NON-POLLEN PALYNOMORPHS CHARACTERISTIC FOR THE DYSTROPHIC STAGE OF HUMIC LAKES IN THE WIGRY NATIONAL PARK, NE POLAND

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Abstract

The numerous dystrophic (humic) lakes are a very important feature of Wigry National Park, NE Poland. As the most recent palaeoecological data indicate, at the beginning of its development (in the Late Glacial and Early and Middle Holocene) these water bodies functioned as harmonious lakes, and their transformation into dystrophic lakes and the stabilization of the trophic state took place at the beginning of the Subboreal. Palynological analysis of sediments from two such lakes (Lake Ślepe and Lake Suchar II), with special emphasis on non-pollen palynomorphs (NPPs), was aimed at a detailed biological characterization of dystrophic lakes during their long-lasting existence. The obtained results allowed for the designation of organisms characteristic for dystrophic lakes, of which representatives appeared with the decreasing pH of the water and the formation of *Sphagnum* peat around lakes. These organisms were divided into four groups: algae, fungi, testate amoebas, and animals. Their representatives appear in various developmental stages of dystrophic lakes.

Key words: NPPs, palaeoecological reconstruction, humic lake, pollen analysis, NE Poland

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INTRODUCTION

Dystrophic lakes are an important component of landscapes in numerous parts of the world, although optimum conditions for forming these lakes are most abundant in the northern regions with a cool, humid climate (Salonen *et al.*, 1983; Kankaala *et al.*, 2006). The numerous dystrophic lakes are a unique feature of the Wigry National Park, but in other regions of Poland they are relatively rare (Kraska *et al.*, 2001; Wilk-Woźniak *et al.*, 2012).

In the Wigry National Park area there are twenty-one dystrophic lakes. They are small, shallow water bodies without outflow. The water of this type of lakes is characterized by specific environmental conditions, such as a deficit in nutrients, higher amount of humic substances (it gives water a brown color), low pH, low level of oxygen and low concentration of calcium in the water and sediments (Kamiński at al. 2001; Górniak 1995). Humic acids in the water react with many microelements and chemical compounds necessary of life for plants and animals, tying them up and as a result make them unavailable in the water. All these factors cause the poor biodiversity and small phytoplankton biomass (Górniak *et al.*, 1999; Gąbka and Owsianny 2006).

Typical for dystrophic lakes is the occurrence of the floating mats with mire plants such as *Menyanthes trifoliata*, *Ledum palustre*, *Eriophorum vaginatum*, *Andromeda poli-* *folia*, *Drosera rotundifolia*, *Scheuchzeria palustris*, *Carex limosa, Carex rostrata, Sphagnum angustifolium*, *Sphagnum fallax* and *Sphagnum magellanicum*. The other characteristic feature of dystrophic lakes is that their catchment areas are covered by coniferous forests with a large proportion of spruce (Kamiński 2002).

Investigations of life in dystrophic lakes has been limited mainly to contemporary flora and fauna (Czeczuga 1995, Zawiska *et al.*, 2013). Also the degree of knowledge on the past changes in the trophic status of this type lakes is not satisfactory and seem a very interesting scientific problem. Until recently, dystrophic lakes were described as not changing during their development (Górniak 1996). The latest studies indicate that a transition from a typical humic state to another state and inversely to that process proves to have been likely in the past as appears from geochemical studies and analysis of macrofossil plant remains (Drzymulska and Zieliński 2013; Drzymulska *et al.*, 2013). The next step is to complement of these studies by research of postglacial succession of vegetation and other organisms existing in these lakes.

Accordingly, interdisciplinary palaeoecological research of several dystrophic lakes located within the Wigry National Park, which has been carried out for a few years in the Department of Botany at the University of Białystok, has an important role in studies of this type of lakes (Drzymulska 2012; Drzymulska and Kupryjanowicz 2012; Fiłoc and Ku-
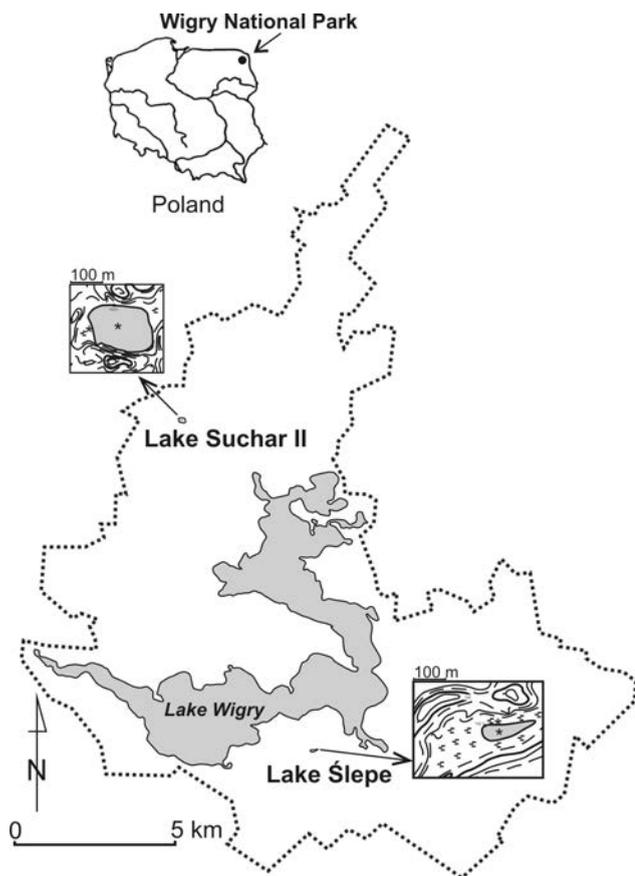
Fig. 1. Location of studied lakes. * – places of the corings.

