biskaborn et al., 2019; Nitzbon et al., 2019; Speetjens et al., 2024) will most likely result in considerable greenhouse gas emissions that may increase further global warming (see Schuur et al., 2013, 2015; Schädel et al., 2016; Turetsky et al., 2019; Ramage et al., 2024).

It is still unclear how Arctic mires will react to the rising temperatures because of a multifaceted interchange of internal and external forcing, direct and indirect effects, and positive and negative feedback mechanisms, affecting frost and thaw processes, microrelief, hydrology, vegetation development, and peat accumulation (Godin et al., 2016; Liljedahl et al., 2016; Millman et al., 2026; Nitzbon et al., 2019; Speetjens et al., 2024). High-resolution palaeoecological studies can contribute to unravel this complexity (De Klerk et al., 2011, 2018;

Teltewskoi et al., 2016).

Ice-wedge polygon mires are a main constituent of the Arctic landscape and consist of relatively dry rims enclosing moist to wet depressions. Furthermore, polygon troughs and collapsed polygon ridges contain moist to wet settings. Vegetation reconstruction using pollen and macrofossil analysis may provide a robust framework for reconstructing polygon development by identifying former wet and dry site conditions, but NPPs often provide more precise information on local hydrological regimes.

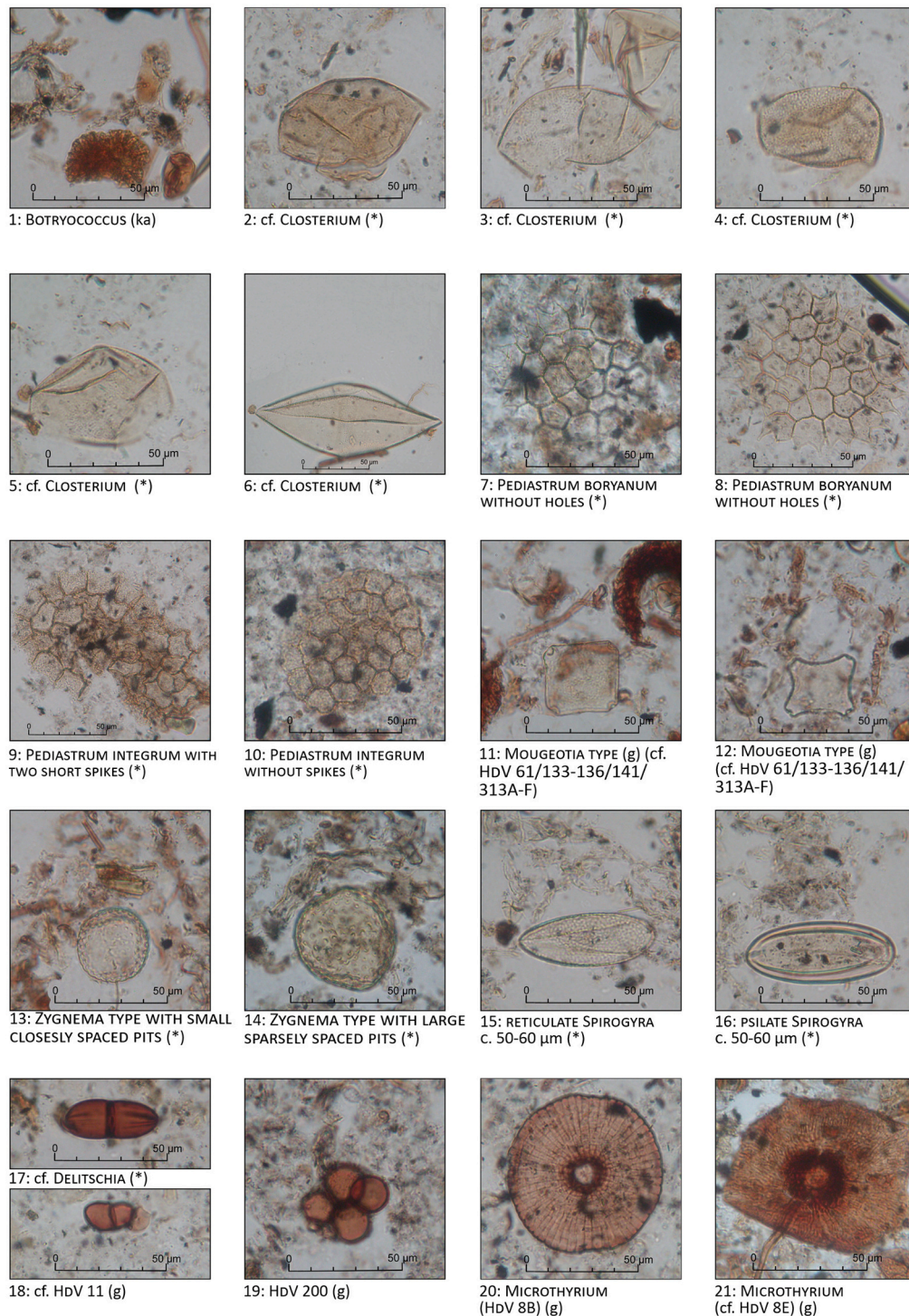
In a long-term project into the development of polygon mires (Minke et al., 2007; De Klerk et al., 2018) we studied short-distance (1 m) distribution patterns of pollen, spores, and NPPs in surface samples along polygon transects (De Klerk et al., 2009, 2014, 2017 and research in progress) to support the palaeoecological recognition of microtopographical elements in peat profiles (De Klerk et al., 2011, 2018; Teltewskoi et al., 2016).

This paper discusses the morphology and indicator value of various NPP-types from ice-wedge polygons in NE Siberia (Fig. 1) and describes the challenges of analysing and interpreting palynomorph data.

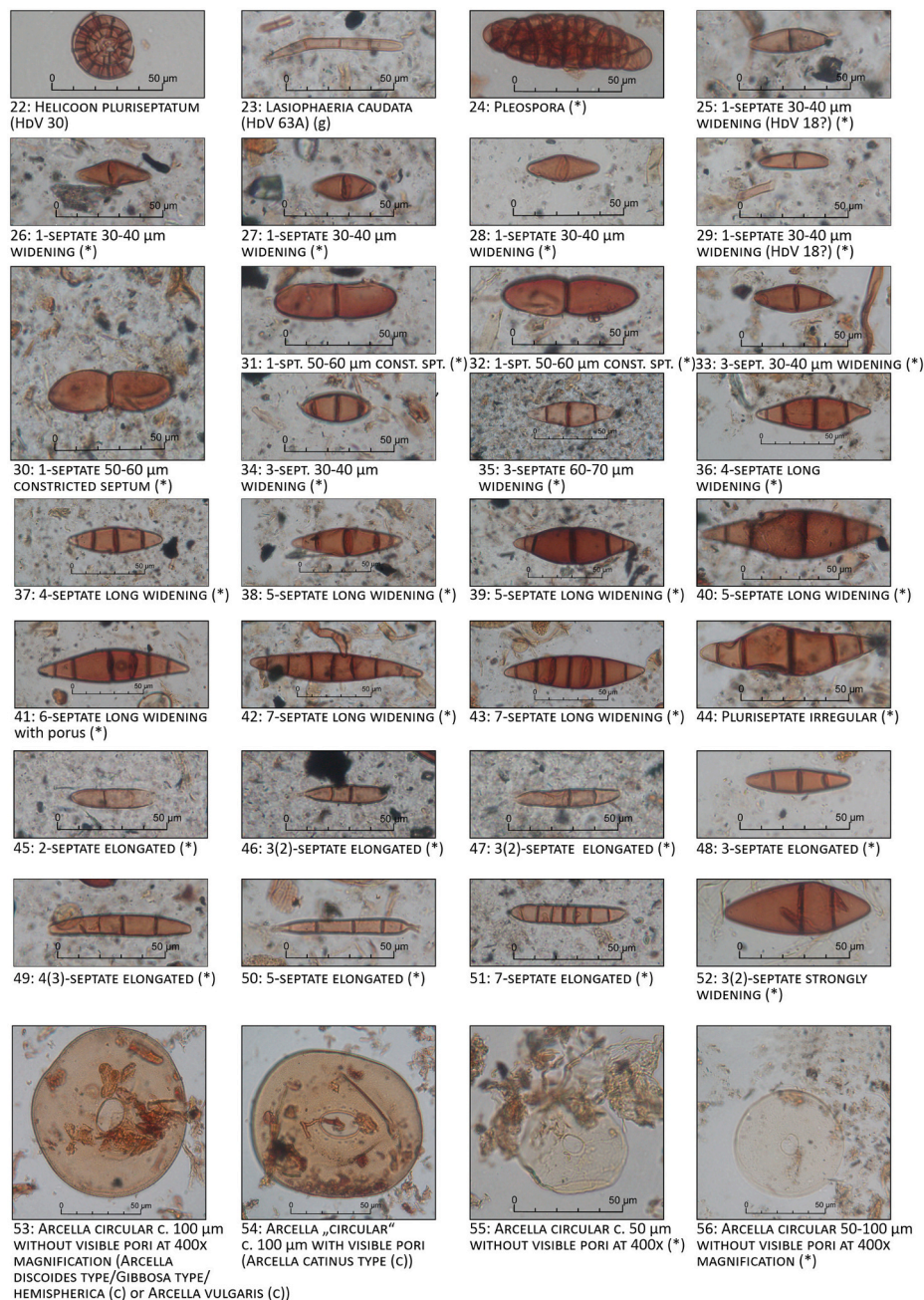
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Photograph 1. Photographs 1-21 of NPP-types encountered during palynological analyses of the ice-wedge polygons discussed in this paper. Note that the photographs were made independently from sample analysis and that several photographs were taken from samples where the types were not found previously. 1: BOTRYOCOCCUS (Mnp12 peat profile AE3 sample 37); 2: cf. CLOSTERIUM (Samoylov surface sample 73); 3: cf. CLOSTERIUM (Samoylov surface sample 73); 4: cf. CLOSTERIUM with clear “punctate-like” wall structure similar to HdV-60 (Samoylov surface sample 73); 5: cf. CLOSTERIUM (Samoylov surface sample 73); 6: cf. CLOSTERIUM (Mnp12 peat profile AX29 sample 20); 7: PEDIASTRUM BORYANUM WITHOUT HOLES (Samoylov profile 83.5 sample 25.5); 8: PEDIASTRUM BORYANUM WITHOUT HOLES (Samoylov surface sample 88); 9: PEDIASTRUM INTEGRUM WITH TWO SHORT SPIKES (Samoylov surface sample 7); 10: PEDIASTRUM INTEGRUM WITHOUT SPIKES (Samoylov surface sample 62); 11: MOUGEOTIA TYPE (Lc04 surface sample U8); 12: MOUGEOTIA TYPE (Lc04 surface sample U8); 13: ZYGNEMA TYPE WITH LARGE CLOSELY SPACED PITS (Lc04 surface sample U8); 14: ZYGNEMA TYPE WITH LARGE SPARSELY SPACED PITS (Mnp12 profile AE3 sample 39); 15: RETICULATE SPIROGYRA c. 50–60 µm (Lhc11 profile J21.20 sample 20.5); 16: Psilate Spirogyra c. 50–60 µm (Lhc11 profile J21.20 sample 21); 17: cf. DELITSCHIA (Samoylov profile 87.1 sample 17); 18: cf. HdV-11; (Samoylov surface sample 94); 19: HdV-200 (Samoylov surface sample 39); 20: MICROTHYRIUM (HdV-8B) (Samoylov surface sample 45); 21: MICROTHYRIUM (cf. HdV-8E) (Samoylov surface sample 3)



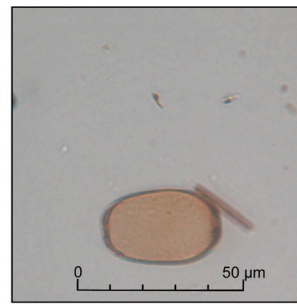
Photograph 2. Photographs 22-56. Note that the photographs were made independently from sample analysis and that several photographs were taken from samples where the types were not found previously. 22: HELICOON PLURISEPTATUM (HdV-30) (Mnp12 surface sample Y42); 23: LASIOPHAERIA CAUDATA (HdV-63A) (Samoylov surface sample 93); 24: PLEOSPORA (Mnp12 profile AE3 sample 8); 25: 1-SEPTATE 30-40 µm WIDENING (Samoylov surface sample 88); 26: 1-SEPTATE 30-40 µm WIDENING (Samoylov surface sample 88); 27: 1-SEPTATE 30-40 µm WIDENING (Samoylov surface sample 88); 28: 1-SEPTATE 30-40 µm WIDENING (Samoylov surface sample 94); 29: 1-SEPTATE 30-40 µm WIDENING (Samoylov surface sample 95); 30: 1-SEPTATE 50-60 µm CONSTRICTED SEPTUM (Samoylov surface sample 4); 31: 1-SEPTATE 50-60 µm CONSTRICTED SEPTUM with only a minor constriction (Samoylov surface sample 94); 32: 1-SEPTATE 50-60 µm CONSTRICTED SEPTUM (Samoylov surface sample 94); 33: 3-SEPTATE 30-40 µm WIDENING with the left septum probably in a state of degeneration or dissolving (Samoylov profile 87.1 sample 11.5); 34: 3-SEPTATE 30-40 µm WIDENING (Samoylov surface sample 88); 35: 3-SEPTATE 60-70 µm WIDENING (Samoylov profile 83.5 sample 17.5); 36: 4-SEPTATE LONG WIDENING (Samoylov profile 83.5 sample 17.5); 37: 4-SEPTATE LONG WIDENING (Samoylov profile 83.5 sample 18.5); 38: 5-SEPTATE LONG WIDENING (Samoylov profile 83.5 sample 17.5); 39: 5-SEPTATE LONG WIDENING (Samoylov surface sample 88); 40: 5-SEPTATE LONG WIDENING (Samoylov surface sample 91); 41: 6-SEPTATE LONG WIDENING, a thick porus is clearly visible (Samoylov surface sample 73); 42: 7-SEPTATE LONG WIDENING (Samoylov surface sample 73); 43: 7-SEPTATE LONG WIDENING (Samoylov surface sample 73); 44: PLURISEPTATE IRREGULAR (Samoylov profile 83.5 sample 17.5); 45: 2-SEPTATE ELONGATED (Samoylov surface sample 63); 46: 3(2)-SEPTATE ELONGATED, i.e. originally 3-septate objects of which one septum has been lost due to taphonomic processes (Samoylov surface sample 62); 47: 3(2)-SEPTATE ELONGATED (Samoylov surface sample 62); 48: 3-SEPTATE ELONGATED (Samoylov surface sample 73); 49: 4(3)-SEPTATE ELONGATED (Samoylov surface sample 94); 50: 5-SEPTATE ELONGATED (Samoylov surface sample 66); 51: 5-SEPTATE ELONGATED (Samoylov surface sample 62); 52: 3(2)-septate strongly widening (Samoylov surface sample 73); 53: ARCELLA CIRCULAR c. 100 µm WITHOUT VISIBLE PORI AT 400X MAGNIFICATION, i.e. ARCELLA DISCOIDES TYPE/GIBBOSA TYPE/HEMISPHERICA (c) or ARCELLA VULGARIS (c) (Lc04 surface sample U24); 54: ARCELLA „CIRCULAR“ c. 100 µm WITH VISIBLE PORI, i.e. ARCELLA CATINUS TYPE (c) (Lc04 surface sample U24); 55: ARCELLA CIRCULAR c. 50 µm WITHOUT VISIBLE PORI AT 400X (Lhc11 profile J18.80 sample 106); 56: ARCELLA CIRCULAR 50-100 µm WITHOUT VISIBLE PORI AT 400X MAGNIFICATION (Lhc11 profile J18.80 sample 106)



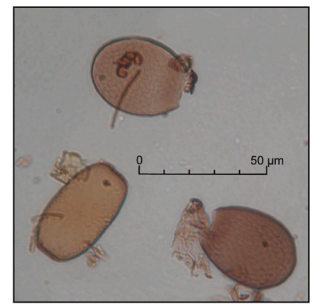
57: ARCELLA CIRCULAR 50-100 µm WITHOUT VISIBLE PORI AT 400X (*)



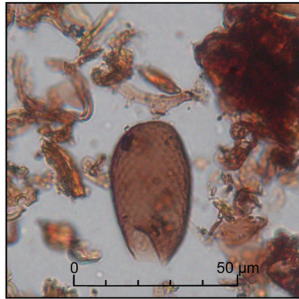
58: ARCELLA OVAL 100-150 µm WITHOUT PORI (*)



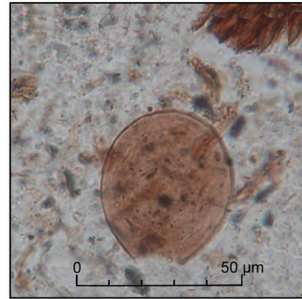
59: AMPHITREMA FLAVUM (c)



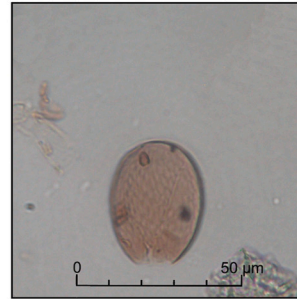
60: AMPHITREMA FLAVUM (c), ASSULINA MUSCORUM TYPE 4 BROAD (*), ASSULINA MUSCORUM TYPE 2 (s)



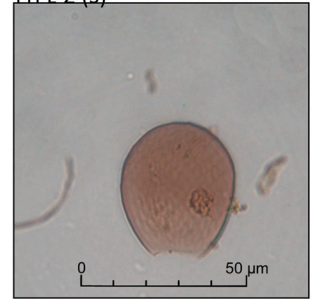
61: ASSULINA MUSCORUM TYPE 1 (*)



62: ASSULINA MUSCORUM TYPE 4 BROAD (*)



63: ASSULINA MUSCORUM TYPE 4 NARROW (*)



64: ASYMMETRICAL ASSULINA MUSCORUM BROAD (*)



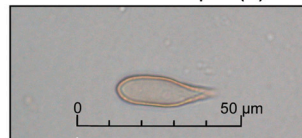
65: COPEPODA >75 µm (*)



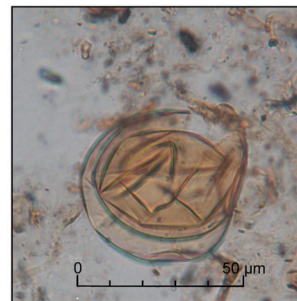
66: COPEPODA >75 µm (*)



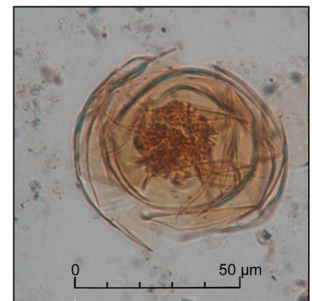
67: COPEPODA <75 µm (*)



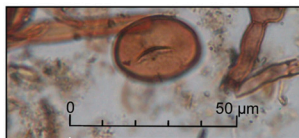
68: COPEPODA <75 µm (*)



69: cf. HdV 91 (g)



70: cf. HdV 91



71: HdV 354 SLIT-LIKE APERT. (*)



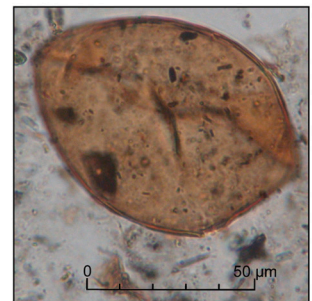
72: HdV 354 LARGE APERTURE (*)



73: HdV 354 WITHOUT APERTURE (*)



74: INAPERTURATE SCABRATISCH GLOBE (*)



75: cf. LARIX TYPE (m)

Photograph 3. Photographs 57-75. Note that the photographs were made independently from sample analysis and that several photographs were taken from samples where the types were not found previously. 57: ARCELLA CIRCULAR 50-100 µm WITHOUT VISIBLE PORI AT 400X; note that with the higher magnification used for photography small pores were revealed (Mnp12 peat profile AX29 sample 20); ARCELLA OVAL 100-150 µm WITHOUT PORI (Samoylov profile 83.5 sample 29.5); 59: AMPHITREMA FLAVUM (Mnp12 surface sample y42); 60: AMPHITREMA FLAVUM (bottom left), ASSULINA MUSCORUM TYPE 4 – BROAD (top centre), ASSULINA MUSCORUM TYPE 2 (bottom right) (Mnp12 surface sample Y42); 61: ASSULINA MUSCORUM TYPE 1 (Lc04 surface sample U24); 62: ASSULINA MUSCORUM TYPE 4 BROAD (Samoylov surface sample 84); 63: ASSULINA MUSCORUM TYPE 4 NARROW (Mnp12 surface sample Y42); 64: ASYMMETRICAL ASSULINA MUSCORUM BROAD (Mnp12 surface sample 42); 65: COPEPODA >75 µm (Mnp12 peat profile AE3 sample 26); 66: COPEPODA >75 µm (Samoylov surface sample 66); 67: COPEPODA <75 µm (Samoylov surface sample 73); 68: COPEPODA <75 µm (Mnp12 peat profile AE3 sample 26); 69: HdV-91 (Samoylov surface sample 73); 70: HdV-91 (Samoylov surface sample 95); 71: HdV-354 SLIT-LIKE APERTURE (Samoylov profile 87.1 sample 11.5); 72: HdV-354 LARGE APERTURE (Samoylov profile 87.1 sample 11.5); 73: HdV-354 WITHOUT APERTURE, note that a weak thinner spot in the wall is clearly visible (Samoylov profile 87.1 sample 11.5); 74: INAPERTURATE SCABRATISCH GLOBE (Samoylov surface sample 91); 75: cf. LARIX TYPE (Samoylov surface sample 94).