Table 1

Radiocarbon dating of the analyzed sediments

Core	Depth [m]	Dated material	Age ^{14}C (BP)	Calibrated age (cal. years BP)	
				range 68.2%	range 95.4%
S_2	4.20	stems of mosses	9560±35	11070–10766	11090–10731
SII_1	2.95		3080±20	3346–3251	3360–3233
SII_2	6.94		1170±80	1180–983	1268–939
SII_2	8.53	sediment	4120±100	4820–4527	4865–4410
SII_2	12.17		10120±30	11916–11626	11987–11508

S_1 – profile from shore of Lake Ślepe, S_2 – profile from central part of Lake Ślepe, SII_1 – profile from shore of Lake Suchar II, SII_2 – profile from central part of Lake Suchar II.

pryjanowicz 2013a, b; Drzymulska *et al.*, 2014, 2015). The study includes a lot of aspects of the history of the examined lakes including changes in trophic state. A part of the project is a pollen analysis of sediments of Lake Ślepe and Lake Suchar II. Its main purpose is to identify organisms limited to dystrophic lakes. Particular emphasis is placed on the identification of non-pollen palynomorphs, which allows for a detailed reconstruction of the changes taking place in these water bodies during dystrophic state.

STUDY AREA

The humic Lake Ślepe (0.6 ha, 5.5 m max. depth, 54°00'35" N, 23°06'46" E) and Lake Suchar II (2.6 ha, 9.5 m

max. depth, 54°05'14" N, 23°01'03" E) are located in north-eastern Poland, in Wigry National Park (WNP), near the shore of Lake Wigry, the largest lake in the national park (Fig. 1). The surface of this area was shaped by the Vistula Glaciation, i.e. Weischelian (Marks 2002). WNP lies on the border two physical-geographical mesoregions, the East Suwałki Lakeland and the Augustów Upland, which are included to the Lithuanian Lakeland (Kondracki 1994). The climate of this area is temperate transitional with a tendency toward continental. It is most severe across the lowland parts of the country (Krzysztofiak and Olszewski 1999).

The investigated lakes are characterized by the zoning of vegetation with mire plants typical for humic lakes along the sublittoral to littoral. The last vegetation zone consists of marshy coniferous forest with *Pinus sylvestris*, *Picea abies* and *Betula pubescens* growing on a peat substratum on the margin of the lakes.

METHODS

Fieldworks

Four sediment cores were collected from the lakes selected for study. The cores from margin parts of lakes (S_1 and SII_1) were collected with a Russian corer (Belokopytov and Beresnevich 1955; Jowsey 1965; Aaby and Digerfeldt 1986) with a length of 50 cm and a diameter of 8 cm. The length of the cores was 4.38 m for Lake Ślepe and 7.00 m for Lake Suchar II. The drillings in central parts of lakes (S_2 and SII_2) were carried out using the Więckowski's probe (Więckowski 1989) with a length of 110 cm and a diameter of 5 cm. The length of the cores was 5.18 m for Lake Ślepe and 6.10 m for Lake Suchar II. It was necessary to supplement the collected profiles with top layers of highly liquefied sediments that could not be collected with a Więckowski's probe. The missing sediments from central part Lake Ślepe – 0.23 m were collected using the Kajak probe. The sediments from central part Lake Suchar II were not collected yet.

Age of sediments

The age of sediments from Lake Suchar Wielki was determined by AMS radiocarbon method in the Gliwice Radiocarbon Laboratory, Poznań Laboratory and Absolute Dating Laboratory in Skała (Tab. 1). OxCal 4.2.3 online software (Bronk Ramsey 2009) was used to calibrate the radiocarbon age of the samples.

Due to a small number of radiocarbon age determinations in the studied profiles, the chronology of events recorded in these profiles has been determined also indirectly, based on a similarity between pollen spectra with the radiometrically well-dated profile from the nearby Lake Wigry (Kupryjanowicz 2007) and it was published (Drzymulska *et al.*, 2014, Fiłoc *et al.*, 2014). The local pollen assemblage zones from the marginal and central parts of lakes were correlated in the earlier paper (Drzymulska *et al.*, 2014).

Pollen analysis

Samples for pollen analysis, 1 cm^3 in size were taken from cores every 2 cm. The preparation of the samples and

their microscopic analysis were carried out in accordance with the standard procedure (Berglund and Ralska-Jasiewiczowa 1986). Each sample was boiled with 5% KOH, and next treated by Erdtman's acetolysis method (Faegri and Iversen 1975). The material was then mounted in glycerine.

In each sample, at least 500 pollen grains of trees and shrubs (AP) and terrestrial herbs (NAP) were counted as well as all other accompanying palynomorphs. Pollen and spores were identified using several keys (e.g. Moore *et al.*, 1991; Beug 2004) and the reference collection of modern pollen slides from the Department of Botany, University of Białystok. The non-pollen palynomorphs (NPPs) were analysed using several keys (e.g. Van Geel 1978; Van Geel *et al.*, 1981; Komárek and Jankovská 2001; http://www.arcella.nl). The percentage value of each pollen and non-pollen taxon has been calculated in relation to the total sum of tree and shrub (AP), and herbaceous plant pollen (NAP). The results are presented as percentage pollen diagrams prepared with POLPAL 2004 ver. 2011 software (Walanus and Nalepka 1999; Nalepka and Walanus 2003). The diagrams were divided into special pollen assemblage zones (S PAZ) (Figs 2, 3) illustrating the changes in the local plant or other organism communities with the use of CONISS application (Grimm 1987).

RESULTS

The analyzed cores had been shortly described during the field works, and then completed after cleaning them in the laboratory (Tab. 2).

In the simplified pollen diagrams 2 special pollen assemblage zones based on changes in water and mire taxa (including NPPs) were distinguished for marginal part Lake Ślepe Lake (S$_1$ profile) and 4 for central part Lake Ślepe (S$_2$ profile) (Fig. 2) and 4 for marginal part Lake Suchar II (SII$_1$ profile) and 4 for central part Lake Suchar II (SII$_2$ profile) (Fig. 3). Their short characteristics are showed in Table 3.

Non-pollen palynomorphs (Fig. 4) had a very important role in determining the special pollen assemblage zones and subzones. These organisms were grouped into four major taxonomic groups (algae, fungi, testate amoeba, animals), which made it possible to trace the changes in trophic status of investigated lakes and development of *Sphagnum* peat.

CHANGES IN THE TROPHIC STATE OF STUDIED LAKES – INTERPRETATION AND DISCUSSION OF RESULTS

Drzymulska *et al.* (2015) proved that the transformation to the dystrophic state in Lake Suchar II took place at the beginning of the Subboreal. This transformation was made possible by the changes in the environment that occurred at this time, e.g. climate change to colder and drier. A decrease in average temperatures and an increase in the amount of precipitation led to the formation of pine forests with a large share of spruce in this region. As we know, the coniferous forests growing in the catchment area are a source of large quantities of humic substances (HS) flowing into the lake (Hagedorn *et al.*, 2000; Górniak and Zieliński 2000). Their significant supply was just one reason for the substantial shift in the trophic state of the lake studied, i.e. the shift to humo-

Table 2

Lithology of analyzed profiles

Depth [m]	Sediment description
Lake Ślepe – marginal part (S$_1$)	
0.00–0.99	*Sphagnum* peat
0.99–3.00	lack of sediment; there is water lens
3.00–4.00	sapropel
Lake Ślepe – central part (S$_2$)	
0.75–5.73	sapropel
Lake Suchar II – marginal part (SII$_1$)	
0.00–1.70	*Sphagnum* peat
1.70–1.90	lack of sediment; there is water lens
1.90–2.20	*Sphagnum* peat
2.20–2.30	lack of sediment; there is water lens
2.30–2.90	*Sphagnum* peat
2.90–4.30	*Sphagnum* peat with *Pinus*
4.40–5.00	sapropel
Lake Suchar II – central part (SII$_2$)	
6.50–12.20	sapropel

In profiles from central parts of lakes, depths are counted from the water surface

trophy (Drzymulska *et al.*, 2015). Based on the results for Lake Suchar II, we concluded that in Lake Ślepe the dystrophic state was also reached in the Subboreal. However, as our data show, in the older and middle part of the Subatlantic (S$_2$-III S PAZs – Fig. 2) this lake temporarily returned to mesotrophy, and then it was finally transformed to the humotrophic state in the younger part of the Subatlantic (S$_1$-I, S$_1$-II, S$_2$-IV S PAZs – Fig. 2). Transition into the state of dystrophy and the deepening of this state were accompanied by changes in various non-pollen palynomorphs in studied sediments.

During the dystrophy stage of both studied lakes, algae (mainly *Botryococcus*) were the group of organisms with the highest percentage share. *Botryococcus* is a genus that includes many species of algae characteristic for small dystrophic, oligotrophic or mezotrophic lakes, and some species are characteristic for eutrophic lakes and bogs (Jankovská and Komárek 2000). This taxon showed a high share, even in the marginal parts of the investigated lakes, where floating mats limited access to light. Another characteristic group of organisms for the dystrophic stage of the studied lakes is *Pediastrum angulosum* var. *angulosum* (Fig. 4A). This cosmopolitan alkaliphilous taxon is associated with eutrophic water bodies and metaphyton of the shallow and littoral parts of various types of lakes (Jankovská and Komárek 2000; Komárek and Jankovská 2001). Our research suggests that *Pediastrum angulosum* var. *angulosum* is the best adapted *Pediastrum* to low trophic conditions. This is confirmed by research on contemporary subarctic lakes in Finland (Weckström *et al.*, 2009), which are also surrounded by spruce-pine forests. Similarly, the study carried out on present-day lakes in Poland indicate that this taxon occurs in lowland lakes with lower trophic status (Lenarczyk 2014).

Fungi such as *Tillietia sphagni*, *Entoplyctis lobata*, *Helicoon pluriseptatum* (Fig. 4B) and the other unidentified taxa, characteristic for mire communities, are the next discussed group of organisms. *Tillietia sphagni* (Fig. 4C) is a parasite

Characteristics of the special pollen assemblage zones (S PAZs) illustrating changes in the local plants or other organism distinguished in analyzed profiles