2. Material and methods

2.1. A note on palynomorph classification and identification

The development of Arctic palynomorph analysis is inextricably linked to the evolution of palynomorph classification. The palynomorph types reported here result from studies over a period of 15 years, over which types were split and lumped as a function of experience, perception, and capability, resulting in changing classifications of the same morphological object. We addressed this issue by adding an epithet to each palynomorph name in the diagrams and photographs to make clear which publication has been used to identify an entity (Joosten and De Klerk, 2002; De Klerk and Joosten, 2007). In the present study, ba stands for Batten (1996) and Batten and Grenfell (1996), c stands for Charman et al. (2000), g for Van Geel (1978), k for Komárek and Jankovská (2001), m for Moore et al. (1991), and s for Schönborn and Peschke (1990). Palynomorphs that do not correspond with well-defined types in the NPP-literature are marked with an asterisk (*) and discussed in this paper.

The taxonomy of testate amoebae, and as a matter of fact also of various algae including *Pediastrum* and *Botryococcus* and algae spores of Zygnematales, is usually based entirely on the morphology of the tests, spores, and coenobia. Therefore, the palynomorphs in palynological samples show all characteristics needed for a full taxonomic identification. We propose that - as far as full testate amoebae analyses are performed that include the complete organisms (De Klerk et al., 2020) - the rules of zoological nomenclature apply (Lingafelter and Nearn, 2013), whereas samples prepared using the much more rigorous processing for palynological analysis in which only the tests of a few taxa survive (as in this study), we use our approach for palynomorphs.

Science demands that facts be distinguished from interpretations and, accordingly, palynology requires a clear conceptual separation

between observed palynomorphs and inferred taxa. To facilitate this distinction, Joosten and De Klerk (2002) and Joosten and De Klerk (2007) have proposed to display the names of palynomorphs in SMALL CAPITALS (see also Erdtman, 1967; Neumann et al., 2019; Shumilovskikh et al., 2026) in contrast to the name of taxa, which should follow the rules of the respective International Codes of Nomenclature (Turland et al., 2025). How NPPs are named is another issue: the name can vary from the name of the taxon that is known to produce the respective palynomorph (Shumilovskikh et al., 2026), it could be a numerical designation (Miola, 2012), or a compilation of the main morphological features of the palynomorph in question.

2.2. Methods

The polygons were subdivided in quadrates of 1 m² using strings, of which the horizontal height was fixed with poles and determined with water level tubes. Depth values below the strings were recalculated to a reference level below the polygon surface (Telteuwskoj et al., 2012; Behrens et al., 2016). Surface samples of moss and litter were taken from the centre of each quadrate (De Klerk et al., 2014, 2017). Only at the Lc04 transect, samples were collected at various places within each quadrate and thoroughly mixed (De Klerk et al., 2009). Peat profiles were excavated with spades, axes, and saws.

Peat profiles were cut into contiguous slices of 0.5 cm thickness with the DAMOCLES-device (Joosten and De Klerk, 2007) from which sub-samples of 2 × 2 × 0.5 cm (= 2 cm³) were taken for palynological analysis.

Processing of all palynological samples included treatment with KOH, sieving (mesh width 125 µm), treatment with HF, and acetolysis (7 min) (see Fægri and Iversen, 1989). Tablets of *Lycopodium* spores were added to the peat profile samples to calculate palynomorph concentrations (Stockmarr, 1971).

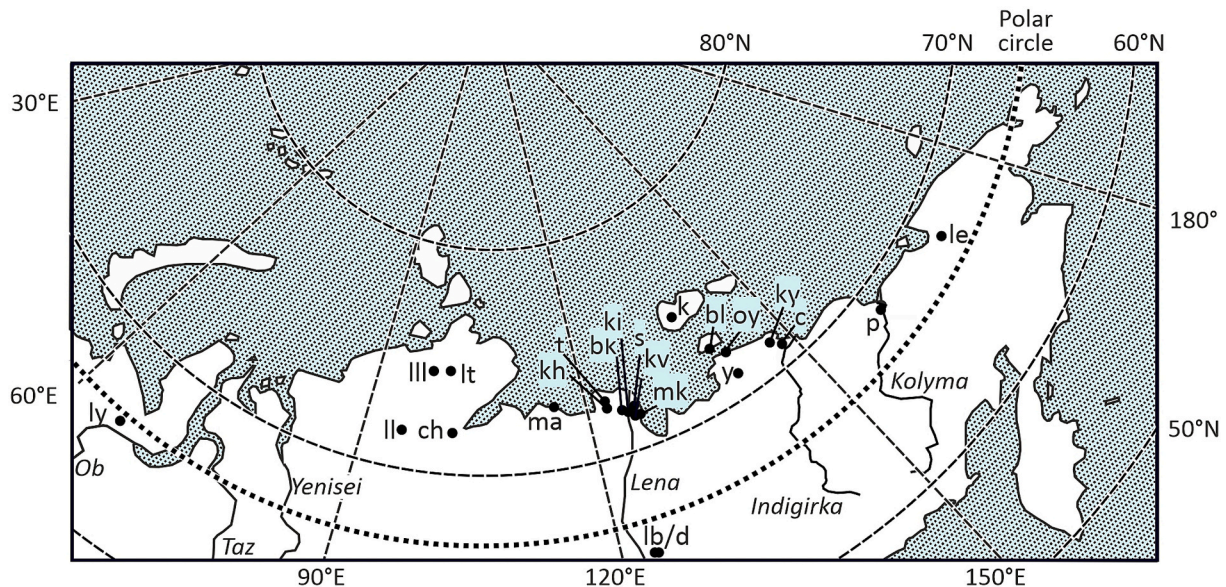


Fig. 1. Locations of analysed sites in NE Siberia with NPP-data: bk: Buor Khaya (Schirrmeister et al., 2003); bl: Bolshoy Lyakhovsky Island, records L14, R8+50, R9+85, R14+40, R17, R18+50, R22+60 (Andreev et al., 2004, 2011), R35 (Ilyashuk et al., 2006), L7-14, L12+30, L7-08, R33 A1 (Wetterich et al., 2009), L7-07, L7-18 (Rudaya et al., 2014); c: Polygon Lc04 (Chokurdakh) (De Klerk et al., 2009, 2011, Minke et al., 2009; this study); ch: 11-CH-17A (Niemeyer et al., 2015); d: Dyanushka River (Zech et al., 2011); k: Koteln Island (Van Geel et al., 2017); kh: Khardang (Lena Delta) (Schirrmeister et al., 2011); ki: Kurungnakh Island (Lena Delta) (Wetterich et al., 2008; Andreev et al., 2011); kv: Khorogor Valley (Grosse et al., 2007); ky: Polygon Lhc11 (Kytalyk) (De Klerk et al., 2014, 2020; Telteuwskoj et al., 2016; this study); l7: L7-14, L7-08, R33 A1 (Wetterich et al., 2009); lb: Lake Billyakh (palaeo-profile and surface samples) (Müller, 2009; Müller et al., 2010); le: Lake El'gygytyn (Andreev et al., 2012, 2014, 2016); ll: Lake Labaz (Andreev et al., 2002); ll: Lake Levinson-Lessing (Andreev et al., 2003); lt: Lake Taymyr (Andreev et al., 2003); ly: findspot mammoth Lyuba (Van Geel et al., 2011); ma: Mamontovy Klyk (Schirrmeister et al., 2008; Andreev et al., 2011); mk: Mamontovy Khayata (Bykovsky Peninsula) (Andreev et al., 2000, 2011); oy: Oyogor Yar (sections Oy7-08 and Oy7-11) (Wetterich et al., 2009; Andreev et al., 2011); p: Polygon Mnp12 (Pokhodsk) (Behrens et al., 2016; De Klerk et al., 2017; this study and research in progress); s: Samoylov Island (Lena Delta) (this study and research in progress); t: Turakh (Lena Delta) (Schirrmeister et al., 2011); y: find spot Yukagir mammoth (Van Geel et al., 2008).

Analysis was with light microscopes Zeiss type Axioskop (Lc04, surface samples and profiles E16, H16 and J16) and a Leitz Dialux 22 EB (all other samples) with 400x magnification; larger magnifications up to 1000× were used for the identification of problematic types. Photographs were taken with a Nikon Coolpix 995 camera with the highest analogue zoom setting. Photographs were taken after counting had ended from different microscopical slides, and incidentally types were photographed in samples where these were not found during palynological analysis.

Palynomorph percentages of the surface samples were calculated relative to a sum including bisaccate pollen grains and pollen grains attributable to *Artemisia* and *Alnus*. NPP concentrations are expressed as palynomorphs 10 mm⁻³ (profiles from Lc04 and Lhc11 and profile AE3 from Mnp12) and 100 mm⁻³ (Samoylov profiles and Mnp12 profiles AE7 and AX29).

The chronology of the palaeo-sequences is based on AMS-¹⁴C-dating of above-ground macrofossils of vascular plants and mosses (De Klerk et al., 2011 and research in progress), calibrated using the software Calib 8.1.0, and refined by non-linear pollen density inter- and extrapolation using selected (extra)regional pollen types (De Klerk et al., 2011, research in progress; Ramezani et al., 2023). For the peat sections of polygon complex Mnp12 no ¹⁴C dates are yet available. Note that dates after “Present” (=1950 CE) are given with negative values, e.g. -18 cal. BP is 1968 CE.

We used the total palynomorph and macrofossil content of the palynomorph diagrams (Figs. 6–13) to infer site conditions as “wet” (W), “dry” (D), “wet with nearby dry conditions” (W/D), and “uncertain” (marked with a question mark).

2.3. Study area and studied polygons

Ice-wedge polygon mires cover c. 250,000 km², i.e. 3% of the Arctic land mass. They develop as a result of frost cracking and ice-wedge growth (Minke et al., 2007; De Klerk et al., 2018). Initial frost cracks of a few millimetres wide develop during winter and fill with water in spring that immediately freezes to form ice veins. Repeated frost contraction and subsequent water fill cause the development of wide ice-wedges after several centuries. Soil material is pushed up against the ice wedges to form ridges of several decimetres height surrounding depressions with a diameter of 10–30 m. Such polygons are called ‘low-centre polygons’, in contrast to ‘high centre polygons’ in which (partial) thawing and collapse of the ice wedge ridges results in a relief inversion. Ice-wedge polygons have long been considered to be hydrologically closed, stable systems (see Boch, 1974; Washburn, 1979; Ellis and Rochefort, 2006). However, recent studies have shown that they may be rapidly changing open systems in which preferential subsurface (melt)waterflow along deeply thawed “hydrological windows” regulates internal polygon hydrology (Minke et al., 2007; Donner et al., 2012). Dependent on their development stage, polygon depressions are moist to aquatic. Polygon rims are dry during ridge phases but may be moist to wet before the ridges are fully developed or when they have collapsed. Accordingly, vegetation and peat formation varies at short distances and over short intervals of time.

The studied polygon Lc04 at Chokurdakh (70°3802N, 147°5515E, 8 m asl., Fig. 2) is a simple low-centred polygon. It is positioned between a yedoma hill and a thaw lake. Peat formation started around 1000 cal. BP in a terrestrialising thermokarst lake. Between 725 and 625 cal. BP a frost mound formed in the present-day polygon centre but collapsed again between 575 and 525 cal. BP (Fig. 7C). The rims at profiles E16, H16, and Q9 collapsed asynchronously during the Little Ice Age, after which the northwestern rim regenerated during the last 2–3 centuries (Fig. 7A/B); the rim at q9 did not regenerate at all (Fig. 7D).

Polygon Lhc11 near the research station Kytalyk (70°4950N, 147°2852E, 5 m asl.; Fig. 3) is in a complex transitional stage between a low-centred and a high-centred polygon. It lies marginally in an alas between two yedoma hills. Seven peat profiles analysed

palaeoecologically run from the centre across the eastern polygon ridge to the three m wide through where the original ridge was located. Around 2000–1000 cal. BP the original outer rims migrated inward and collapsed at their original position. This secondary ridge-growth terminated differently at various locations resulting in depositional hiatuses of different lengths (Fig. 9C/D/E). A short-lived dry phase is discernible in the polygon centre around 100 cal. BP (Fig. 9A). The two outer trough profiles display a wet setting after 2000–1600 cal. BP with nearby dry conditions from the expanding ridge (Lhc11 J20.20 and -21.20; Fig. 9F/G). Whereas Lhc-J21.20 experienced dry conditions between 91–18 cal. BP, the top part of both sections is characterised by very rapid accumulation of *Sphagnum* peat since 42 and -18 cal. BP.

Polygon complex Mnp12 near Pokhodsk (69°0539N; 160°5555E, 8 m asl.; Fig. 4) - located in a landscape with numerous thaw-lakes - originally consisted of six individual polygons of which the ridges have collapsed resulting in a merged large depression that at present is rather dry. Of the five collected peat profiles, only three have been analysed but radiocarbon dates are not yet available, which prevents a detailed spatio-temporal interpretation (Fig. 11A–C). The depression profile AE7 (Fig. 11B) displays mainly wet conditions throughout except for the top 6 cm that show the recent drying-out. Profile AE3 (Fig. 11A) shows an alternation of dry and wet phases that may reflect ridges and ridge collapses but may also represent general dry and wet phases independent of polygon morphology. Profile AX29 (Fig. 11C) was taken at a still perceivable ridge remnant and shows a dry phase at its base followed by a wet phase after ridge collapse. The current drying-out is not registered.

Samoylov Island in the Lena Delta (72°2213N, 126°296E, 15 m asl., Fig. 5A) - is an island with at the northwest an active river flood plain adjacent to a plateau with numerous low-centred polygons (Fig. 5B). 122 surface samples were analysed in a transect crossing nine contiguous polygons (Fig. 5C). Profile 83.5 from the ridge part of polygon 7 (Fig. 13A) experienced wet conditions starting around 640–580 cal. BP followed by dry conditions from a mature ridge since 45 cal. BP. The part from the same ridge belonging to polygon 8 (profile 87.1; Fig. 13B) shows dry conditions at its base, which dates to 280–230 cal. BP. The upper part of the section shows dry ridge conditions since 130–100 cal. BP. Profile 161.5 from the centre of polygon 7 (Fig. 13C) shows a continuous wet setting for the period after c. 200–100 cal. BP.

3. Morphology and indicator value of NPP-types in NE Siberian polygon mires

3.1. NPPs attributed to algae

3.1.1. BOTRYOCOCCUS

BOTRYOCOCCUS colonies (photograph 1) are roughly spherical and consist of numerous cells between 5 and 15 µm long and 2.5 and 6 µm wide that have their broad ends outward (Batten and Grenfell, 1996).

Botryococcus dwells in more-or-less eutrophic freshwater bodies of mires, temporary pools, ponds and lakes, but also in saltwater settings (Batten and Grenfell, 1996). In our surface samples BOTRYOCOCCUS occurs only sporadically (Figs. 6, 8, 10, 12). Some BOTRYOCOCCUS, probably originating from the water consumed by the animals, was found in the intestines of the Lyuba and Yukagir mammoths (c. 42,000 and 18,500 cal. BP, respectively), as well as in a related horse dropping (Aptroot and Van Geel, 2006; Van Geel et al., 2008, 2011). BOTRYOCOCCUS occurs widespread in the other palynologically analysed sites in NE Siberia (Fig. 1) covering all time periods dating back to the Pliocene (e.g. Andreev et al., 2014, 2021).

3.1.2. cf. CLOSTERIUM

Objects generally interpreted as zygospores of *Closterium idiosporum*, e.g. HdV-60, are characterised by an irregular to angular/roundish shape, often having a longitudinal furrow, and a somewhat punctate wall structure, with sizes around (39-)42-63 × (17-)26-34(-43) µm (Van Geel et al., 1980/1981). Taxonomic literature shows that spores of

Closterium species have different shapes varying from circular to rectangular/quadratic, indented or more tapering sides, and with variable length/width proportions (Förster, 1982; Dillard, 1990). Van Geel et al. (1980/1981) mention that there are morphologically transitional morphs between the zygospores of *C. idiosporum* ssp. *idiosporum* and

C. idiosporum ssp. *punctatum*. The spore types, thus, are morphologically rather diverse, which hampers the establishment of sharply defined morphotypes.

The objects observed in the ice-wedge polygons (photographs 2–5) are 60–70 × 40–45 µm large, i.e. somewhat broader than the objects

A: Lc04 (Chokurdakh)

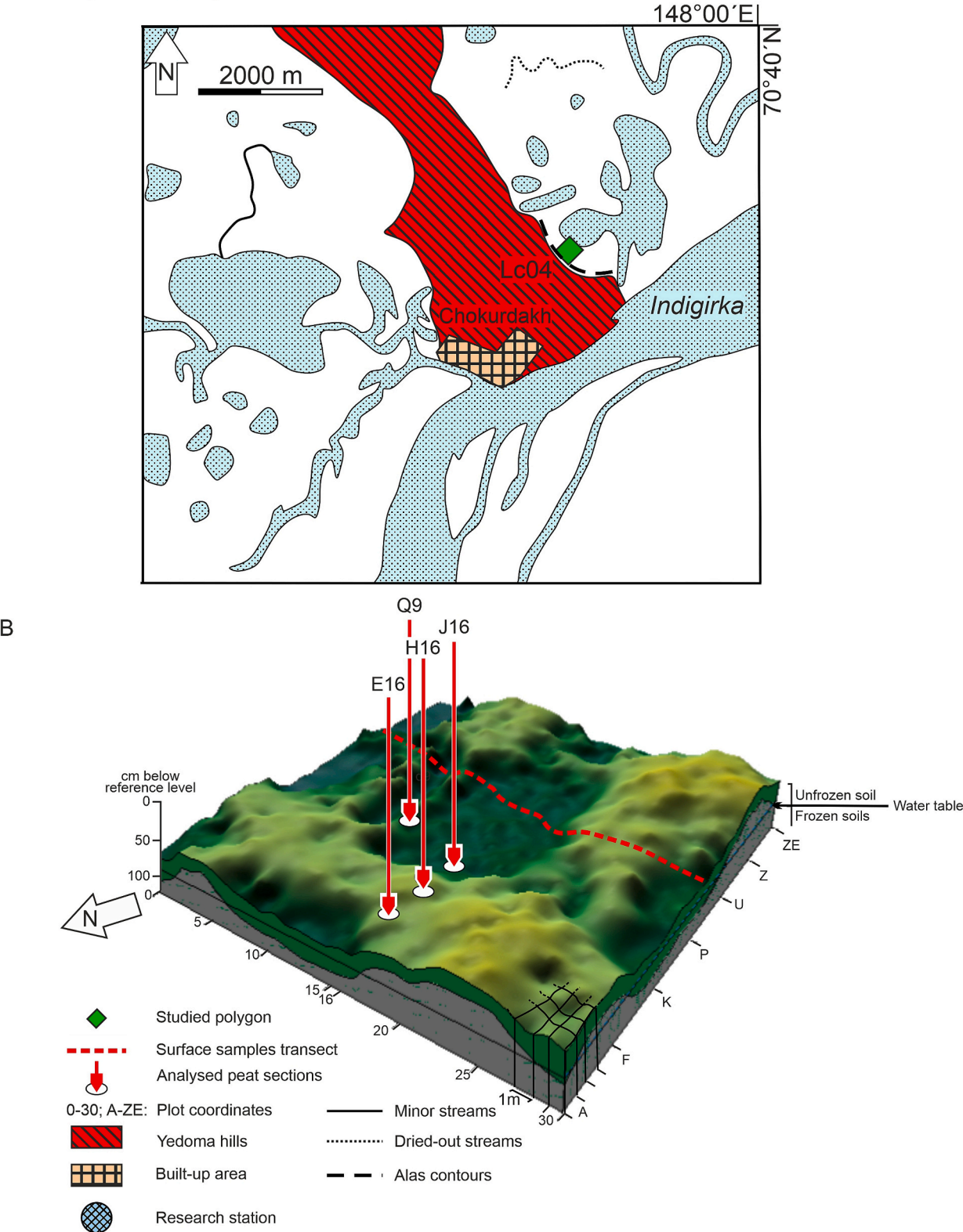
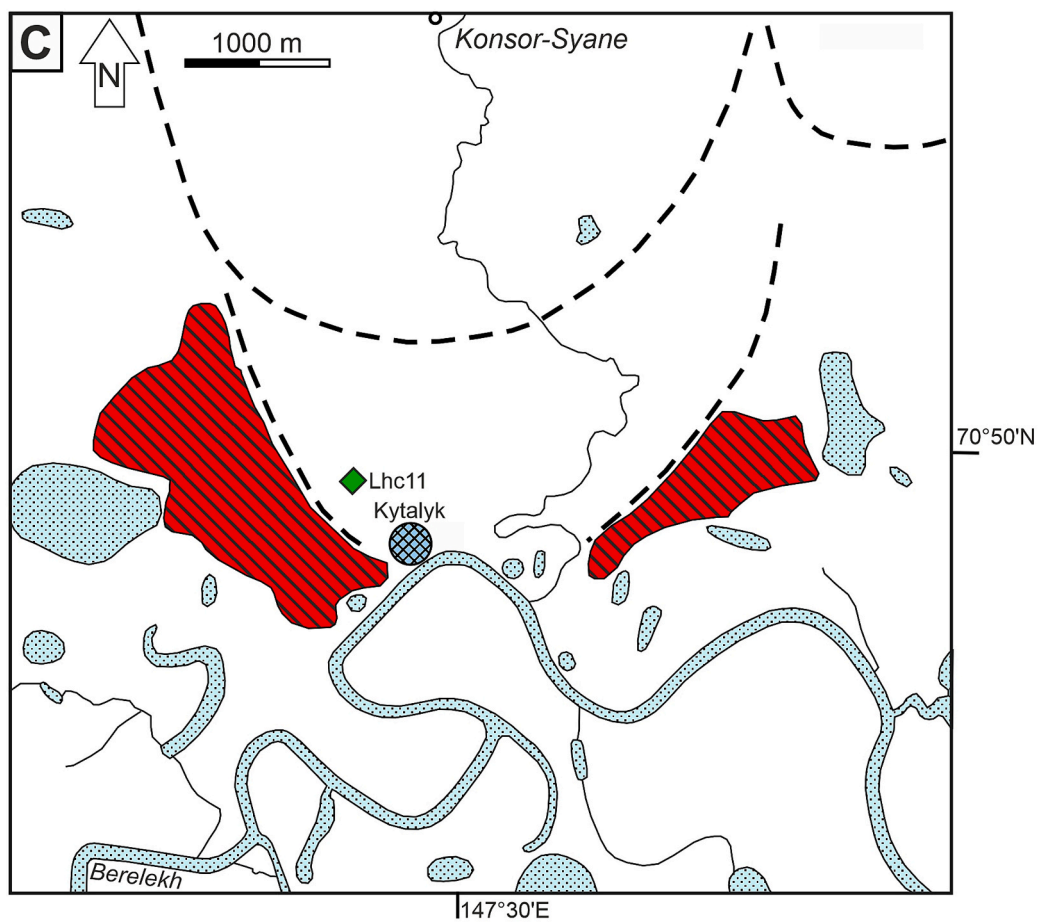


Fig. 2. Geomorphological map (A) and three-dimensional model (B) of polygon Lc04 near Chokurdakh, after De Klerk et al. (2011).

A: Lhc11 (Kytalyk)



B

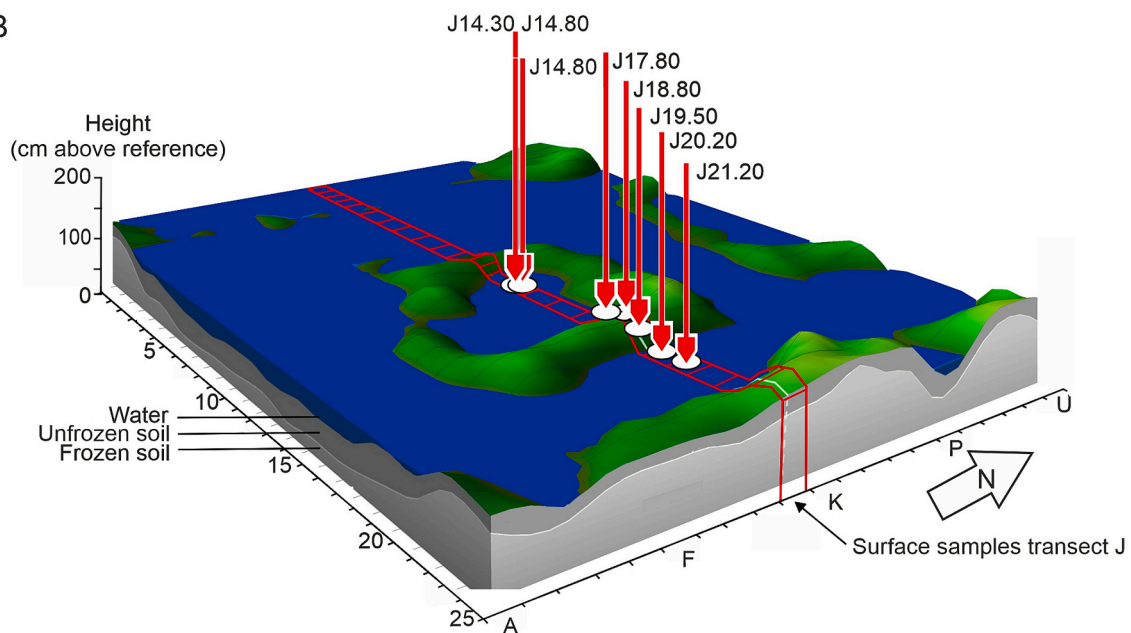


Fig. 3. Geomorphological map (A) and three-dimensional model (B) of polygon Lhc11 near the research station Kytalyk, after De Klerk et al. (2014) and Teltewskoi et al. (2016).

A: Mnp12 (Pokhodsk)

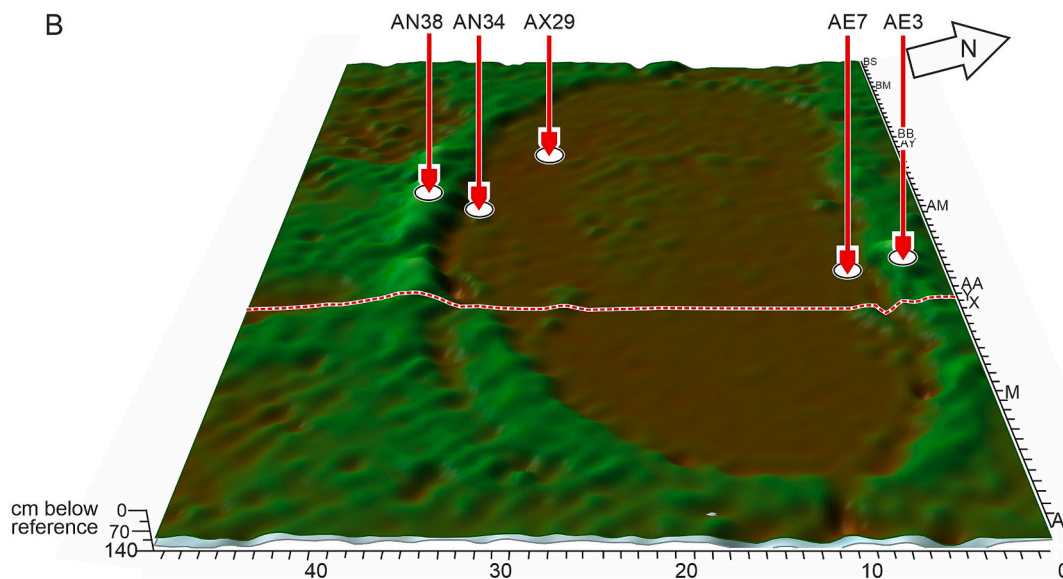
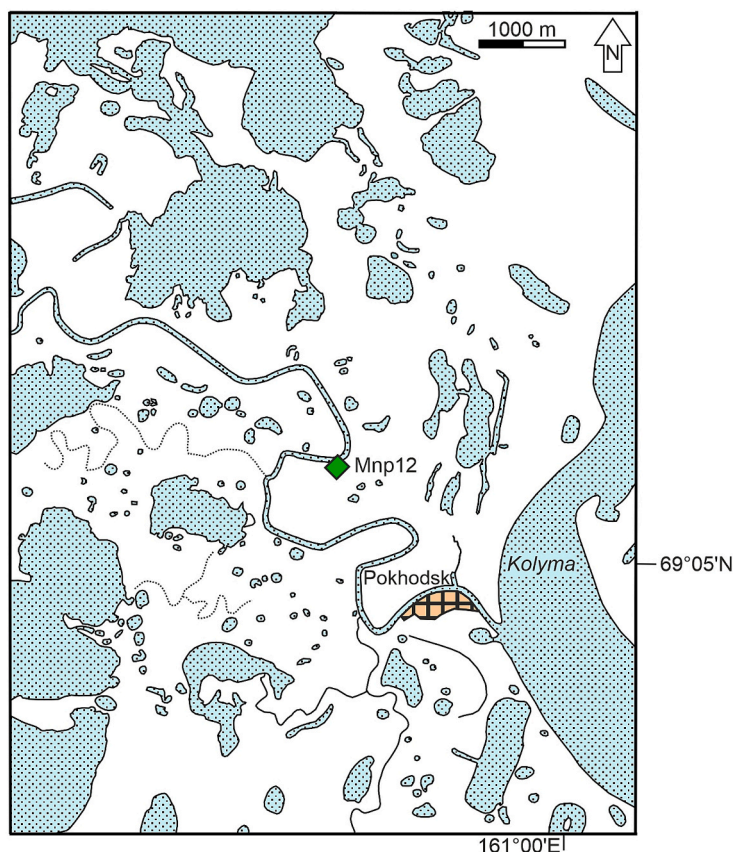


Fig. 4. Geomorphological map (A) and three-dimensional model (B) of low-centred polygon Mnp12 near Pokhodsk, after De Klerk et al. (2017).

described in the literature. Only the object in photograph 4 displays a punctate wall structure. Photograph 6 shows a c. 135 μm long folded object that has at some places a distinguishable punctate structure similar to HdV-60. We do not rule out that some of the observed objects derive from other *Closterium* species than *C. idiosporum*. *Closterium* cf. *rostratum* (HbV-372; Van Geel et al., 1980/1981) can be ruled out as a parent organism for our cf. *CLOSTERIUM* in the polygons because of its smooth wall structure and rather irregular angular outline, which

appears as if parts were “cut-off”.

Closterium idiosporum occurs in more or less mesotrophic open water, avoids relatively warm areas, and has been mentioned to prefer somewhat acidic habitats (Van Geel et al., 1980/1981; Medeanic and Silva, 2010).

We only recognized cf. *CLOSTERIUM* in polygon Lhc11, on Samoylov Island, and in the fossil peat sections of Mnp12. The type was found abundantly in both wet and dry settings, but more prominently in wet

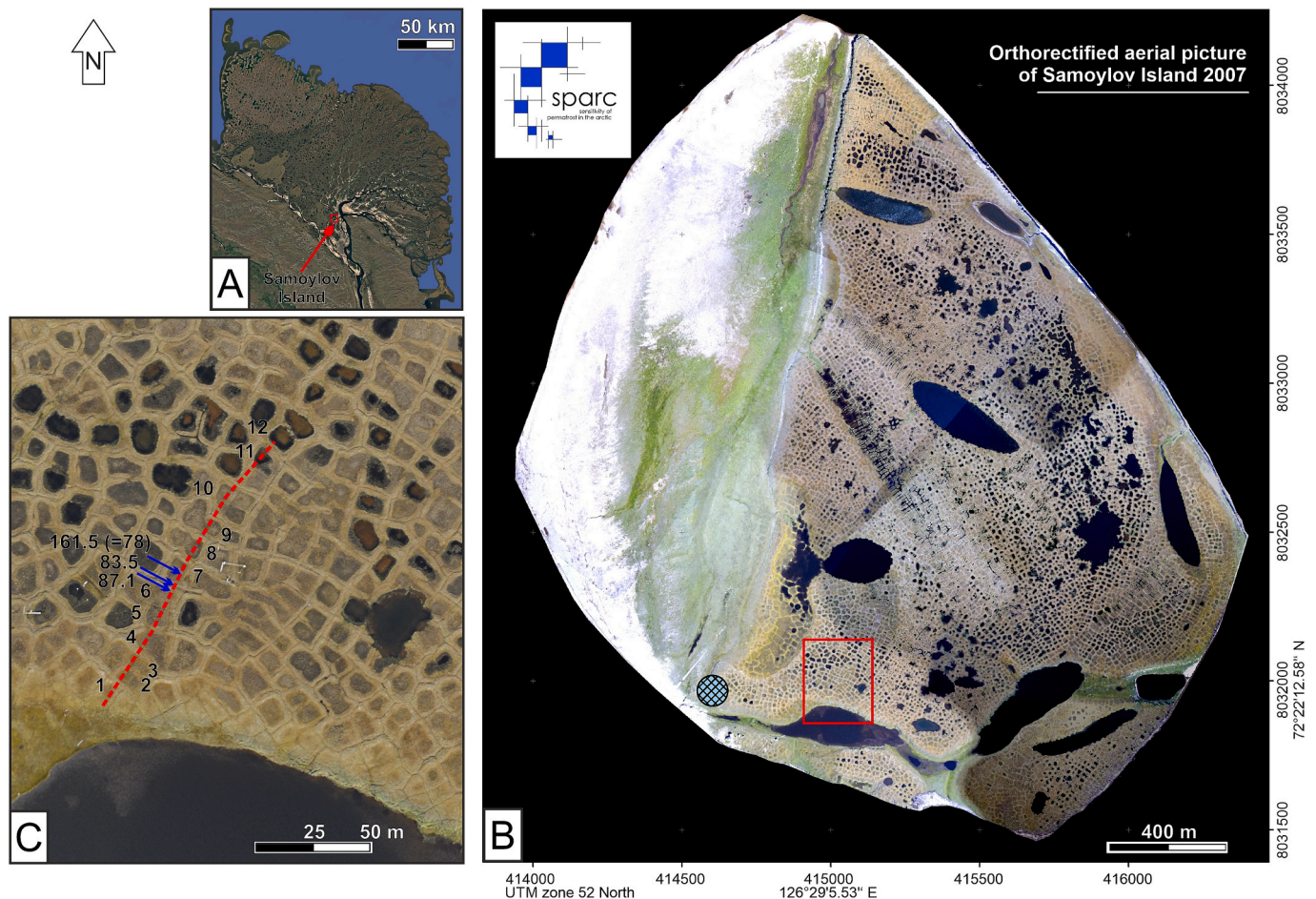


Fig. 5. Aerial photograph of the Lena Delta (A; © GoogleEarth Image Landsat/Copernicus Image IBCAO, January 1st 2021), Samoylov Island (B), modified after Boike et al. (2008) and Scheritz et al. (2008), with the analysed surface sample transect and the palynologically analysed profiles (C).

habitats. In Lhc11, the type was found in low values only in one surface sample from a lower polygon rim part. It occurs in clear ranges in interpreted wet settings, with in J18.80 and J21.20 nearby dry habitats (Fig. 9D/G), and in the latter also in an interpreted dry phase. It was not observed in the other profiles from polygon Lhc11. In Mnp12 profile AE3 cf. *Closterium* occurs with substantial values in a clear dry setting, and in AX29 with high values in a wet phase. On Samoylov Island, cf. *Closterium* was found with high amounts in the polygon depressions along the surface sample transect (Fig. 12A). In the fossil profiles the type occurs with high values in the profile Sam 161.5 (Fig. 13C) from the continuously wet polygon centre profile. In the other peat profiles from Samoylov, it occurs in wet phases (Fig. 13A/B). In our study area, thus, cf. *Closterium* dwells predominantly in wet settings but in low amounts in dry settings too, which is a somewhat broader range than known from NPP literature.

Other palynomorphs attributed to *Closterium* were found in NE Siberia in sediments from Lake Levinson-Lessing on the Taymyr peninsula (Andreev et al., 2025). At the other Siberian palynological records the type may have been overseen or not distinguished.

3.1.3. *Pediastrum* types

Coenobia of *Pediastrum* are radially symmetrical and consist of clusters of cells that are contiguous or interrupted by openings, with the rim of outer cells containing different kinds of processes (see Batten, 1996; Jankovska and Komárek, 2000; Komárek and Jankovská, 2001; Van Geel, 2001). Whereas these morphological characteristics are used for the distinction of different (sub)species, we observed several types that do not completely fit these described taxonomical entities.

PEDIASTRUM BORYANUM WITHOUT HOLES (photographs 7/8) includes the coenobia described for most *Pediastrum boryanum* subspecies without holes between the individual cells, i.e. effectively excluding the coenobia of *P. boryanum* ssp. *cornutum* and ssp. *perforatum*, which do have such interruptions (Komárek and Jankovská, 2001).

According to Komárek and Jankovská (2001), some specimens of *Pediastrum integrum* have short spikes in the outer rim of cells, and others where such spikes do not occur, but they do not distinguish different taxa. Following the morphological characteristics, we split palynomorphs attributable to *Pediastrum integrum* into *PEDIASTRUM INTEGRUM* WITH TWO SHORT SPIKES (photograph 9) and *PEDIASTRUM INTEGRUM* WITHOUT SPIKES (photograph 10).

P. kawraiskyi and *P. orientale* coenobia have two spikes in the outer cell rim, which are positioned perpendicular to the coenobium, and no apertures between the individual cells (in contrast to *P. musteri* and *P. patagonicum*, which also have perpendicularly positioned processes). A distinction between *P. kawraiskyi* and *P. orientale* is possible using the morphology of the individual cells (Komárek and Jankovská, 2001). However, in the polygon research such distinction was not made, and both taxa may be covered by the morph *PEDIASTRUM KAWRAISKYI/ORIENTALE* (no photograph).

Furthermore, we found *PEDIASTRUM* WITHOUT HOLES WITH ONE SPIKE (no photograph) with one clear spike in each cell of the outer rim that, which - because of absence of openings between the individual cells - cannot represent the taxon *P. simplex* of Komárek and Jankovská (2001).

PEDIASTRUM undiff. consists of morphs that could not be further classified because of such severe damages to the outer cell rim that no visible processes remained.