Number	Depth [m]	Description
Lake Ślepe – marginal part (S₁)		
S₁-I	0.99–0.60	Maximum of Cyperaceae (4.7%); continuous curve of *Equisetum*, *Entoplyctis lobata*, *Assulina muscorum/seminulum*, *Centropyxis*, *Hyalosphenia papilio*, *Helicoon pluriseptatum*, *Tillietia sphagni* and fungal remains; high values of *Sphagnum* (17.5%); fall of *Botryococcus* (5–35.5%).
S₁-II	0.40–0.05	Maxima of *Sphagnum* (32.5%), *Entoplyctis lobata* (10%), *Helicoon pluriseptatum* (4.8%), *Tillietia sphagni* (2.6%), *Assulina muscorum/seminulum* (1.7%) and fungal remains (31.5%).
Lake Ślepe – central part (S₂)		
S₂-I	3.50–3.10	Proportion of *Botryococcus* between 2 and 20.5%; values of Filicales monolete and Turbellaria very low (to 0.6% and 1%, respectively).
S₂-II	3.14–2.70	Relatively low values of *Botryococcus* with peak of 38%.
S₂-III	2.60–1.20	Maximum of *Botryococcus* (6–69%).
S₂-IV	1.10–0.75	Increase of *Sphagnum* to 4.2%; high values of Cyperaceae with maximum 1.3%; fall of *Botryococcus* (3–46.5%).
Lake Suchar II – marginal part (SII₁)		
SII₁-I	5.00–3.70	Maximum of *Botryococcus* (20%); beginning of continuous curve of Cyperaceae; culmination of *Pediastrum angulosum* var. *angulosum* with maximum 0.5%; low values of *Amphitrema flavum* (0.5%).
SII₁-II	3.60–3.20	Decrease of *Botryococcus* (3–0.6%); continuous curve of Filicales monolete (0.1–0.2%); maximum of *Scheuchzueria palustris* (2.7%); low values of *Sphagnum* (0.1–0.9%).
SII₁-III	3.10–1.35	Maxima of Cyperaceae (5.5%), *Amphitrema flavum* (43%) and *Assulina muscorum/seminulum* (8.0%); rises of *Sphagnum* to 14%.
SII₁-IV	1.20–0.00	Maxima of *Sphagnum* (25.5%), *Tillietia sphagni* (12%), *Entoplyctis lobata* (4%) and *Hyalosphenia subflava* (6.5%). The zone was divided into tree subzones:
SII₁-IVa	1.20–0.80	values of *Assulina muscorum/seminulum* higher than other subzones;
SII₁-IVb	0.70–0.40	peak of *Botryococcus* and depression of Sphagnum;
SII₁-IVc	0.30–0.00	depression of Cyperaceae.
Lake Suchar II – central part (SII₂)		
SII₂-I	9.80–9.40	Maximum of *Botryococcus* (24%); continuous curve of Cyperaceae; decrease of Bryales (0–2.5%) and Filicales monolete (1–4%); high values of *Pediastrum angulosum* var. *angulosum* (to 4.5%).
SII₂-II	9.30–8.70	Maxima of *Sphagnum* (1.7%) and *Pediastrum* (5.5%); high values of *Pediastrum angulosum* var. *angulosum* with maximum 4.5%; proportion of *Botryococcus* between 2 and 21%. The zone was divided into two subzones:
SII₂-IIa	9.30–8.88	values of *Botryococcus* very higher than upper subzone;
SII₂-IIb	8.88–8.70	depressions of *Botryococcus* and Filicales monolete; high peak of *Sphagnum*.
SII₂-III	8.66–7.34	High values of *Botryococcus* (2.3–22.5%); fall of Filicales monolete; culmination of *Pediastrum angulosum* var. *angulosum* in the top part of the zone.
SII₂-IV	7.30–6.65	Relatively low values of *Botryococcus* (1–4%); culmination of Cyperaceae with maximum 1.5%.

of various species of *Sphagnum* (Dickson 1973; Van Geel 1978), whose spores are represented in large numbers in the sediments from the shores of both examined lakes. In the case of Lake Suchar II, the *Sphagnum* genus was represented by *S. magellanicum* and *S. fallax* (Drzymulska *et al.*, 2015). *Entoplyctis lobata* (Fig. 4E) occurs commonly on *Oxycoccus palustris*, *Polytrichum* sp., *Erica tetralix* and other Ericaceae growing on the shores of dystrophic lakes (Van Geel 1978). These fungi were also found inside the cells of the aquatic leaves of *Sphagnum imbricatum* (Van Geel 1978), which forms spreading floating mats. Based on the results obtained from both lakes (Fig. 2 and 3), it can be concluded that *Entoplyctis lobata* frequently appears in the final stage of the formation of the floating mats, when the proportion of the *Sphagnum* is very high. Other remains of fungi identified as Type 96A/B (Fig. 4F) were found on living leaves of *Oxycoccus palustris* (Van Geel 1978), similar to the previous. They can be represented by the fungal remains of one or more species of the dark-coloured genera *Beltrania, Beltraniopsis, Beltraniella, Ellisiopsis, Pseudobeltrania* and *Hemibeltra-*

nia (Ellis 1971). On the diagram from the shore of Lake Suchar II Type 96A/B has not been counted yet, although it was present in all samples between 0 and 300 cm SII₁. The presence of *Helicoon pluriseptatum* conidia may be due to the intense inflow from the catchment area (Van Geel 1978). This fungus was found growing on decaying leaves of birch and needles of pine and spruce (Van Beverwijk 1954), and the occurrence of its remains in sediments is usually linked to an increase in the share of *Pinus* and *Picea* pollen (Yeloff *et al.*, 2007). Moreover, in the shore sediments of both studied lakes, especially in Lake Suchar II, the high share of pine and spruce pollen correlates very well with the occurrence of *Helicoon pluriseptatum* conidia (Drzymulska *et al.*, 2015). This fungus was also recently recorded in another dystrophic lake in Wigry National Park (Czeczuga 1995).