Lc04 - surface samples transect

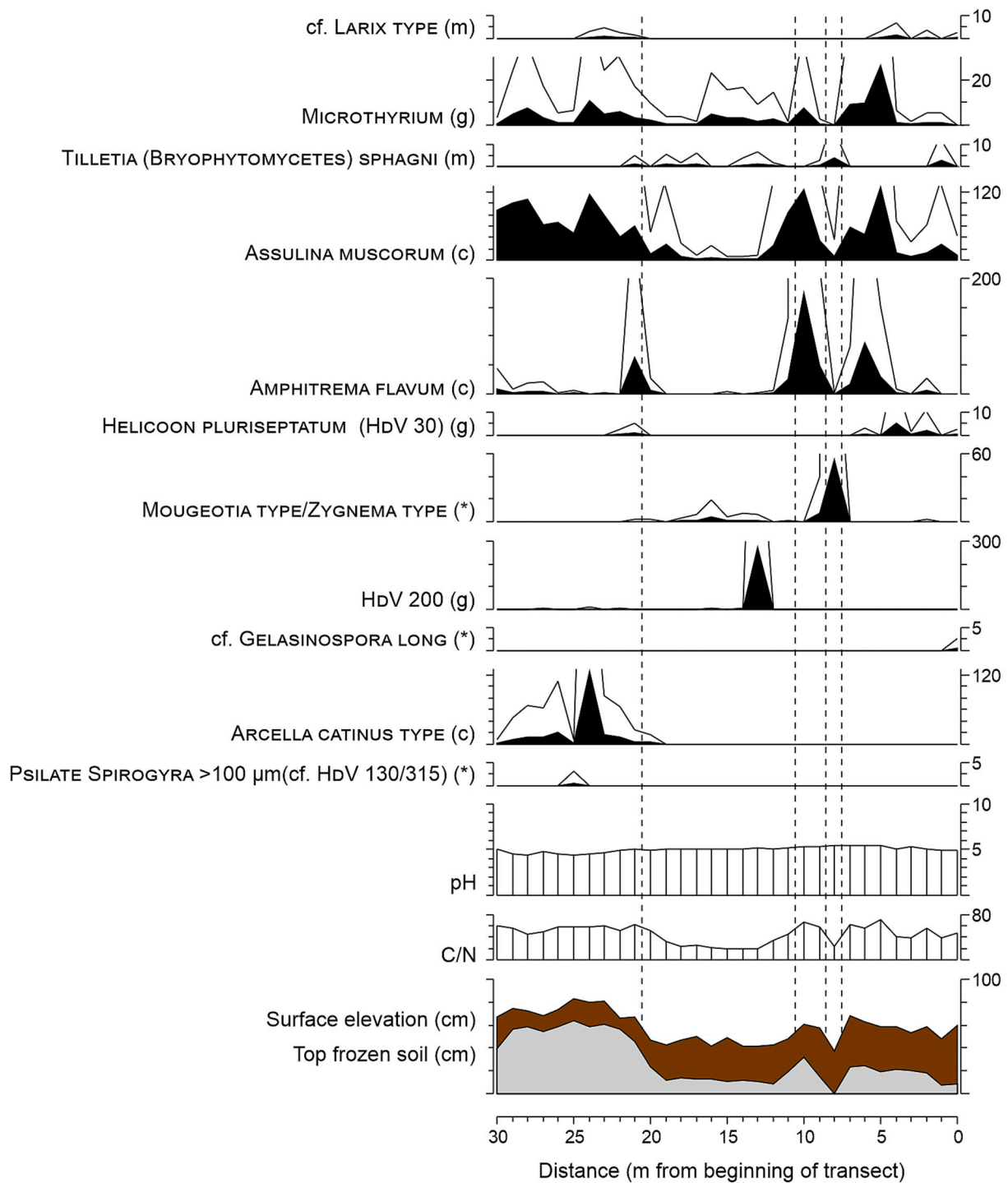


Fig. 6. NPPs in the surface sample transect of polygon Lc04 (Chokurdakh), calculated relative to a pollen sum consisting of pollen types attributable to *Alnus*, *Artemisia*, *Pinus*, *Picea*, and *Abies* (after De Klerk et al., 2009).

In the studied ice-wedge polygons, remains attributable to *Pediastrum* are infrequent indicating that the habitats are suboptimal for these algae. Only in profile Mnp12 AE7, somewhat more substantial values of *PEDIASTRUM* WITH ONE SPIKE and *PEDIASTRUM* INTEGRUM WITHOUT SPIKES occur in an interpreted wet phase.

At another site on the NE Siberian Taymyr peninsula (Lake 11-CH-

17A), Niemeyer et al. (2015) distinguished ten rather frequent *PEDIASTRUM* morphotypes that were ascribed to *P. boryanum* (four morphotypes), *P. angulosum*, *P. orientale* (two morphotypes), *P. kawraiskyi*, *P. integrum*, and *P. duplex* and were linked to temperature and trophic conditions.

Some *PEDIASTRUM* was found in the intestines of the Lyuba and Yukagir

mammoths and in a related possible horse dropping (Aptroot and Van Geel, 2006; Van Geel et al., 2008, 2011) and will have been present in the water consumed by the animals. Coenobia attributable to *Pediastrum* were found widespread at the other palynologically analysed sites in NE Siberia (Fig. 1) covering all time periods dating back to the Pliocene. They occur incidentally or in distinct phases, in both low and high numbers.

3.1.4. Types attributed to Zygnemataceae taxa

Zygnemataceae are known for their large variety in zygospore types (see Kadłubowska, 2009) and their taxonomy is partly based on zygospore morphology (Kolkwitz and Krieger, 1971; Hoshaw and McCourt, 1988; Dillard, 1990; Kadłubowska, 2009). A thorough evaluation of taxonomic studies may yield additional information on the total variety in spore morphology useful for describing and identifying NPP types. However, the acetolysis procedure commonly used in palynological sample preparation may modify spore wall ornamentation (Hoshaw and McCourt, 1988) and caution is, therefore, necessary.

We expect that many Zygnemataceae species in the NE Siberian Arctic have not yet been studied so that an attribution to types known from other regions may be flawed.

Zygnemataceae algae generally occur in shallow, clean, stagnant, oxygen-rich open water of pools, ponds, ditches, or the littoral zones of lakes (Kolkwitz and Krieger, 1971; Hoshaw and McCourt, 1988; Van Geel and Grenfell, 1996; Kadłubowska, 2009). Similar environments occur in the only few dm deep polygon troughs and depressions. It is assumed that also trophic differences influence the distribution of the taxa (Van Geel and Grenfell, 1996; Van Geel, 2001). According to Van Geel and Van der Hammen (1978), Van Geel et al. (1980/1981) and Van Geel (2001), Zygnemataceae need relatively high water temperatures for reproduction, which seemingly contradicts their occurrence in the (Sub)Arctic. Kolkwitz and Krieger (1971) and Kadłubowska (2009), however, note that Zygnemataceae reproduction depends on the amount of light penetrating the water. Since shallow water is easily warmed by summer sunlight, also in the Arctic, both factors may play together.

3.1.4.1. MOUGEOTIA TYPE and ZYGNEMA TYPE. MOUGEOTIA TYPE morphs (photographs 11/12) are mainly rectangular/quadratic and have straight or concave spore walls, with broad depressed corners, whereas the hyaline surfaces are smooth or beset with small pits (Van Geel, 1976, 1978; Van Geel and Van der Hammen, 1978; Pals et al., 1980; Van Geel et al., 1980/1981, 1982/1983). The generic type, judging from photographs, covers HdV-133-136/141/313A-F.

ZYGNEMA TYPE zygospores (cf. HdV-213/314) (photographs 13/14) are described as a heterogenous group of circular, hyaline objects with small pits in the surface (Van Geel, 1976; Van Geel and Van der Hammen, 1978; Van Geel et al., 1980/1981). HdV-213 differs from HdV-314 in having pits with a larger diameter (Van Geel et al., 1989). However, there is a large morphological variety within the “heterogenous groups” attributed to *Mougeotia* and *Zygnema* in NW Europe (see the photographs of Pals et al., 1980; Van Geel et al., 1980/1981, 1982/1983, 1989; Bakker and Van Smeerdijk, 1982; Van der Wiel, 1982; Kuhry, 1997), especially concerning the shape, which varies between rectangular and circular, and the number and size of the pits. Illustrations in the algal flora of Kadłubowska (2009) show that various *Mougeotia*, *Mougeotiopsis*, *Zygnemopsis*, and *Debarya* species produce circular smooth spores or oval structured spores, which in the palynological practice will probably be identified as ZYGNEMA TYPE. On the other hand, *Temnoganetum* and some other *Zygnema*, *Debarya*, and *Zygnemopsis* taxa seem to produce angular zygospores that may be included in the various MOUGEOTIA “heterogenic groups” described in the NPP literature. Unfortunately, in the polygon studies such “heterogenous” groups were initially lumped together. In later stages of the polygon research, increasingly more morphological characteristics were included to separate different morphs. These morphs deviate from the described morphs of HdV-313A-F and are not

unambiguously attributable to one of the HdV-types. Fig. 14 shows how morphs identified in the various polygon diagrams hierarchically relate to each other with an increasing number of features resulting in an increasing number of (sub)types with each a narrower set of morphological characteristics.

In the studied ice-wedge polygons, MOUGEOTIA TYPE and ZYGNEMA TYPE occur abundantly in the wet polygon depressions of Lc04 and Lhc11 (Figs. 6/8), whereas in the fossil peat sections the types occur sometimes with considerable, sometimes with low prominence in inferred wet phases. Although counted as a lumped entity, a re-inspection of some surface samples of Lc04 showed both MOUGEOTIA TYPE and ZYGNEMA TYPE (photographs 11–13). In polygon complex Mnp12, MOUGEOTIA TYPE occurs only incidentally, as can be expected considering its rather dry character. However, also in the wet polygon elements of Samoylov Island the types were found only sporadically (Figs. 12B, 13A–C).

MOUGEOTIA has been reported only rarely from other NE Siberian sites. A single specimen was noted for Lake Billiyakh sediments (Müller, 2009; see Müller et al., 2010) and few specimens were found in Pliocene sediments of Lake El'gygytyn (Andreev et al., 2014). ZYGNEMA TYPE zygospores were found frequently in Weichselian sediments of exposure L7–18 on Bolshoy Lyakhovsky Island (Rudaya et al., 2014). In sediment sections of Lake El'gygytyn finds date back to the Pliocene (Andreev et al., 2012, 2014, 2016). This all seems to imply that only few habitats in Arctic NE Siberia there are only few habitats suitable for the relevant taxa.

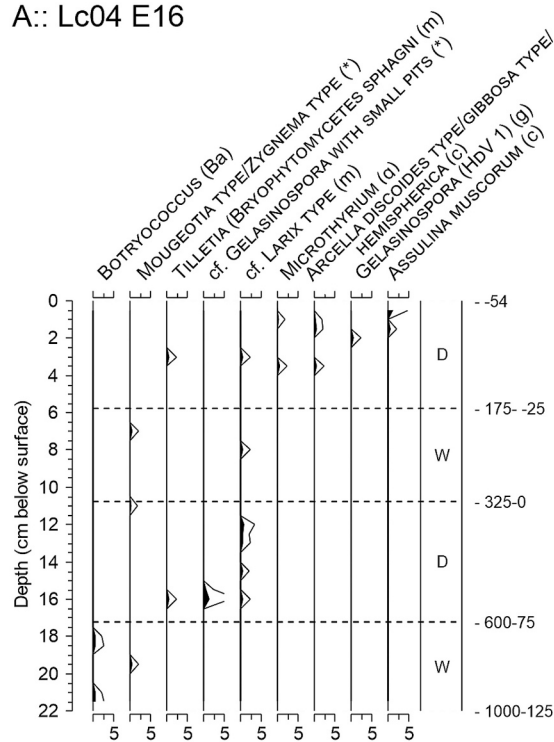
3.1.4.2. NPPs attributed to Spirogyra. The *Spirogyra* genus produces highly diverse morphs (see e.g. Van Geel and Van der Hammen, 1978; Pals et al., 1980; Kuhry, 1997; Fig. 15). Most types have rather large sizes (>100 µm) and psilate, reticulate, or rugulate-like walls and are elongated with slits. However, judging from the illustrations in Kadłubowska (2009), *Spirogyra* species produce also circular to oval spores, and spores with other wall structures, which are not covered by the SPIROGYRA types in the NPP-literature.

RETICULATE SPIROGYRA >100 µm morphs (no photograph) that resemble HdV-132 were found incidentally in wet settings in NE Siberian ice-wedge polygons, but with a reticulate structure finer than on the photographs of Pals et al. (1980) but coarser than on the photographs of Van Geel (1976). For that reason, we are not convinced that the morphs from the polygon wetlands are identical with HdV-132. RETICULATE SPIROGYRA c. 50–60 µm (photograph 15) has been found with substantial amounts in profile sections of the Kytalyk polygon Lhc11 that were interpreted to represent wet peatland phases. The type is hardly present in the Chokurdakh, Pokhodsk, and Samoylov polygons, but it remains unclear why the Kytalyk polygon Lhc11 provides a more favourable habitat for the producers of these morphs than the other sites.

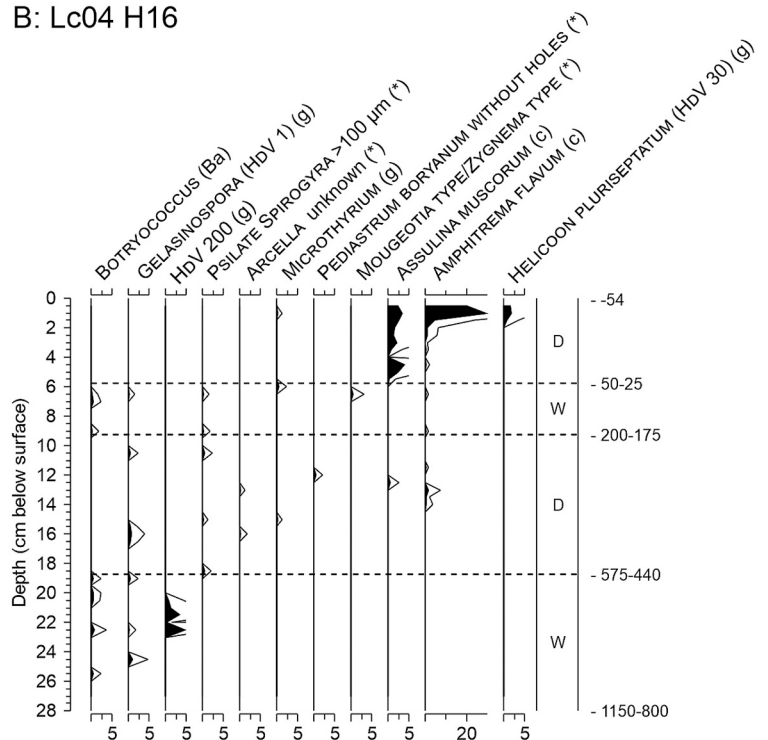
PSILATE SPIROGYRA (i.e., HdV-130/315; Type C in Van Geel, 1976) - which is mentioned to have sizes of (52-)61-90(-110) × 26-37 µm - occurs in the studied sites in two size classes. PSILATE SPIROGYRA c. 50–60 µm (photograph 16) occurs regularly but not in high amounts in the studied polygons (Figs. 6–13). PSILATE SPIROGYRA >100 µm (no photograph) has been observed incidentally, but often with a wider size than reported in the literature, and with furrows or slits that do not clearly resemble the furrows on the photographs of Van Geel et al. (1980/1981), Van Geel and Grenfell (1996), and Van Geel (2001). We did not observe objects with lengths between 60 and 100 µm except in profile Mnp12 AE7 where several specimens with a length of around 80 µm were seen. In Mnp12 AE7, one PSILATE SPIROGYRA specimen with a length of c. 150 µm was seen. Specimens with lengths exceeding 170 µm were reported by Van Geel et al. (1982/1983) but such large objects were not observed in the polygon samples.

Palynomorphs attributed to *Spirogyra* were found regularly in the Lake El'gygytyn sediments dating back to the Pliocene (Andreev et al., 2012, 2014).

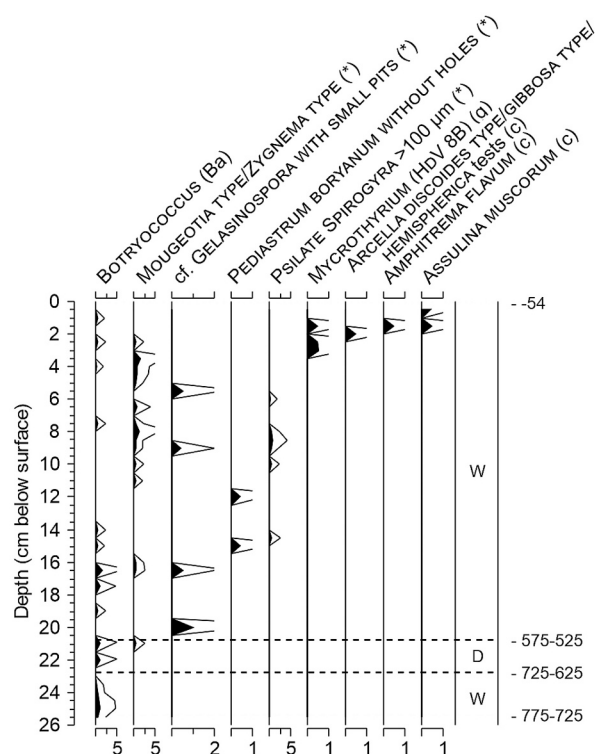
A.: Lc04 E16



B: Lc04 H16



C: Lc04 J16



D: Lc04 Q9

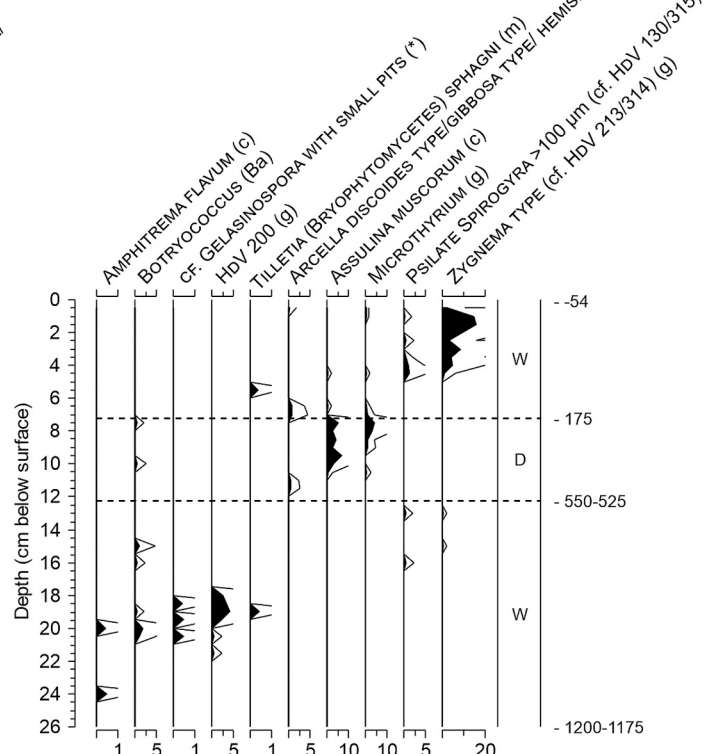


Fig. 7. (A–D) NPP concentrations (palynomorphs 10 mm⁻³) of the palynologically analysed peat profiles of polygon Lc04 (Chokurdakh) (after De Klerk et al., 2011).

3.2. Types attributed to fungi

3.2.1. cf. *DELITSCHIA*

Objects attributed to *DELITSCHIA* (photograph 17) have been described

by Gelorini et al. (2011) for east African lake sediments as UG-1066. The objects are uniseptate, ellipsoid to broadly fusiform, and unsymmetrical, psilate, thick-walled, and have size dimensions of 20–30(37) × 9–10 (15) µm, with slits along the cells.

Lhc11 - surface samples transect

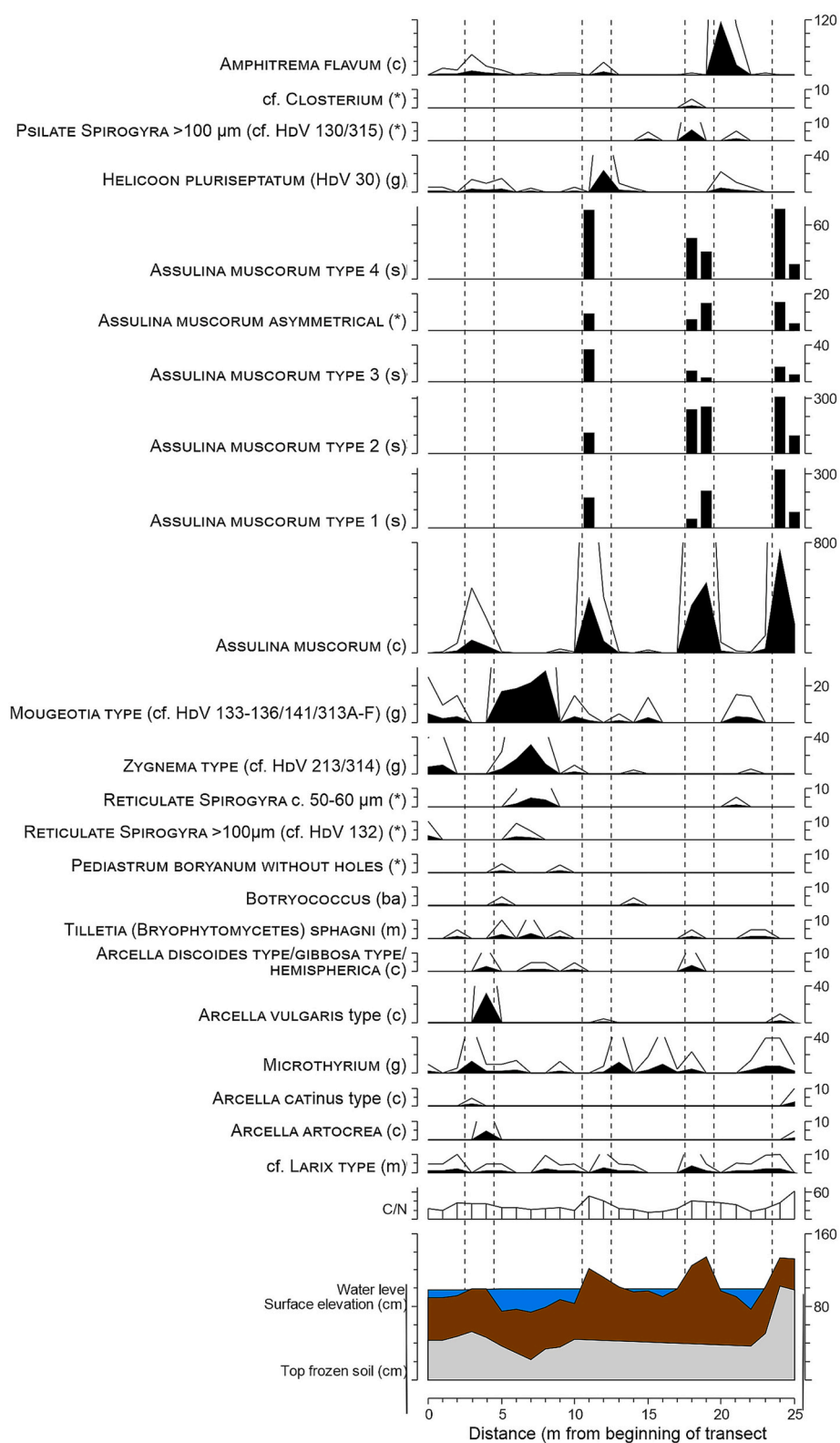
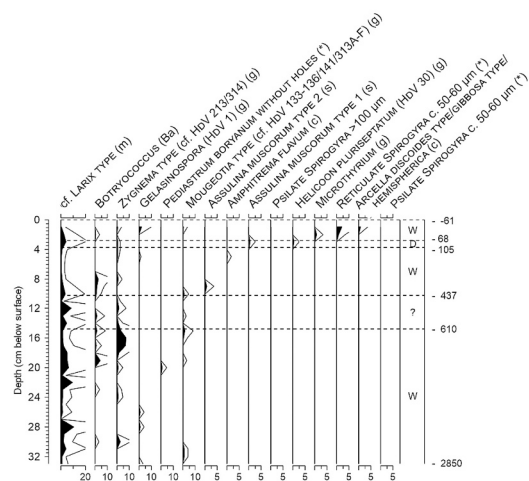
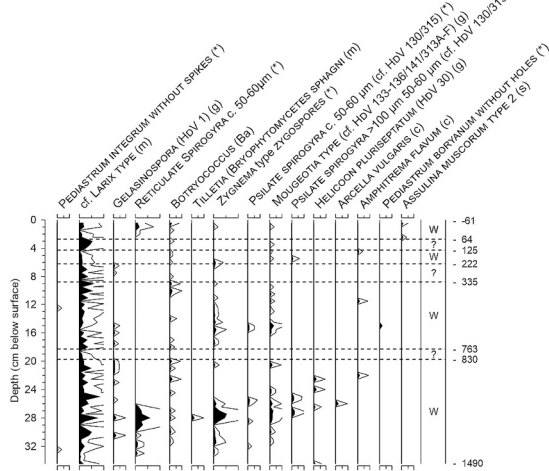


Fig. 8. NPPs in the surface sample transect of polygon Lhc11 (Kytalyk), calculated relative to a pollen sum consisting of pollen types attributable to *Alnus*, *Artemisia*, *Pinus*, *Picea*, and *Abies* (after De Klerk et al., 2014).

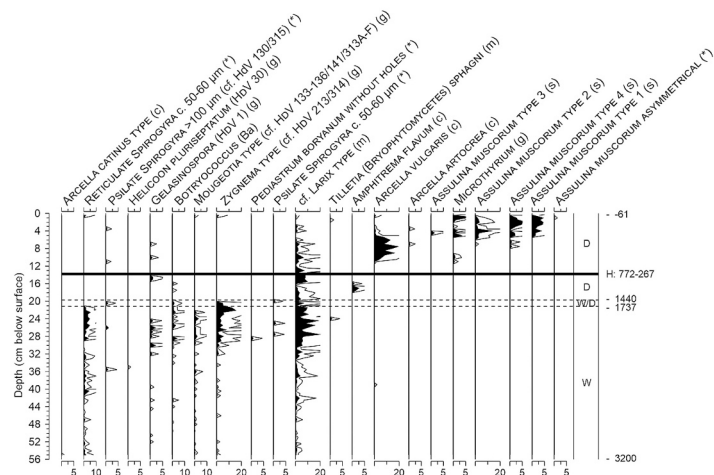
A: Lhc11 J14.30



B: Lhc11 J14.80



C: Lhc11 J17.80



D: Lhc11 J18.80

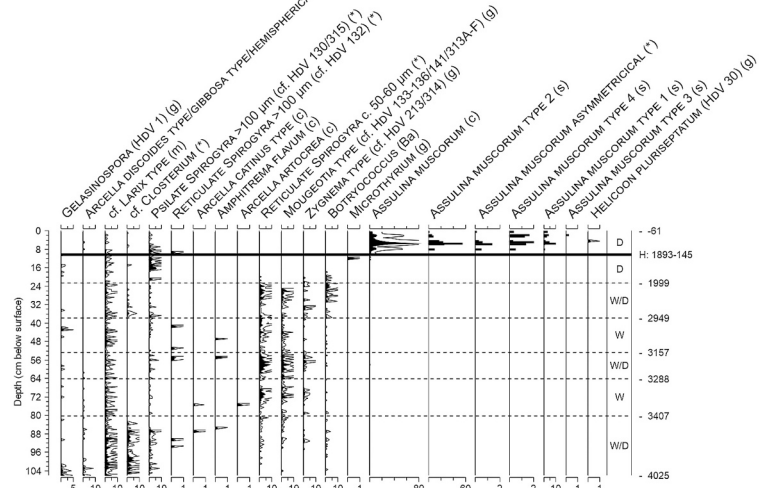
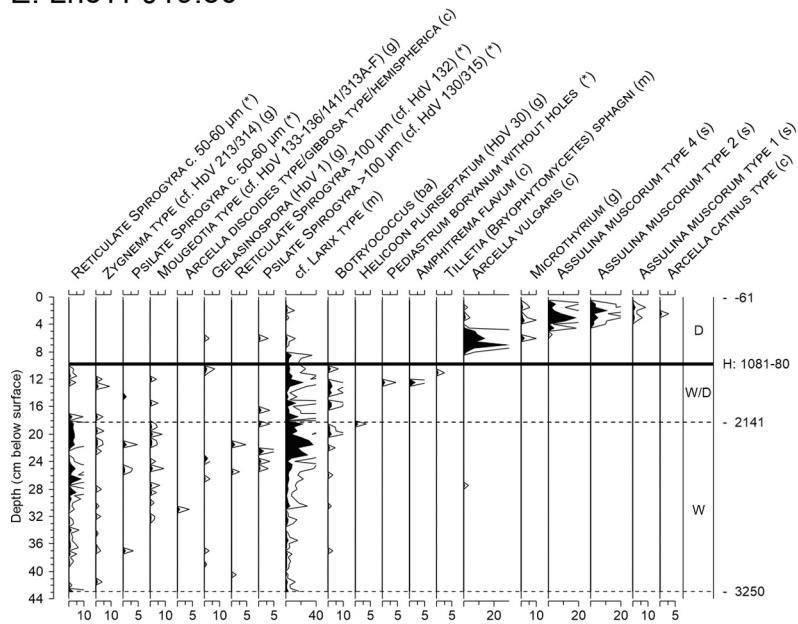
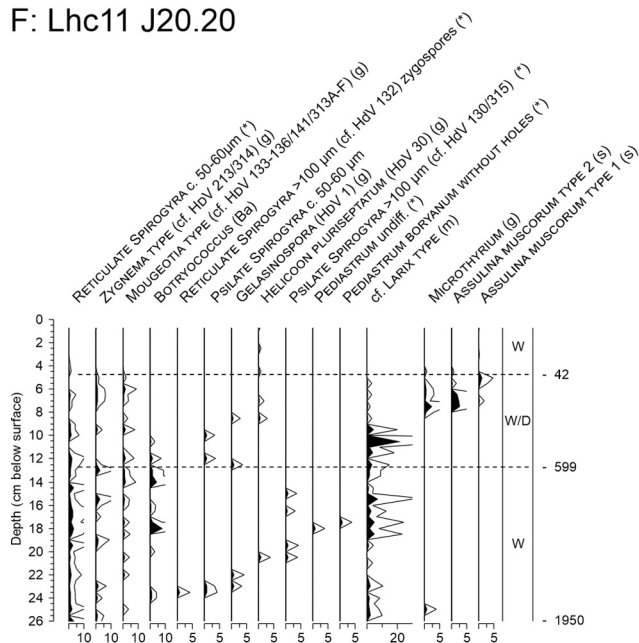


Fig. 9. (A–G) NPP concentrations (palynomorphs 10 mm⁻³) of the palynologically analysed peat profiles of polygon Lhc11 (Kytalyk) (De Klerk et al., research in progress).

E: Lhc11 J19.50



F: Lhc11 J20.20



G: Lhc11 J21.20

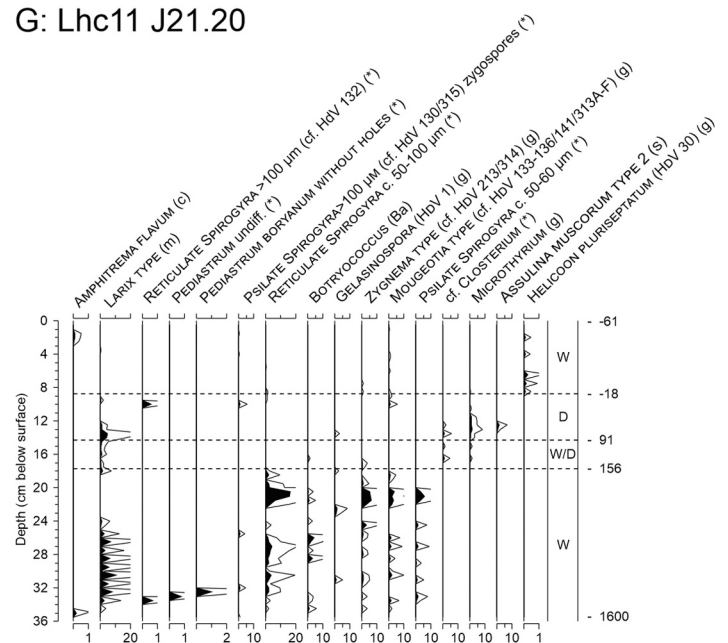


Fig. 9. (continued).

cf. *DELITSCHIA* was found incidentally in profile Mnp12 AE3 in interpreted dry settings (Fig. 11A) and was ignored during the analysis of the other polygons. In contrast to the NPP-type described by Gelorini et al. (2011), the objects seen in the polygon mires are with lengths of 40–50 µm longer than UG-1066 and may be a different type derived from other *Delitschia* taxa than UG-1066.

In NE Siberia, spores attributed to *Delitschia* were furthermore reported for Lake Billyakh (Müller, 2009; see also Müller et al., 2010).

3.2.2. *GELASINOSPORA* (HdV-1), cf. *GELASINOSPORA* LONG, cf. *GELASINOSPORA* with small pits

GELASINOSPORA (HdV-1) (no photograph) includes oval fungal spores with sizes of ca. 22–30 × 14–20 µm and with evenly distributed hyaline pits (Van Geel, 1978). The type is fimicolous but may be carbonicolous

and lignicolous as well (Van Geel, 1978).

GELASINOSPORA occurs sporadically in all polygons. Only in peat profile Lhc11 J14.80 the type occurs more regularly. A single similarly looking spore (named cf. *GELASINOSPORA* LONG by us) which we found in a surface sample of Chokurdakh polygon Lc04 (Fig. 6) (De Klerk et al., 2009) is ca. 3-times longer than the entities described by Van Geel (1978) but has a similar width and similar pits. Furthermore, we found spores in peat profiles Lc04 E16, -J16 and -Q9 of the Chokurdakh polygon Lc04 with smaller pits than the spores described by Van Geel (1978). We assume that both latter morphs derive from *Gelasinospora* or closely related taxa that are possibly absent in the regions where HdV-1 occurs.

At other sites in NE Siberia the type was found only rarely in the surface samples and Lake Billyakh samples of Müller (2009, see Müller et al., 2010) and in samples from Turakh, Mamontov, and Kurungnakh

Mnp12 - surface samples transect

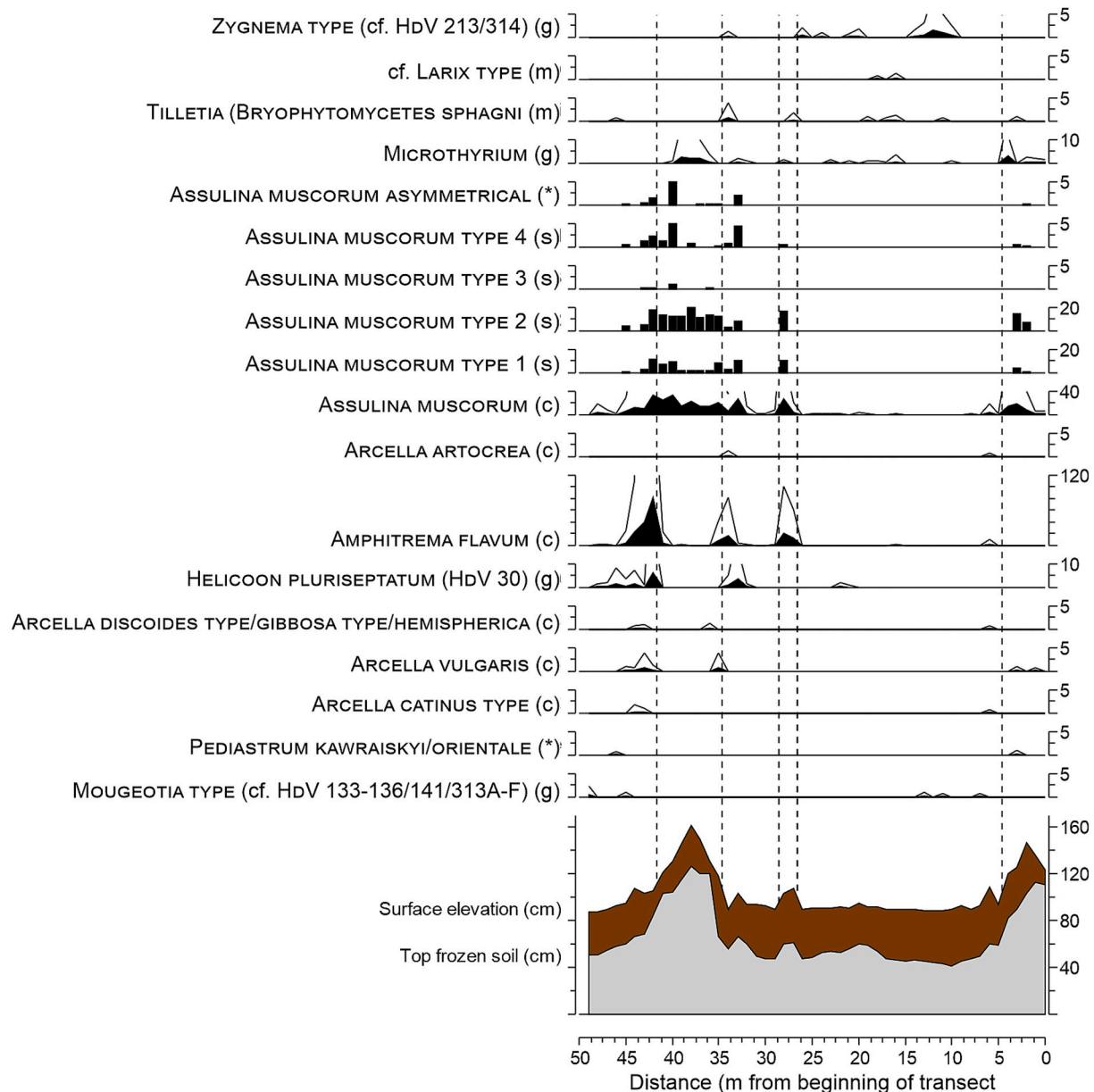


Fig. 10. NPPs in the surface sample transect of polygon Mnp12 (Pokhodsk), calculated relative to a pollen sum consisting of pollen types attributable to *Alnus*, *Artemisia*, *Pinus*, *Picea*, and *Abies* (after De Klerk et al., 2017).

Islands (Schirmer et al., 2008, 2011; Wetterich et al., 2008). Finds date back to the Pliocene in the sediments of Lake El'gygytyn (Andreev et al., 2012, 2014).

3.2.3. cf. HdV-11

Van Geel (1978) describes HdV-11 as mostly 1-2 septate, occasionally constricted at the septa and 23–40 μm (mostly 27–30 μm) long and 10–20 μm (mostly 14–17 μm) wide in the apical cell; the basal cell is hyaline and has a truncate end. Van Geel (1978) assumes that the type is a chlamydospore but puts a question mark to this assessment. We found the type (photograph 18) incidentally in the Samoylov surface sample transect and in sediment profile Sam 87.1 in both dry and wet peatland settings, but the identification may be flawed. The type was neither distinguished in Lc04 and Lhc11 nor in the surface samples of Mnp12. It

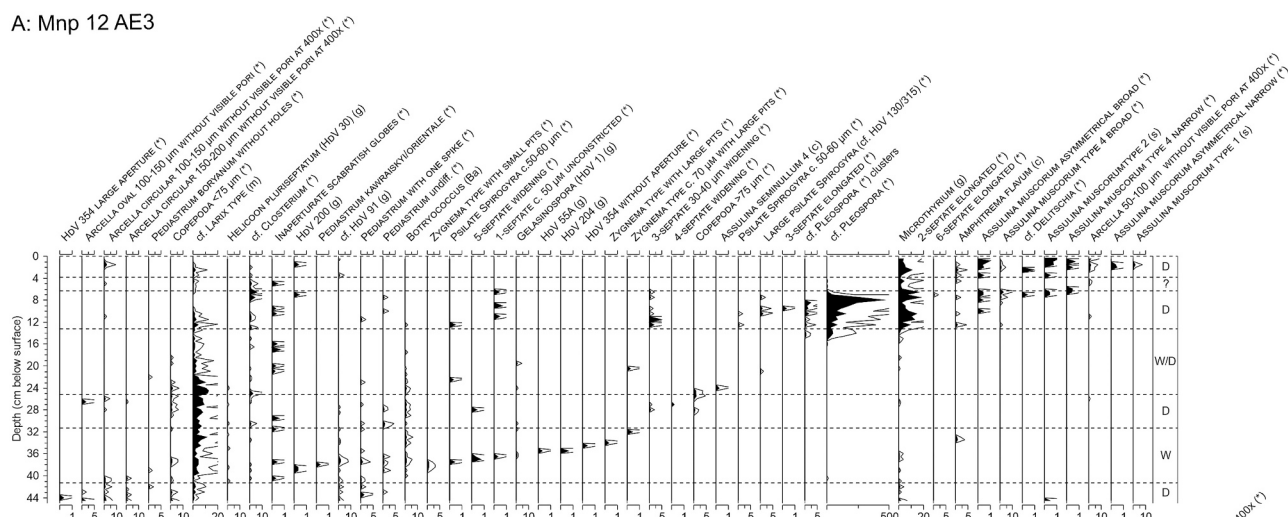
may be connected to Cyperaceae (Van Geel, 1978).