Testate amoeba like *Amphitrema flavum* (Fig. 4L)*, Assulina muscorum/seminulum* (Fig. 4G, 4H), *Centropyxis*, *Hyalosphenia subflava* (Fig. 4J), *Hyalosphenia papilio* (Fig. 4K), *Arcella*, *Nebela* (Fig. 4N), *Heleopera* (Fig. 4M), and *Difflugia* are connected with different species of *Sphagnum*.
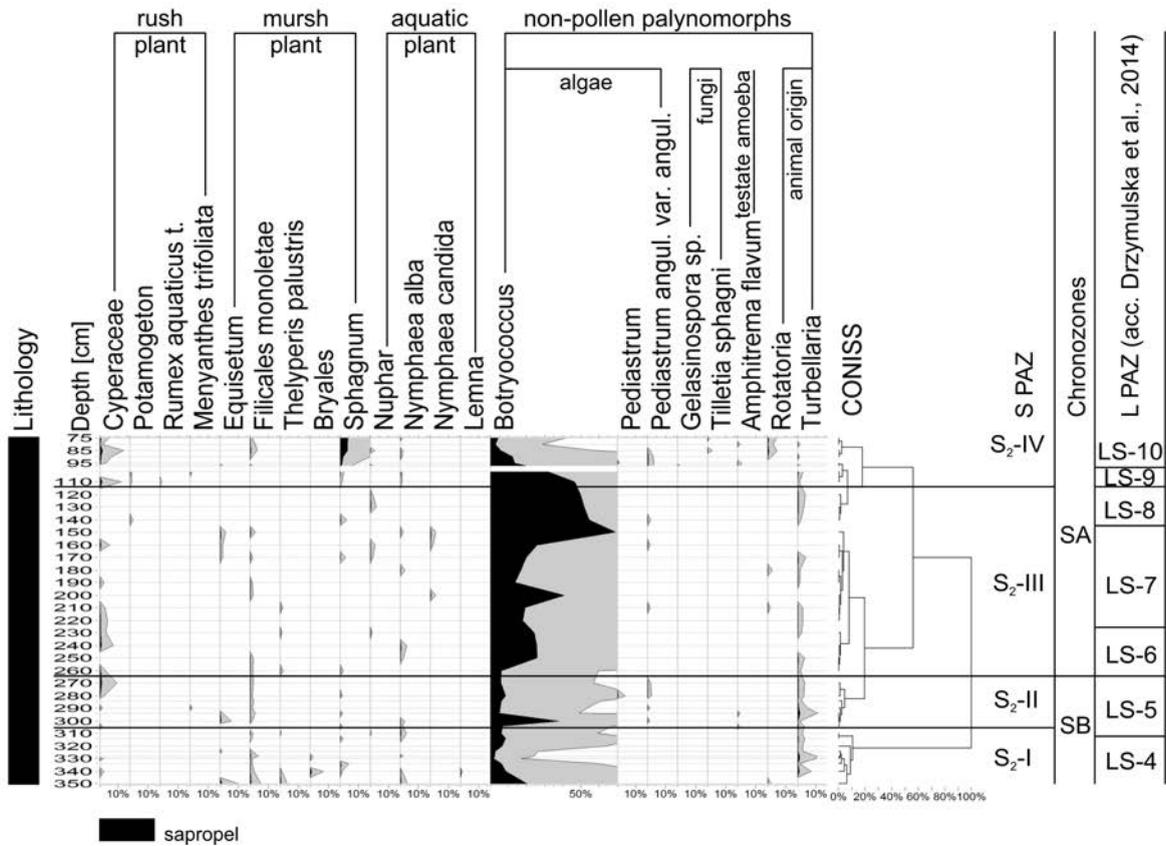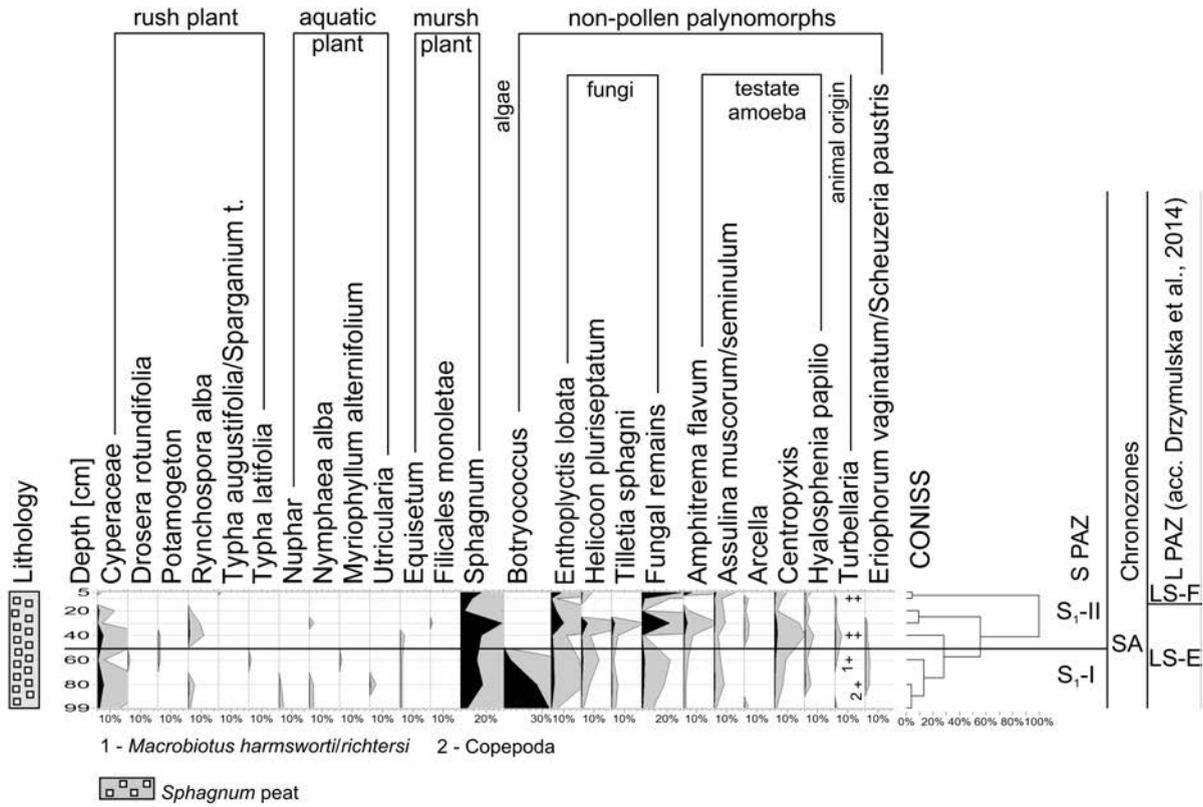
Fig. 2. Lake Suchar II. Simplified pollen diagrams illustrating changes of the local plants and other organisms.
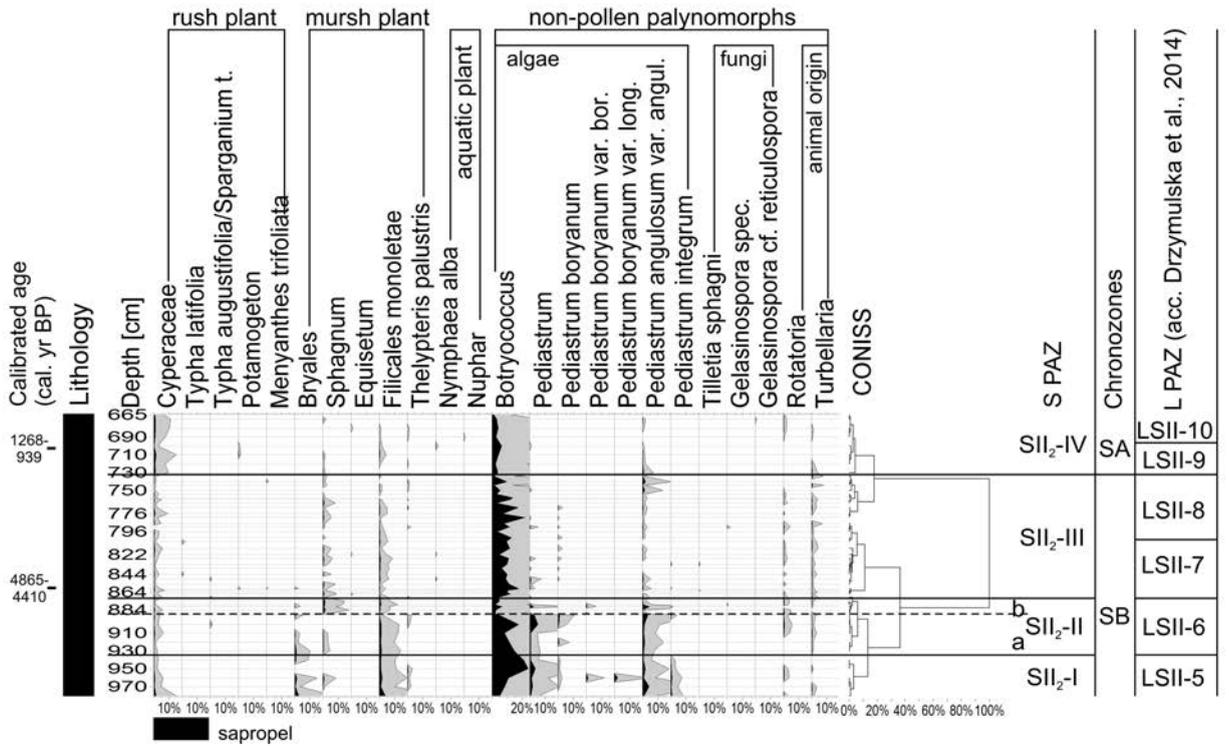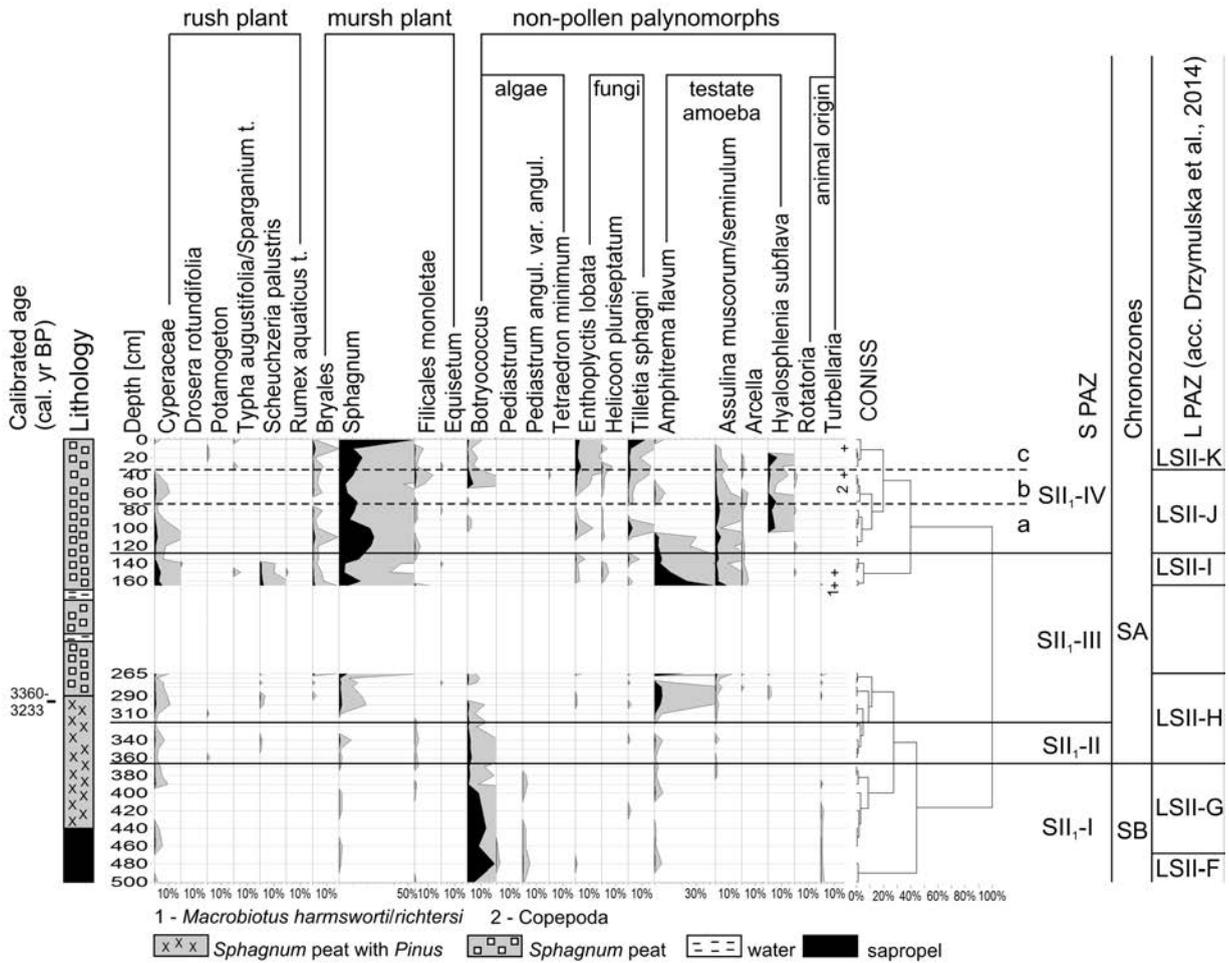
Fig. 3.   Lake Ślepe. Simplified pollen diagrams illustrating changes of the local plants and other organisms.