3.2.4. HdV-200

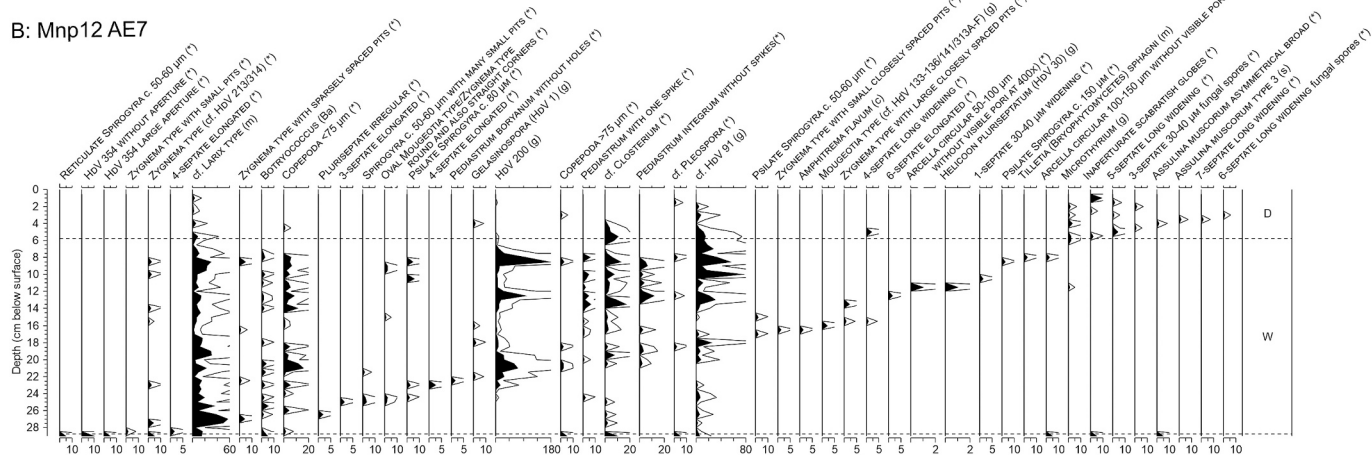
HdV-200 (g) (photograph 19) consists of clusters of globose cells with a cluster diameter of 20–45 μm and with individual cells of different sizes (Van Geel et al., 1989). It is assumed to occur on dry parts of helophytes or on plant remains of bottoms of pools that incidentally dry-out (Van Geel et al., 1989). Gelorini et al. (2011) ascribe it to relatively dry microhabitats.

In the NE Siberian ice-wedge polygons the type occurs regularly with very high values in the polygon depressions of Chokurdakh (Lc04), in submerged depressions on Samoylov Island as well as in interpreted wet phases of the peat profiles of Lc04 and Mnp 12 (Figs. 7A–D, 11A–C). In peat profile Mnp12 AE7 (Fig. 11B), the type also occurs in low amounts

A: Mnp 12 AE3



B: Mnp12 AE7



C: Mnp12 AX29

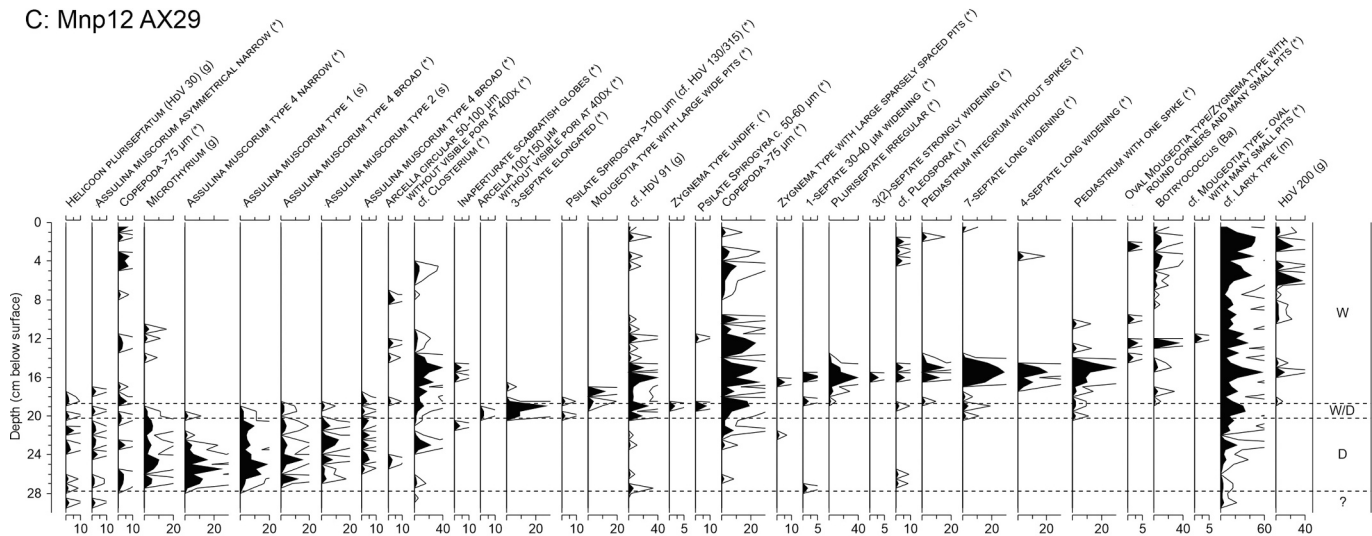


Fig. 11. (A–C) NPP concentrations (AE3: palynomorphs 10 mm^{-3} ; AE7 and AX29: palynomorphs 100 mm^{-3}) of the palynologically analysed peat profiles of polygon complex Mnp12 (Pokhodsk) (De Klerk et al., research in progress).

in an interpreted dry peatland habitat. The type was initially not distinguished in the surface samples of polygon Lhc11, but a re-inspection of a sample from the central submerged depression revealed HbV-200 in very high amounts. It was not found in the peat profiles of Samoylov Island.

3.2.5. *HELICOON PLURISEPTATUM* (HdV-30)

HELICOON PLURISEPTATUM (HdV-30) (photograph 22) is helically coiled around 8–9 times and forms a bioconical body of (30)–58–73 μm diameter (Van Geel, 1978). The type is well-known under various names in the literature (discussed by Van Geel, 1978) and occurs predominantly just above the water film on leaves of plants (see Van Geel, 1978). The type is generally larger in settings where it occurs prominently than in

A: Sam - surface samples transect (part 1)

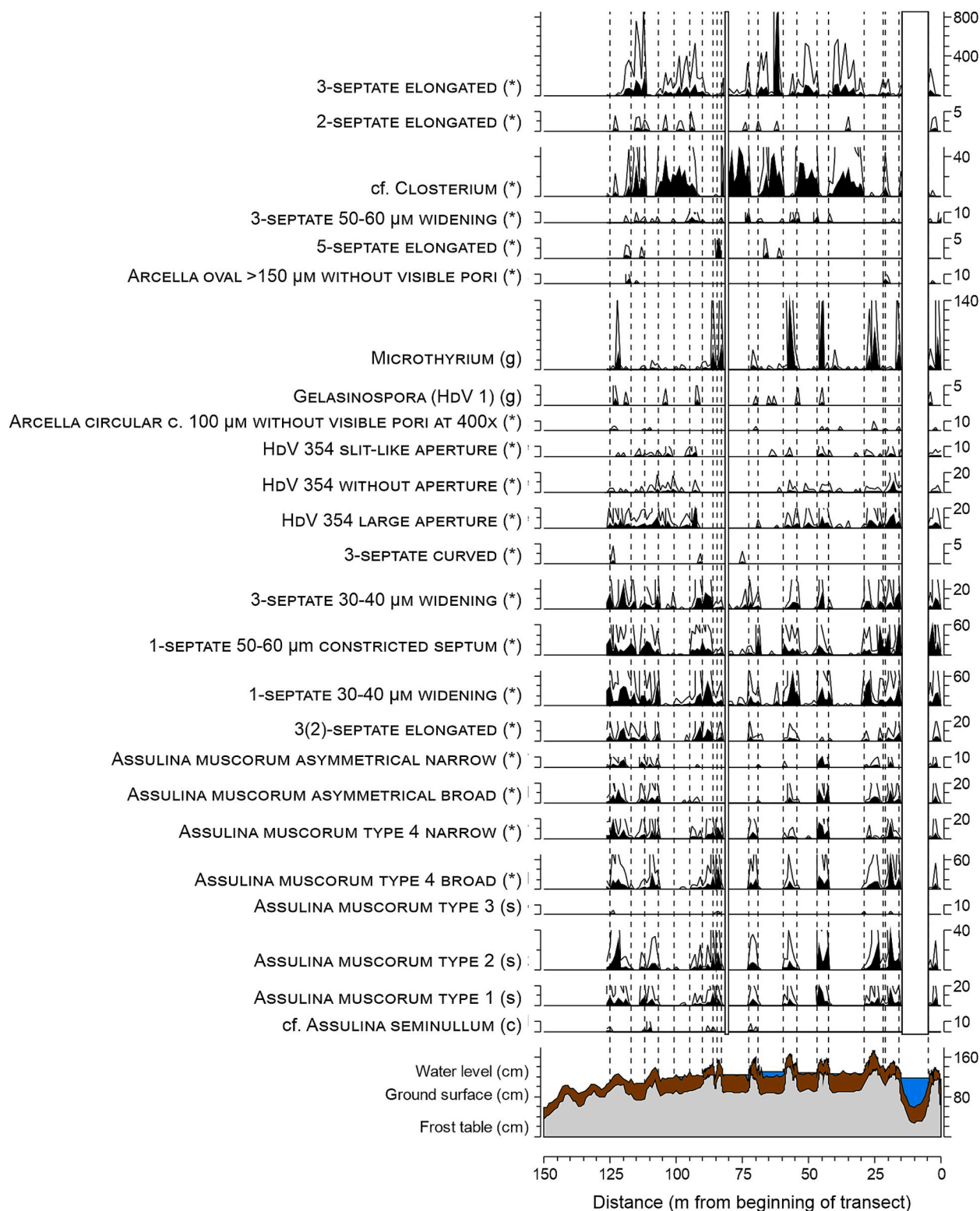


Fig. 12. (A/B) NPPs in the surface sample transect of Samoylov Island, calculated relative to a pollen sum consisting of pollen types attributable to *Alnus*, *Artemisia*, *Pinus*, *Picea*, and *Abies* (De Klerk et al., research in progress).

B: Sam - surface samples transect (part 2)

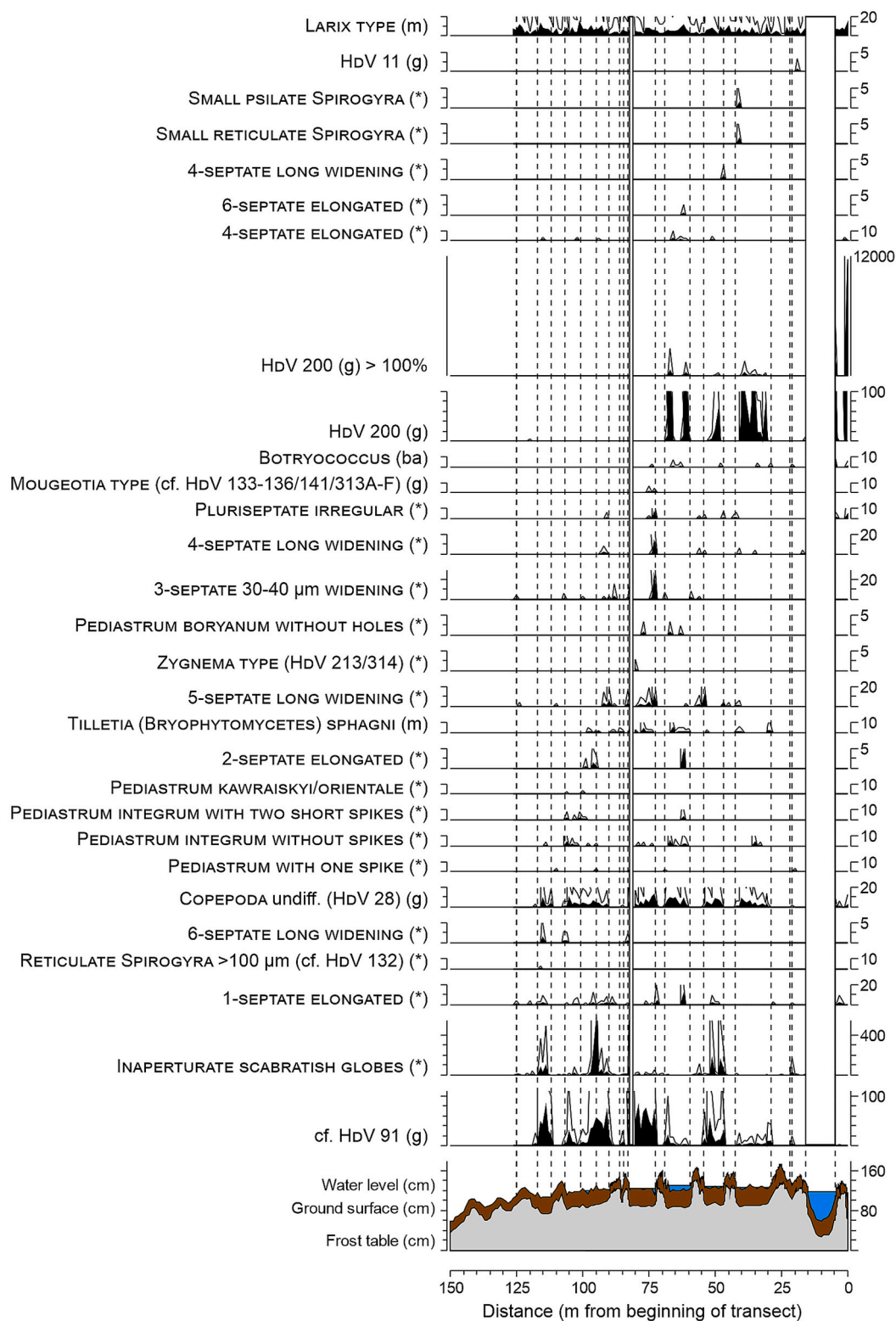
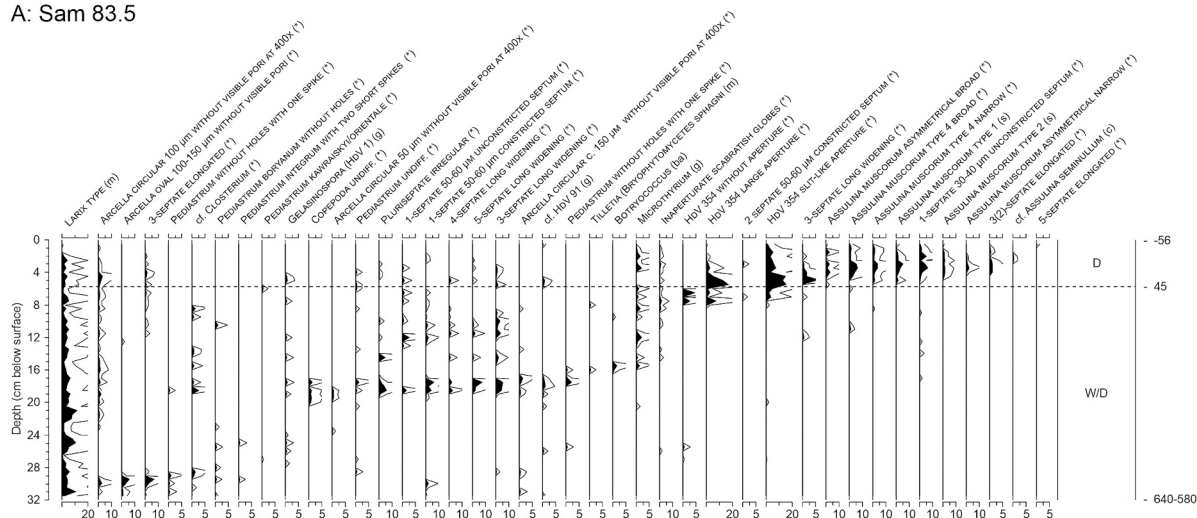
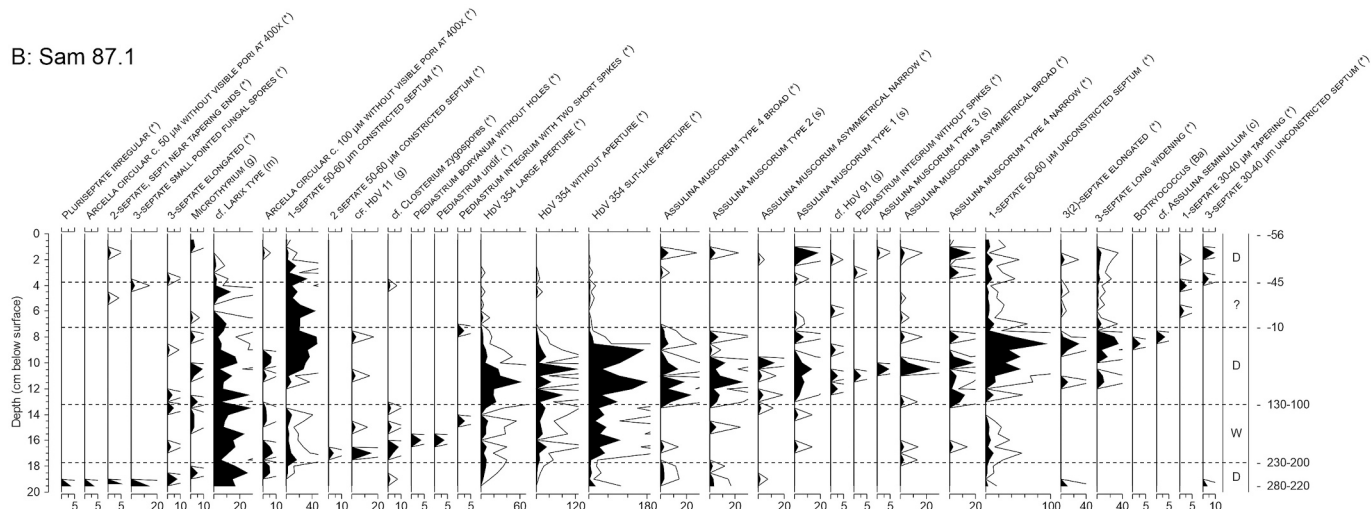


Fig. 12. (continued).

A: Sam 83.5



B: Sam 87.1



C: Sam 161.5

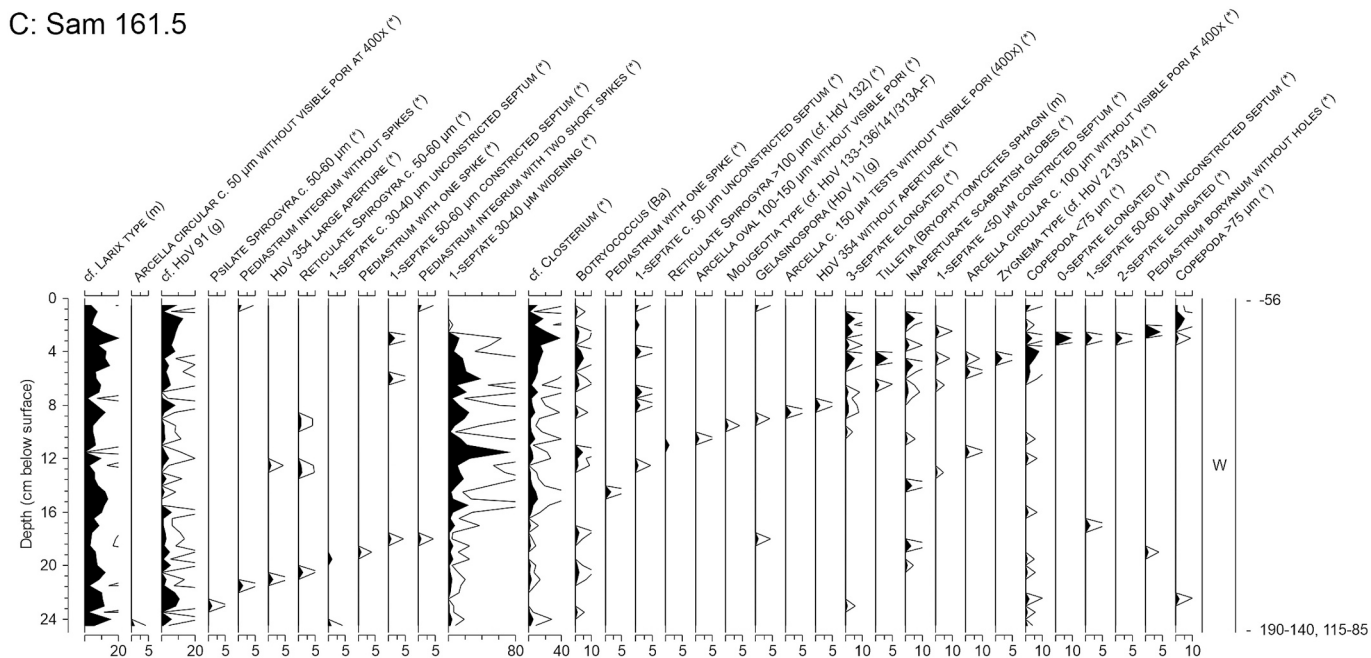


Fig. 13. (A–C) NPP concentrations (palynomorphs 100 mm⁻³) of the palynologically analysed peat profiles of Samoylov Island.