The shell-forming *Arcella* occurred commonly in bryophyte peat, particularly among peat mosses (Hoogenraad and Groot 1979; Chardez and Beyens 1987), for example, *S. fuscum* (Van Geel *et al.*, 1981) or *S. fallax* (Lamentowicz *et al.*, 2007a). There are many different species of this genus, and they are difficult to differentiate in the subfossil material. Most likely, at least one of the species of this genus was *A. artocrea* (Fig. 4Ł), as evidenced by its size, 188–211 μm, and appearance (http://www.arcella.nl). *Arcella* and *Centropyxis* are the most common testate amoebae among epiphytic bryophytes (Glime 2013). At least one of the species of *Centropyxis* was of the *Centropyxis aculeata* type (Fig. 4I), which appeared on the *Sphagnum* mat dominated by *S. fallax*, and preferred higher ground water levels (Lamentowicz *et al.*, 2007a). Some species of *Centropyxis* are associated with high pH, e.g. *Centropyxis aculeata*, *C. hirsuta*, *C. aerophila* and *C. ecornis*, but *Centropyxis aculeata* has a wide range of tolerance for environmental conditions (Lamentowicz *et al.*, 2005). *Arcella artocrea* and *Centropyxis aculeata* type were found in Lake Ślepe and Lake Suchar II, for example, on *S. fallax* (Drzymulska *et al.*, 2015, and unpublished data). *Hyalosphenia subflava* (Fig. 4J) is supposed to give an indication of serious disturbances in peat growth (Van Geel 1978), and prefers relatively dry conditions compared to other species (Booth 2001). In our research this taxon was found only in Lake Suchar II after a longer period of formation of the floating mats. In high humidity, *Hyalosphenia papilio* (Fig. 4K) is one of the most numerous species of peat bog (Lamentowicz *et al.*, 2007a, Glime 2013), and is associated with acid habitats (Lamentowicz *et al.*, 2007a). *H. papilio* was present only in Lake Ślepe. *Assulina muscorum/seminulum* are closely related to *Sphagnum* (Van Geel 1978). *Assulina muscorum* appears in spring, and *A. seminulum* in summer (Glime 2013). These oligotraphentous thecamoeba are an additional indicator of low nutrient content, such as in the drier poor fens (Van Geel *et al.*, 1989). *Assulina muscorum/seminulum* inhabit both communities described by Mazei and Tsyganov (2007/08) in the *Sphagnum* peatlands of Russia: bottom sediments of the drainage and the *Sphagnum* quagmire (acc. Glime 2013). The results from Lake Suchar II (Fig. 3) confirmed that the early stages of *Sphagnum* peatlands were characterized by widespread species such as *Assulina muscorum* and *Arcella arenaria*, whereas the sphagnobionts, such as *Hyalosphenia*, were absent (Mazei and Bubnova 2007; Glime 2013). Another amoeba species, *Amphitrema flavum*, is characteristic for young *Sphagnum* peat, for example, *Sphagnum* cf. *rubellum* peat formed in the Subatlantic (Van Geel 1978). This amoeba is an indicator of a low-nutrient substratum (Van Geel *et al.*, 1989) and wet conditions (Schnitchen *et al.*, 2003). In our study this species reaches its maximum occurrence in the early phase development of *Sphagnum* peat, when the water level increases, as also demonstrated by a study on Jelenia Wyspa mire (Lamentowicz *et al.*, 2007b). Low pH is a characteristic feature of dystrophic lakes, and in our investigations such conditions were indicated by acidophilic taxa such as *Arcella artocrea*, *Assulina muscorum*, *Amphitrema flavum* and *Hyalosphenia* sp.. This is consistent with other studies (Lamentowicz and Mitchell 2005; Glime 2013). It has to be pointed out, however, that genera of amoeba such as