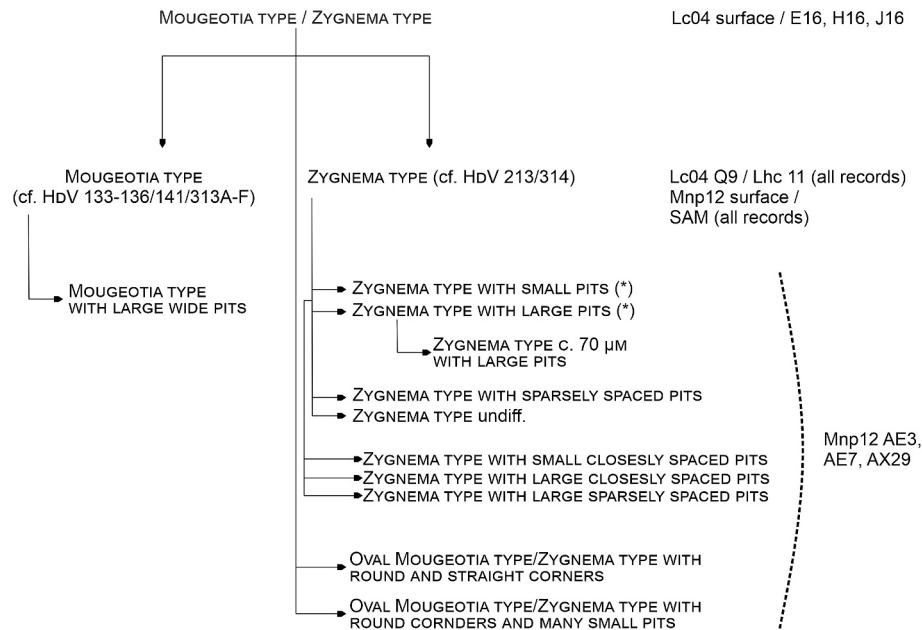


Fig. 14. Hierarchical model of morphotypes attributable to *Mougeotia* and *Zygnema*.

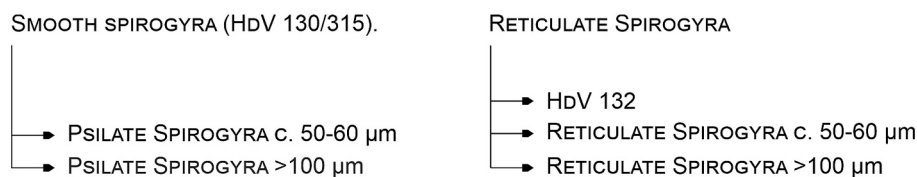


Fig. 15. Hierarchical model of morphotypes attributable to *Spirogyra*.

habitats where it is only sporadically present, which is attributed to more favourable growth conditions in the former (Van Geel, 1978).

In the NE Siberian ice-wedge polygons the type was found only sporadically in both wet and dry settings, with higher values on polygon ridges from Lhc11 and Mnp12 (Figs. 8, 10). The type was not seen in the samples from Samoylov Island.

3.2.6. HdV-55A

HdV-55A (sensu Van Geel, 1978) (no photograph) is a small oval monocellular object associated to sordarioaceous fungi. Later the type was subdivided into HdV-55A1 and HdV-55A2 of which the former is shorter and the latter longer than 20 µm; both types are typical for mammal excrements (Van Geel et al., 1980/1981). The type was found only once in peat profile Mnp12 AE3. It could therefore have been blown in from far outside the polygon complex and, thus, does not necessarily indicate grazing (of e.g. reindeer) in the polygon directly.

3.2.7. LASIOPHAERIA CAUDATA (HdV-63A)

The type (photograph 23) is 3-, rarely 4-septate, at one end geniculate and tapering into a point, and at the other end narrowly rounded (Van Geel, 1978). *Lasiosphaeria caudata* specimens were found on decaying wood of *Picea*, but fossil spores have also been found in deposits from time-periods where *Picea* was not present in the study areas. It is therefore assumed that the parent species may also occur in treeless peatlands (Van Geel, 1978; Van Geel and Aptroot, 2006).

The type was only found in the samples from Samoylov Island but lumped with other 3-SEPTATE ELONGATED morphs, which as a complex occurs predominantly in the moist – but not submerged – polygon depressions (Fig. 12A).

3.2.8. MICROTHYRIUM

MICROTHYRIUM (photographs 20, 21) consists of circular objects with diameters between 40–100 µm and a distinct dark rim surrounding a circular aperture in its centre (Van Geel, 1978). Cell structures radiate from the centre to the margin (Van Geel, 1978). Different morphological varieties may represent fruit bodies of different species of the genus depending on the host plant taxon (Van Geel, 1978) but these varieties have not been worked out into different palynomorphs yet. The type was found superficially attached to fossil remnants of various plant species including *Scheuchzeria palustris*, and cf. *Eriophorum vaginatum* (Van Geel, 1978). The latter species occurs locally in the studied polygons.

In the samples from the ice-wedge polygons, distinct differences in size and structure are discernible (photographs 20, 21), e.g. the object on photograph 21 has considerably narrower radiating cells than the object on photograph 20. A similar difference seems to exist between HdV-8B and HdV-8E, for the latter of which no parent species is known. We found palynomorphs attributed to MICROTHYRIUM frequently in samples from both dry and wet peatland habitats, but prominently on the polygon ridges along the surface sample transects and in profile sections interpreted as dry phases (Figs. 6, 8, 10, 12A).

Objects attributed to *Microthyrium* are mentioned for Bolshoy Lyaikhovsky Island sediment sections (Andreev et al., 2004, 2009, 2011; Wetterich et al., 2009; Rudaya et al., 2014), and were also found regularly in low amounts in Mamontov Klyk (Schirmeister et al., 2008; Andreev et al., 2011) and at the Oyogos Yar (Wetterich et al., 2009) and Dyanushka River outcrop sections (Zech et al., 2011), the Central Yakutian surface samples of Müller (2009), at Lake Billyakh (see Müller et al., 2010) and in Lake El'gygytyn dating back to the Pliocene (Andreev et al., 2012, 2014, 2021).

Lc04 all records, Lhc11 all records, Mnp12 surface samples:

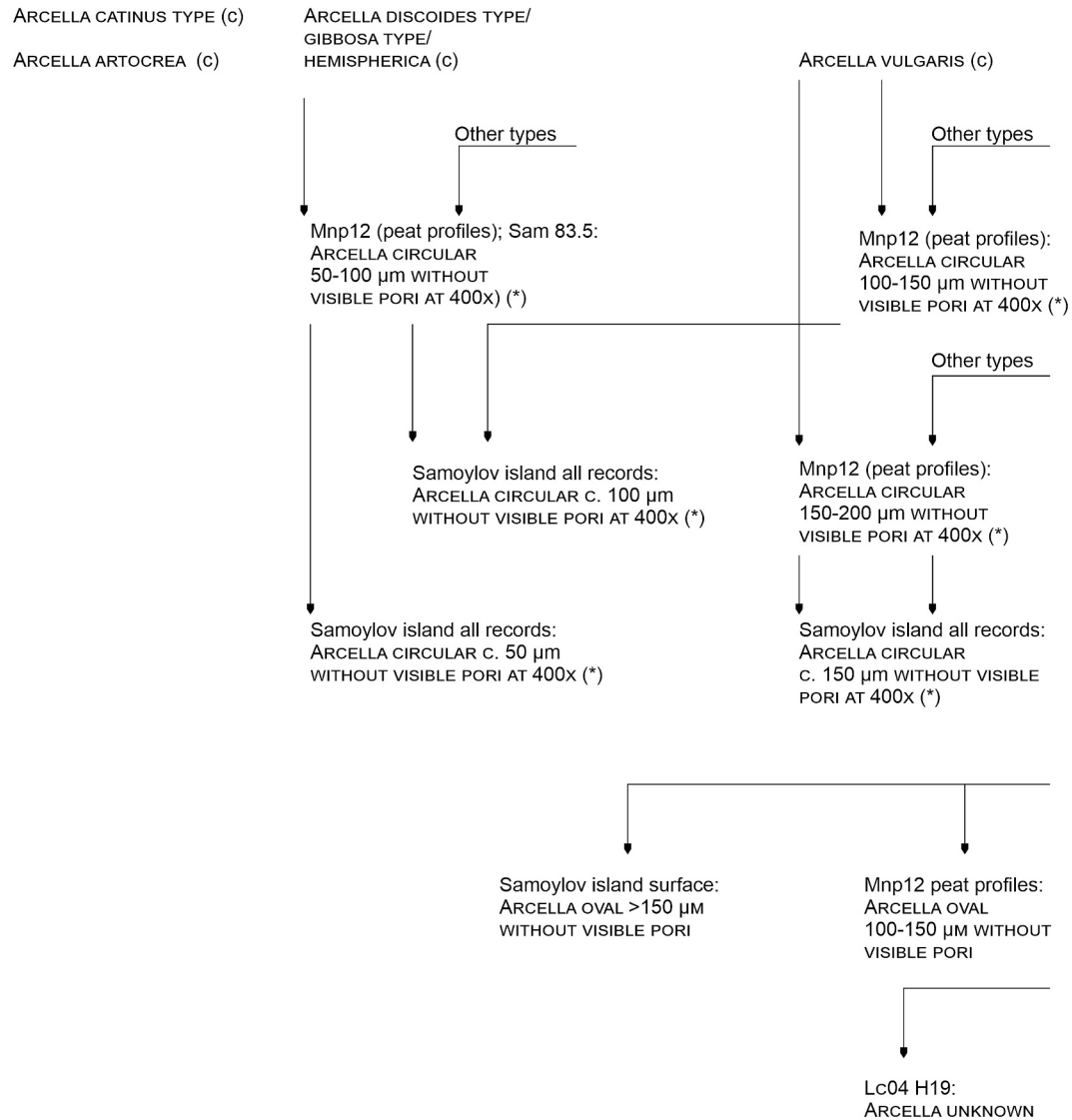


Fig. 16. Hierarchical model of morphotypes attributable to *Arcella*.

Lc04 (all data), Lhc11 surface:

ASSULINA MUSCORUM (c)

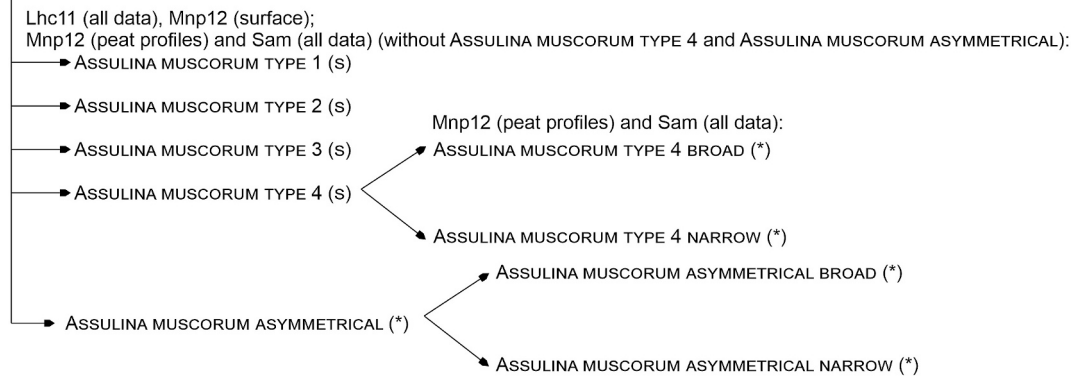


Fig. 17. Hierarchical model of morphotypes attributable to *Assulina muscorum*.

3.2.9. cf. *PLEOSPORA*

HdV-3B, interpreted as fruit bodies from various *Pleospora* species, has sizes around $150\text{--}290 \times 225\text{--}320 \mu\text{m}$ with short, $2.5 \mu\text{m}$ thick septate hairs (Van Geel, 1978). Similarly looking ascospores range between $25\text{--}43 \mu\text{m} \times 10\text{--}14 \mu\text{m}$ (Van Geel, 1978; Van Geel and Aptroot, 2006). The type occurs in relatively dry ombrotrophic peatland vegetation and on dead plant remains (Van Geel, 1978; Van Geel and Aptroot, 2006).

The objects seen by us (photograph 24) - of which frequently also clusters were observed - are present with very high numbers in samples of the Pokhodsk peat profile AE3 in a dry phase. However, the size of the observed objects (c. $80 \times 30 \mu\text{m}$) ranges between those of the described ascospores and fruit bodies mentioned by Van Geel (1978). In general, ascospores of *Pleospora* taxa are diverse in morphology (Crivelli, 1983). We expect that the objects of Mnp12 are spores from *Pleospora* taxa not known from the well-studied areas in NW and C Europe. The spores were not found in the Samoylov polygons and were ignored during the analysis of the Lc04 and Lhc11 records, and the surface samples of Mnp12.

Aptroot and Van Geel (2006) and Van Geel et al. (2008) found objects in the intestines of the 18,500 cal. BP Yukagir mammoth that they interpreted as spores of *Pleospora herbarum*.

3.2.10. *TILLETIA* (BRYOPHYTOMYCETES) SPHAGNI

TILLETIA (BRYOPHYTOMYCETES) SPHAGNI (m) spores (no photograph) are small circular spores with a net-like fissural wall structure that are produced by fungi that parasite on peat moss (*Sphagnum*). They are well-known from pollen samples (e.g. Van Geel, 1978; Moore et al., 1991). The type was found only sporadically in the Siberian ice-wedge polygons, and a confusion with similar-looking spores from other *Tilletia* species seems feasible (De Klerk et al., 2009).

3.2.11. 1-SEPTATE 30–40 μm WIDENING

We observed 1-SEPTATE 30–40 μm WIDENING objects with smooth surfaces and a length between 30 and 40 μm that widen conspicuously (photographs 25–28) or slightly (photograph 29). The variety among the objects suggests that they originate from different taxa with possibly different ecological requirements.

1-SEPTATE 30–40 μm WIDENING was only counted for Samoylov Island where it occurs in high amounts in the surface samples of the ridges and in the interpreted continuously wet profile 161.5, and in low numbers in 87.1. In the peat sections of Mnp12 the type occurs only sporadically in AE7 and AX29 in phases that are interpreted as wet, but also in one sample of an interpreted dry phase.

3.2.12. 1-SEPTATE 30–40 μm TAPERING

1-SEPTATE 30–40 μm TAPERING was only found in profile Sam 87.1 where it occurs in three samples. The type was not observed in the other Samoylov samples and the peat profiles of Mnp12.

3.2.13. 1-SEPTATE 50–60 μm CONSTRICTED SEPTUM, 1-SEPTATE < 50 μm CONSTRICTED SEPTUM, 1-SEPTATE 50–60 μm UNCONSTRICTED SEPTUM, 2-SEPTATE 50–60 μm CONSTRICTED SEPTUM, 1-SEPTATE c. 50 μm UNCONSTRICTED SEPTUM, 1-SEPTATE c. 30–40 μm UNCONSTRICTED SEPTUM

1-SEPTATE 50–60 μm CONSTRICTED SEPTUM (photographs 30–32) is c. $50\text{--}60 \mu\text{m}$ long and around $15\text{--}20 \mu\text{m}$ wide. The septum is markedly or slightly constricted. Similarities exist with spores on photographs of TM-4088 and TM-4091 (Cugny, 2011) that both were categorised as Didymoascospores, but the former has more blunt and the latter more tapering ends than the objects seen by us.

The objects were only counted in the records from Samoylov Island where they occur partly in high amounts on dry polygon ridges and in much lower numbers in the polygon depressions. The taxa from which these NPPs originate are - at least on Samoylov Island - most likely xerophilic. The objects were not encountered in the peat profiles of Mnp12.

Some sporadically occurring objects have some resemblance to 1-

SEPTATE 50–60 μm CONSTRICTED SEPTUM, including conspicuously smaller specimens (named 1-SEPTATE < 50 μm CONSTRICTED SEPTUM) (Sam 161.5; Fig. 13C) and with an unstricted septum (named 1-SEPTATE 50–60 μm UNCONSTRICTED SEPTUM (Sam 83.5, 87.1 161.5; Fig. 11A–C; photograph 31). Furthermore, we found 2-SEPTATE 50–60 μm UNCONSTRICTED SEPTUM (Sam 83.5/87.1) and 1-SEPTATE 30–40 μm UNCONSTRICTED SEPTUM, both with straight sides. If these are not morphological varieties within the types produced by one taxon, these objects might derive from closely related taxa. All these types were only found in the Samoylov records and not in the peat profiles of Mnp12.

Similar palynomorphs of which photographs have been published are interpreted as originating from *Delitschia* species (Montoya et al., 2012, pl. 1-35; Shumilovskikh et al., 2015, Fig. 6C), but without systematic description in these papers we are not sure whether our type is actually the same.

3.2.14. 2-SEPTATE, SEPTA NEAR TAPERING ENDS

2-SEPTATE, SEPTA NEAR TAPERING ENDS (no photograph) are objects consisting of three cells, of which the outer ones have sharply pointed ends. The septa are positioned near to these ends and the central cell is, thus, clearly larger than the outer cells. The type was found in only three samples of peat profile Sam 87.1 (Fig. 13B).

3.2.15. 3-SEPTATE 30–40 μm WIDENING

3-SEPTATE 30–40 μm (photograph 33/34) morphs are oval and somewhat stocky and may include remains from different taxa, or morphological varieties of one taxon. In the object on photograph 33 the left septum seems to be in a state of dissolving. The type was ignored in the analysis of polygons Lc04 and Lhc11, and the surface samples of Mnp12. It occurs often in the surface samples from Samoylov Island mainly on the polygon ridges and in the dry polygon depressions at the southwestern reach of the transect (Fig. 12A), and a dry phase from section 81.7 (Fig. 13B) of that polygon. Most likely the connected taxon/taxa are xerophilic.

3.2.16. 3-SEPTATE 50–60 μm WIDENING

3-SEPTATE 50–60 μm WIDENING objects were found only in Samoylov profile 83.5 where the type occurs in several samples of a zone interpreted as a dry phase, and in a zone we cannot identify as wet or dry. The type was not observed in the other Samoylov records and in the peat profiles of Mnp12.

3.2.17. 3-SEPTATE CURVED

3-SEPTATE CURVED (no photograph) is characterised by a distinct arched form and was found only three times in the surface sample transect of Samoylov Island. It may correspond to HdV-17 or HdV-99 (Van Geel, 1972, 1978), or to UG-1145, which is cautiously attributed to *Fusarium* (Gelorini et al., 2011).

3.2.18. 3-SEPTATE SMALL POINTED

3-SEPTATE SMALL POINTED (*) (no photograph) is conspicuously short and has similarly sharp outer cells as 2-SEPTATE, SEPTA NEAR TAPERING ENDS. Further morphological notes were not made. The type occurs in some samples of Sam 87.1 (Fig. 13B) but in too low numbers to allow meaningful ecological inference.

3.2.19. 3-SEPTATE LONG WIDENING, 4-SEPTATE LONG WIDENING, 5-SEPTATE LONG WIDENING, 6-SEPTATE LONG WIDENING, 7-SEPTATE LONG WIDENING

We found a number of relatively long ($60\text{--}115 \mu\text{m}$) and widening objects with 1–7 septa (photographs 35–43). Some septa appear to be slightly constricted. In one case a clear porus with thickened rim is visible (photograph 41). The clear morphological differences between the objects indicate that they originate from different fungal taxa or from the one or a few taxa that produce polymorphic objects. The various types were only counted in the Samoylov data and the Mnp12 peat profiles.

The types occur predominantly on the lower rim parts and depression margins of the Samoylov surface transect but were also found in low numbers in the depressions. The various types may, thus, relate to taxa of transitional settings. In profile Mnp12 AX29 high values of 4-SEPTATE LONG WIDENING and 7-SEPTATE LONG WIDENING co-occur in some samples with high values of PLURISEPTATE IRREGULAR and with coenobia-morphotypes attributed to *Pediastrum*. The types occur only a few samples above an interpreted dry phase when the depression was still shallow.

3.2.20. PLURISEPTATE IRREGULAR

A few observed morphs have a length of c. 80 µm, a variable number of septa, and a pronounced irregular outline (photograph 44). In the Samoylov surface transect the type occurs in low amounts along the depression margins, and in the peat profiles of Samoylov it is only sporadically present. In profile Mnp12 AX29 the type occurs in high values at the base of a wet phase together with two *PEDIASTRUM* types. The type was not distinguished in the samples of polygons Lc04, Lhc11, and the surface samples of Mnp12

3.2.21. 0-SEPTATE ELONGATED, 1-SEPTATE ELONGATED, 2-SEPTATE ELONGATED, 3-SEPTATE ELONGATED, 3(2)-SEPTATE ELONGATED, SMALL 3(2)-SEPTATE ELONGATED < 30 µm, 4-SEPTATE ELONGATED, 5-SEPTATE ELONGATED, 6-SEPTATE ELONGATED, 7-SEPTATE ELONGATED, 8-SEPTATE ELONGATED

Various elongated objects with 0 to 8 septa (photographs 45–51), a smooth wall and a length between c. 40 and 80 µm, which may derive from related taxa (including *LASIOPHAERIA CAUDATA* with its clearly distinguishable with its bend, see photograph 23), were lumped in distinct groups based on the number of septa. Septa may have gone lost (photographs 46/47) or be in the state of disappearing (photograph 49) probably due to taphonomical processes. For the case that the loss of septa may reflect specific ecological conditions, we added the number of remaining septa between brackets to allow for future interpretation (i.e., 3(2)-SEPTATE ELONGATED). Apart from objects with a length exceeding 40 µm, also objects that range around 30 µm were encountered (Sam profile 87.1).

These types were only analysed for the records from Samoylov Island and the peat profiles of Mnp12. Apart from 3-SEPTATE ELONGATED remains, all types occur only sporadically in both dry and wet peatland settings. 3-SEPTATE ELONGATED remains occur predominantly in wet habitats in the surface samples of Samoylov Island (Fig. 12A) and in profile AX29 from the Pokhodsk polygon complex Mnp12 (Fig. 11C). 3-septate morphs of which one septum is lost abound in the surface samples of the polygon ridges and in the southwestern dry polygon depressions of Samoylov Island as well as in an interpreted dry phase of profile Sam 87.1 (Fig. 13B). This may indicate that in the case of Samoylov Island the loss of a septum relates to the drier peatland habitats.

3.2.22. 3(2)-SEPTATE STRONGLY WIDENING fungal spores

We sporadically found c. 65 × 25 µm large fungal spores that widen conspicuously towards their centres (photograph 52). The outline and the position of the septa give the impression as if the type is actually 3-septate with one septum missing. The type occurs in sample 73 of the Samoylov surface samples on a polygon ridge (Fig. 12) and in one sample of Mnp12 AX29 (Fig. 11C) in an interpreted wet peatland phase.

3.3. Testate amoebae

3.3.1. Morphs attributed to *Arcella*

The morphs of the genus *Arcella* are normally round or oval with a large central aperture. Based on test size and on the presence of small pores around the central aperture, we initially identified *ARCELLA CATINUS* TYPE, *ARCELLA ARTOCREA*, *ARCELLA DISCOIDES* TYPE/*GIBBOSA* TYPE/*HEMISPHERICA*, and *ARCELLA VULGARIS* after Charman et al. (2000) in the records from Lc04, Lhc11 and the surface samples of Mnp12. *ARCELLA CATINUS* TYPE and *ARCELLA DISCOIDES* TYPE/*GIBBOSA* TYPE/*HEMISPHERICA* are of similar size, but the former has clear small pores around the central aperture, whereas such pores

are absent in the latter (which could not be further identified because a possible dome shape of the tests could not be observed in the microscopic slides because of the flattening weight of the cover glasses. *ARCELLA VULGARIS* is large (> 100 µm) and may contain pores scattered over the surface but not around the central aperture. *ARCELLA ARTOCREA* has a diameter exceeding 180 µm and numerous small pores around the central aperture.

The key of Charman et al. (2000) does not cover all species of the *Arcella* genus (see Beyens and Meisterfeld, 2001; Mitchell et al., 2008; Mazei and Tsyganov, 2006; Payne et al., 2012), which limits its suitability for NPP identification in palynological research. Indeed, in the Lc04 peat profile H16 we found morphs, which did not fit any description, and were therefore labelled “*ARCELLA* unknown”.

On Samoylov Island, some *ARCELLA* tests don't display small pori during standard microscopy with 400×, but do at magnifications of 1000× (e.g. photograph 57; note that this morph has a broader aperture rim than the other morphs which gives the impression that the pori are positioned on this rim). Therefore, we added morphological characteristics to the names of the *ARCELLA* morphs, including test diameter and whether pores are visible with standard 400× magnification. We initially used size ranges, but later gave a specific size as the diameter of *ARCELLA* types appeared to be constant and intermediate sizes were hardly encountered. Whereas most *ARCELLA* palynomorphs are brown (photographs 53, 54, 58), also rather light-coloured specimens were seen (photographs 55–57). However, this feature was not used for distinguishing different types. Apart from *ARCELLA CATINUS* TYPE and *ARCELLA ARTOCREA* in the Lc04 and Lhc11 records and the Mnp12 surface samples, we did not observe any morphs with apertures visible at 400× magnification. Such categorisation does not solve the question of which taxa may have been observed but facilitates future identification when knowledge on Arcellidae morphology progresses further. Fig. 16 presents the relationship between the different type names used for objects attributed to *Arcella*.

In the polygon records, *ARCELLA* abound on the dry polygon ridges of the Lc04 and Lhc11 surface transects (Fig. 8). The type also occurs along the lower rim parts in the Mnp12 transect. In the dry peatland phases of peat profiles Lhc11 J17.80 and J19.50, *ARCELLA VULGARIS* (sensu Charman et al., 2000) peaks before morphs attributed to *Assulina muscorum* increase (Fig. 9C/E), suggesting a succession related to (hitherto unknown) changing ecological conditions.

On Samoylov Island and in peat profile Mnp12 AE3, *ARCELLA* OVAL 100–150 µm WITHOUT VISIBLE PORI (photograph 58) was found. The type resembles tests of *A. ovaliformis* considerably (Chardez and Beyens, 1987) but it has no visible pores even at 1000× magnification. It may, thus, represent a previously unknown taxon, or a mere morphological variation due to unknown ecological factors (L. Beyens, pers. com. April, 2020). The presence or absence of these pores may allow future identification of these factors if the knowledge of *Arcella* morphology increases.

In NE Siberia, morphs attributed to *Arcella* were furthermore found regularly in surface samples from both (sub)arctic Yakutia and further southward (Müller, 2009; see Müller et al., 2010). *ARCELLA* morphs were also found in low numbers in Weichselian deposits of Mamontov Klyk (Schirrmeister et al., 2008), Eemian deposits of the Oyogos Yar sites (Wetterich et al., 2009; Andreev et al., 2011) and incidentally in Pliocene sediments of Lake El'gygytyn (Andreev et al., 2016).

3.3.2. AMPHITREMA FLAVUM

AMPHITREMA FLAVUM is longitudinal, around 30–40 µm long with a dark-yellow colour and flattened ends with large pores (photographs 59/60). Many decades ago it has been proposed to rename the taxon *Amphitrema flavum* to *Archerella flavum* (Loeblich and Tappan, 1961), but it took a long time before this name entered standard testate amoebae literature (e.g. Mazei and Tsyganov, 2006). Following the principle that the name of a palynomorph should not change when the name of the related taxon changes (Joosten and De Klerk, 2002), we

retain the name *AMPHITREMA FLAVUM*.

AMPHITREMA FLAVUM is predominantly known from wet *Sphagnum* habitats (Chardez, 1965; Payne et al., 2012), which implies that there is a strong dependency of the taxon to peat mosses, although this dependency has not yet been explained (see Avel-Niinemets et al., 2011). In surface sample 24 from the transect of the Kytalyk polygon Lhc11 where *Sphagnum* does not occur, the taxon was found in *Dicranum groenlandicum* and *D. acutifolium* vegetation (De Klerk et al., 2020), which indicates that it is in NE Siberia not restricted to peat moss. Furthermore, we found the morph predominantly in dry peatland settings in the surface transects (Figs. 6, 8, 10, 12) and peat profiles. In the surface samples of Lhc11 (Fig. 8), the type occurs with a high peak at the transition between a submerged polygon and its ridge. In the surface sample transect of Mnp12 (Fig. 10) the highest *AMPHITREMA FLAVUM* values occur on lower rim parts and - with somewhat lower values - on a minor degrading rim. The type was not found in the records from Samoylov Island, which may be a biogeographical feature.

Other palynological studies from NE Siberia hardly report *AMPHITREMA FLAVUM* tests. The type was found sporadically in Pliocene and early Pleistocene sediments of Lake El'gygytyn (Andreev et al., 2016).

3.3.3. *ASSULINA* types

ASSULINA MUSCORUM is ovoid, flattened and covered with oval, regularly arranged plates, and ranges between 28–60 µm length (Grospietsch, 1972; Charman et al., 2000; Clarke, 2003). Schönborn and Peschke (1990) introduced four types of *A. muscorum* based on the variety in shell width (photographs 60–64). *ASSULINA MUSCORUM* TYPE 1 has the largest width in the top third part of the shell, is narrow and has a small aperture. *ASSULINA MUSCORUM* TYPE 2 also has its maximum width in the top third part but is broad and has a broad aperture. The largest width of *ASSULINA MUSCORUM* TYPE 3 is in the centre, and the lower part of the test is narrower than the upper part. *ASSULINA MUSCORUM* TYPE 4 also has the maximum width in the shell centre, but the upper and lower parts are equally wide. The related species *Valkanovia elegans* produces tests similar to *ASSULINA MUSCORUM* TYPE 4, but with a somewhat different rim around the aperture (Schönborn and Peschke, 1990). If the occurrence of the different morphological types would be random, they would occur with rather similar values within populations. However, Schönborn and Peschke (1990) found also in monocultures of *A. muscorum* – where the species reproduced by cloning only – that the different morphotypes developed after some time. This implies that not genetics but environment regulates test morphology. Polymorphism has been frequently observed for many testate amoebae taxa in different ecological settings (Schönborn, 1992; Bobrov and Mazei, 2004; Mitchell et al., 2008; Smith et al., 2008) and the different morphotypes of *A. muscorum* may be sharp (palaeo)ecological indicators if the regulating factors would be known.

The hierarchical relationship between the various types attributable to *Assulina muscorum* as observed in the polygon mire studies is shown in Fig. 17. In the surface samples and peat profiles of Lc04 we counted all tests attributable to *A. muscorum* as a single type after Charman et al. (2000). In selected surface sample transects of polygons Lhc11 (Fig. 8) and Mnp12 (Fig. 10) as well as in peat profile Lhc11 J18.80 (Fig. 9D), we additionally estimated the proportion of the four types of Schönborn and Peschke (1990) and added an *ASSULINA MUSCORUM* ASYMMETRICAL for tests with the widest axis running more or less diagonally from the top third at one side to the middle of the opposite wall. Continuing studies showed that this five-type scheme is insufficient to cover the full morphological variety of *ASSULINA MUSCORUM* TYPE 4, of which - similar to *ASSULINA MUSCORUM* TYPE 1 and *ASSULINA MUSCORUM* TYPE 2 - broad and narrow varieties occur. Similarly, both narrow and broad specimens of the asymmetrical morphs were distinguished separately.

The specimens of Samoylov Island are conspicuously longer and darker with individual plates of the tests more difficult to observe (photographs 61/62) compared to those of the polygons further east (photographs 60, 63, 64). This cannot be a sample preparation artifact

since laboratory processing was identical in all samples.

Assulina muscorum occurs in dry peatland habitats (Charman et al., 2000; Prager et al., 2006; Payne et al., 2012). In the Siberian polygons, *ASSULINA MUSCORUM* occurs prominently on the polygon ridges and only sporadically in the depressions. Since *ASSULINA MUSCORUM* is ubiquitous with high values on all studied polygon ridges, it is one of the most valuable NPP types for the inference of dry phases in fossil peat profiles.

Light-coloured tests that probably represent *Assulina seminulum* were found extremely rarely in the ice-wedge polygons: the size is, however, much smaller than that of the European specimens. The rareness of these tests does not allow a comprehensive evaluation for the NE Siberian realm.

In other sites in NE Siberia, *ASSULINA MUSCORUM* was found in high amounts in numerous palynological surface samples from arctic and central Yakutia and regions further south (Müller, 2009; see Müller et al., 2010). Undifferentiated *ASSULINA* tests were found in Weichselian sediments of Mamontov Klyk (Schirmer et al., 2008) and date back to the Pliocene in Lake El'gygytyn (Andreev et al., 2014).

3.4. Other objects

3.4.1. *COPEPODA* UNDIFF., *COPEPODA* < 75 µm; *COPEPODA* > 75 µm

COPEPODA (HbV-28) spermatophores have lengths between 30–160 µm and widths between 10–50 µm. They originate from different *Copepoda* species, which all occur in (temporary) open water (Van Geel, 1978; Shumilovskikh et al., 2015).

Abramova et al. (2017) identified 36 *Copepoda* species in water pools on Samoylov Island and noted that these, together with Cladocera, are the dominant zooplankton taxa in the wet polygon depressions.

In the Samoylov surface samples (Fig. 12B) and in peat profile 83.5 (Fig. 13A) from that island, we made no size differentiation of *COPEPODA* and labelled the morph *COPEPODA* UNDIFF. The morph was not seen at all in profile 87.1 (Fig. 13B). In profile Sam 161.5 and the peat profiles of polygon complex Mnp12, an arbitrary distinction was made between *COPEPODA* < 75 µm and *COPEPODA* > 75 µm. The morphs occur in both wet and dry peatland settings, although the highest values are in wet habitats. Future research on *Copepoda* may reveal whether different sizes have a taxonomic or ecological significance.

Fossils attributed to *Copepoda* were reported for the Lake Billyakh sediments (Müller, 2009; see Müller et al., 2010) where they occur in low amounts.

3.4.2. cf. HbV-91

HbV-91 is described by Van Geel (1978) as globose, with lamellate walls, and consisting of very thin loosely arranged layers. HbV-1402 (Van Geel et al., 2010) is morphologically similar. Taxonomic affiliation and ecological indication value are still unknown.

The objects observed in the pollen samples from Samoylov Island (photographs 69/70) resemble these types but are not completely similar to the objects on the photographs of Van Geel (1978): morphological modifications by taphonomic processes, however, are well conceivable for such thin-walled objects. For that reason, we use the designation cf. HbV-91.

On Samoylov Island cf. HbV-91 occurs with very high values in various polygon depressions (Fig. 12B). In profiles Mnp12 AE7 (Fig. 11B) and AX29 (Fig. 11C), and Sam 161.5 (Fig. 13C), the type is numerous in interpreted wet phases but is also present in lower numbers in the adjacent interpreted dry peatland phases. The type also occurs sporadically in the Mnp12 AE3 (Fig. 11A) and Sam 83.5 (Fig. 13A) profiles. The type was not counted in the other records.

3.4.3. HbV-354 LARGE APERTURE, HbV-354 SLIT-LIKE APERTURE, HbV-354 WITHOUT APERTURE

HbV-354 consists, according to Van Geel et al., (1980/1981), of flattened microfossils that often have a fissure in the centre of one or both sides. The type is probably a moss spore.

HdV-354 was counted in the major part of the surface sample transect on Samoylov (except samples 70–91; Fig. 12A) and in the peat profiles of that island (Fig. 13A–C) and of Mnp12 (Fig. 11A–C). It was divided into three morphotypes depending on whether they have a large gaping opening, a slit-like aperture, or no aperture (HdV-354 LARGE APERTURE, HdV-354 SLIT-LIKE APERTURE, HdV-35 WITHOUT APERTURE, respectively). Morphs of the latter type, however, often have weak spots.

In the Samoylov surface sample transect the types occur in depressions as well as on rims (Fig. 12A). The types occur with high values in both interpreted dry and wet peatland phases in peat profiles Sam 83.5 and 87.1 (Fig. 13A/B). The three different morphs show distinctly different distribution patterns, which means that the morphological diversity is not random but relates to still unidentified taxonomic, taphonomic, or ecological factors. In the peat profiles of polygon complex Mnp12 and profile Sam 161.5 the morphs occur only sporadically.

Some not further differentiated specimens were reported for Lake Billyakh, in (sub)arctic surface samples as well as in some samples from Central Yakutia (Müller, 2009; Müller et al., 2010).

3.4.4. INAPERTURATE SCABRATISH GLOBES

INAPERTURATE scabratish GLOBES (photograph 74) are around 50–60 µm in diameter. The wall elements are not easy to determine but most resemble scabrae.

Along the surface sample transect of Samoylov Island, the type occurs with high peak values up to 400% in some of the less-wet polygon depressions, but also in low amounts on rims (Fig. 12B). The type was not found in profiles Sam 87.1 and Sam 161.5 but occurs sporadically in the peat profiles of polygon complex Mnp12 and in Sam 83.5. It was not counted in the samples of the other polygons.

3.4.5. cf. LARIX TYPE (m)

Although strictly a pollen type, a remark on LARIX TYPE pollen (photograph 75) is necessary. LARIX TYPE pollen is described by Moore et al. (1991) as inaperturate, psilate, usually circular but very often crumpled or split, and with a size exceeding 50 µm and mostly even exceeding 100 µm. Moore et al. (1991) remark explicitly that many fungal, animal, or algal objects may key-out as their LARIX TYPE. It is, thus, likely that during standard pollen analysis various non-pollen palynomorphs are counted as LARIX TYPE.

At first sight judging from photographs, we do not rule out that LARIX TYPE pollen and cocoons of various non-parasitic flatworms of the Rhabdocoela order are confused, i.e. HdV-29 and HdV-35 (Van Geel, 1972, 1978; note that in the latter paper HdV-29 was discarded because no discriminating morphological characteristics were seen), and HdV-353D (Van Geel et al., 1980/1981; see also López-Vila et al., 2014, who present a photograph of a NEORHABDOCOELA oocyte).

Since *Larix* is a major constituent of the regional vegetation in many parts of NE Siberia, inherently its pollen is deposited in all polygon settings. However, some samples have such high values, compared to other sites from the same polygons, that a local source is likely (Lhc11 J17.80, -J19.50, -J20.20, Mnp12 AE3, -AE7, -AX). In these cases, flatworm cocoons may have been encountered.

4. Concluding remarks

The NPPs in NE Siberian ice-wedge polygon mires are as diverse as in other parts of the world. The strategy of studying surface samples with a distance of 1 m allows the inference of short distance distribution patterns and, thus, a connection to microhabitats especially with respect to hydrology.

NE Siberia is situated far from the well-studied wetlands of Europe and the Americas, so that NPP types have been observed that have not yet been described morphologically and could not yet be identified. Nonetheless, various of these “unknown” NPPs appear to have a sharp indication value, making them valuable for reconstructing the developmental history of ice-wedge polygons without knowing their

taxonomic affiliation.

The various types attributable to algae and testate amoebae show a morphological diversity unknown from the NPP literature. Our approach of naming them with morphological designations rather than with numbers will facilitate their future identification and interpretation when knowledge on NPPs progresses.

As TILLETIA (BRYOPHYTOMYCETES) SPHAGNI (m) and AMPHITREMA FLAVUM illustrate, NPP types (and their species) in the Arctic may occur in other habitats than known from “classic” NPP-studies. This may reflect different conditional factors resulting in the same operational factor (cf. Grootjans et al., 1996), e.g. thawing permafrost on rims providing similar continuously wet and cool micro-habitats as wet hollows in temperate mires, different genetic varieties of the same species, but also totally different taxa with a similar morphology.

Our study presents the first systematic inventory of NPP types from ice-wedge polygons in NE Siberia and, thus, provides an addition to the NPP data from other regions.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Data availability

All descriptions and images are submitted to the NPP-ID (Shumilovskikh et al., 2022; <https://non-pollen-palynomorphs.uni-goettingen.de/index.html>) for open access. Complete raw palynological data of all investigated surface samples and peat profiles will be offered to an international palynological database after the relevant diagrams have been published in full in (palaeo)ecological journals.

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