Arcella, *Assulina*, *Amphitrema* and *Hyalosphenia* are dominant for peatland communities. *Amphitrema flavum*, *Assulina muscorum*, *Assulina seminulum* and *Hyalosphenia papilio* are associated with the upper parts of *Sphagnum* specimens, as described by Mazei and Tsyganov (2007/08). This is indicated by other studies in Poland on peatlands at different stages of succession, where the dominant species were *Amphitrema flavum*, *Assulina muscorum*, *Arcella discoides* type, and *Hyalosphenia papilio*, which together represented around 60% of the total community count (Lamentowicz and Mitchell 2005). Singly, in the analyzed marginal profiles (S_1 and SII_1), *Nebela* (Fig. 4N), *Heleopera* (Fig. 4M) and *Difflugia* occurred. These taxa are characteristic for *Sphagnum*-dominated peatlands (Lamentowicz and Mitchell 2005). However, their designation only to the genus does not give enough information.

Microremains, such as eggs and lorica of Rotatoria, cocoons of Turbellaria, spermatophore of Copepoda, and eggs of Tardigrada were non-pollen pallynomorphs of animal origin. The remains of Turbellaria were more numerous in sediments from the central parts of the studied lakes than in sediments from the marginal parts. Eggs of the rotifer *Fillinia*, recognized only to the genus, do not provide relevant information. Lorica of the rotifer *Habrotrocha angusticollis* (Fig. 4R) occurred frequently in the sediments of the marginal parts of the investigated lakes (not included in the diagrams). They are associated with mosses in *Sphagnum* bogs, marshes, and with floating mats and another emergent vegetation along the shores of lakes and ponds throughout the world (Murray 1906; Bartos 1951; Haigh 1963; Chengalath and Koste 1983; Francez 1986; Koste and Shiel 1986; Warner and Chengalath 1988, Lamentowicz *et al.*, 2007b). The results of our study also indicate that this rotifer is most characteristic for *Sphagnum* habitats. Also spermatophores of Copepoda appeared in *Sphagnum* peat from the studied profiles (Fig. 4O). These remains probably represent different species (Van Geel 1978). Present-day copepods have been found, among other places, in the waterlogged moss layer on peatlands (Rybak and Błędzki 2005). The results of our research suggest that they are sphagnobionts, and appear in the late-stage of development of *Sphagnum* bogs. *Macrobiotus harmsworti/richtersi* (Fig. 4P), classified by Jankovská (1991) (acc. Montoya *et al.*, 2010), appeared only in a few samples. Eggs of this Tardigrada have been found in moss and foliose lichen (Mayer 2013).

SUMMARY AND CONCLUSIONS

The transformation of both studied lakes, Lake Ślepe and Lake Suchar II, into a dystrophic state at the beginning of the Subboreal resulted in the appearance of organisms typical for water with low pH and poor access to light. During this stage, *Sphagnum* peat started to accumulate in the marginal parts of the lakes. This has given rise to the formation of numerous moss communities forming floating mats, which create a habitat for many new organisms.

In the first stage of dystrophy, before the development of *Sphagnum* bog, mainly algae (*Botryococcus* and *Pediastrum angulosum* var. *angulosum*) and some Rotatoria and Turbellaria were observed.
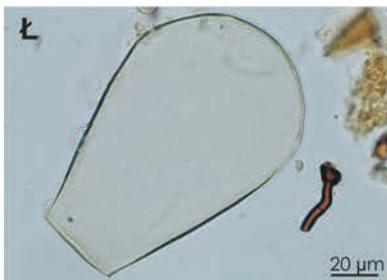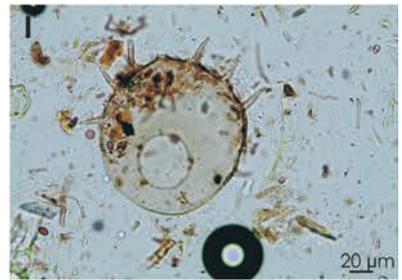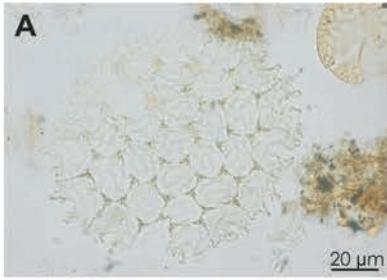
The second stage begins with an increase in the share of *Sphagnum*. Where the *Sphagnum* peat was formed, the share and diversity of non-pollen palynomorphs in the marginal parts of both investigated lakes become higher than in their central parts. In the early part of the stage, *Sphagnum* bogs were characterized by the spread of testate amoeba species such as *Amphitrema flavum*, *Assulina muscorum* and *Arcella arenaria*, whereas the sphagnobionts were absent. In a later part of these stage, organisms associated with *Sphagnum* floating mat, such as species of testate amoeba: *Assulina seminulum*, *Hyalosphenia subflava, Hyalosphenia papilio, Arcella*, *Nebela*, *Heleopera*, *Difflugia*, single representatives of Rotatoria: *Habrotrocha angusticollis*, and Tardigrada: *Macrobiotus harmsworti/richtersi*, some Copepoda and *Tillietia sphagni*, a parasite fungus of *Sphagnum* appeared. At this time, on floating mats different mire plants and the *Entoplyctis lobata* fungi associated with them also existed. The presence of *Helicoon pluriseptatum* conidia in the analyzed sediments suggests an intensification of inflow from the catchment area, where, since the beginning of the Subboreal, the share of coniferous trees has increased, and this fungus was found on the needles of pine and spruce.

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Fig. 4. The selected taxa of non-pollen palynomorphs (NPPs) registered in profiles from Lake Ślepe and Lake Suchar II: A – *Pediastrum angulosum* var. *angulosum* (SII₂ – 8.80 m); B – *Helicoon pluriseptatum* (S₁ – 0.40 m); C – *Tilletia sphagni* (S₁ – 0.30 m); D – *Entoplyctis lobata* (S₁ – 1.00 m); E – *Entoplyctis lobata* (SII₁ – 0.10 m); F – unidentified fungi characteristic for mire communities (Type 96A/B), (S₁ – 0.20 m); G – *Assulina muscorum* (S₁ – 0.20 m); H – *Assulina seminulum* (S₁ – 0.10 m); I – *Centropyxis aculeate* type (S₁ – 0.30 m); J – *Hyalosphenia subflava* (SII₁ – 1.50 m); K – *Hyalosphenia papilio* (S₁ – 0.60 m); L – *Amphitrema flavum* (SII₁ – 1.60 m); Ł – *Arcella artocrea* (S₁ – 0.99 m); M – *Heleoptera* (S₁ – 0.05 m); N – *Nebela* (S₁ – 0.10 m); O – spermatopore of Copepoda (S₁ – 0.10 m); P – eggs of *Macrobiotus harmsworti/richtersi* (S₁ – 0.60 m); R – lorica of *Habrotrocha angusticollis* (SII₁ – 0.40 m).

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