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LATE PLEISTOCENE VEGETATION HISTORY AND CLIMATIC CHANGES AT HOROSZKI DUŻE EASTERN POLAND: A PALAEOBOTANICAL STUDY

Wojciech GRANOSZEWSKI

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EDITORIAL OFFICE
W. Szafer Institute of Botany, Polish Academy of Sciences,
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Late Pleistocene vegetation history and climatic changes at Horoszki Duże, eastern Poland: a palaeobotanical study

WOJCIECH GRANOSZEWSKI

W. Szafer Institute of Botany, Polish Academy of Sciences, Lubicz 46, 31-512 Kraków, Poland;
e-mail: wgranoszewski@pigok.com.pl

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ABSTRACT. In the present study, 197 samples from one core were examined by pollen analysis, and 157 for plant macroscopic remains; and lithological analyses (loss on ignition and grain size distribution) of the sediment were carried out. 408 plant taxa of various levels were determined. The results of the palaeobotanical analysis are presented graphically in diagrams and in a floristic list. As presented in the Table 5 thirty-nine biostratigraphic units (HD-1 – HD-39) were distinguished at the level of local pollen assemblage zones (L PAZ) and on the basis of this it was determined that the sediment sequence from Horoszki Duże spans the closing phase of the late Wartanian (Saalian) Glacial, the Eemian interglacial, the Early Vistulian (Weichselian) and a part of the Plenivistulian (Middle Weichselian). The vegetation history and climatic changes as reflected in sections of this part of the Pleistocene in the region of Horoszki are presented on the basis of these data.

KEY WORDS: pollen analysis, plant macrofossils, palaeoclimate, steppe-tundra, vegetation history, Eemian interglacial, Brörup interstadial, Odderade interstadial, Vistulian (Weichselian), Pleistocene

CONTENTS

INTRODUCTION

The North European plain is rich in fossil lakes with sediments deposited during various stages of the Pleistocene, i.e. interglacials, interstadials and glacials. This makes the area especially suitable for palaeoecological studies.

In the palaeoecological literature of the last

10–20 years, there has been an increased interest among researchers studying the last interglacial-glacial cycle, spanning the Eemian interglacial and the subsequent Vistulian Glaciation including stadial and interstadial phases.

This interest is not only the result of efforts to solve problems of historical plant geography and to clarify climate changes and vegetation history during the Late Pleistocene, but also the need to compare the Eemian with the present interglacial, i.e. the Holocene. The similarity in plant succession of these two stages of the Quaternary makes it possible to predict future changes in vegetation and climate during the Holocene, and their potential disruption associated with the accelerating human impact on the global ecosystem.

In this context, most attention is paid to sediment sequences with long and more or less complete stratigraphical records of palaeoenvironmental changes spanning the last interglacial-glacial cycle. These sequences make it possible to separate not only changes within the Eemian interglacial but also around the interglacial-glacial boundary and during the Vistulian glaciation including interstadial and stadial phases. If the above presumptions are to be fulfilled, the investigation of such sections should be multidisciplinary in order to receive the most complete data.

The core of studied lake sediments from Horoszki Duże in Podlasie (Fig. 1) largely seems to fulfil the above conditions.

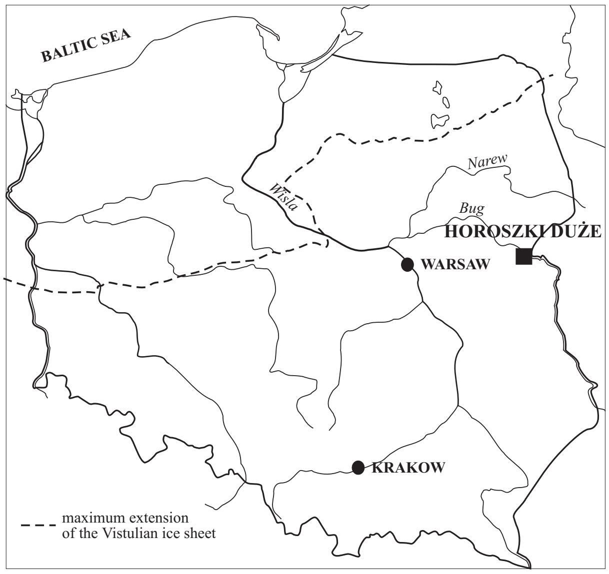

Fig. 1. Localization of the site studied

PREVIOUS PALAEOBOTANICAL RESEARCH AT HOROSZKI DUŻE

The first palaeobotanical study of lake sediments from Horoszki Duże was carried out by Bitner (1954), who examined 35 samples by pollen analysis. In the pollen diagram only 22 spectra are presented due to very low frequency of sporomorphs in the lowermost sediments and in top most 9 metres of silts. Today we know that it was not possible to extract enough pollen from these sediments using the maceration method of the time (Bitner having used only 10% KOH, and, in carbonate sediments, also HCL). The spectra shown were calculated on a basic sum of 200 grains AP. The following pollen taxa were identified: *Pinus*, *Betula*, *Salix*, *Corylus*, *Ulmus*, *Tilia cordata*, *T. platyphyllos*, *Quercus*, *Alnus*, *Carpinus*, *Picea*, *Abies*, Gramineae, Ericaceae, and spores of *Sphagnum* and Filicinae. *Salix* and *Artemisia* were given as one curve. Due to the fragmentary nature of the core, no analysis was made of macroscopic plant remains.

On the basis of the palynological results, Bitner (op. cit.) correlated the lower part of the sediments studied to the Masovien II, or the Eemian interglacial. He drew the attention to the uppermost ca 13 m of the profile above the interglacial layer represented the Vistulian Glaciation.

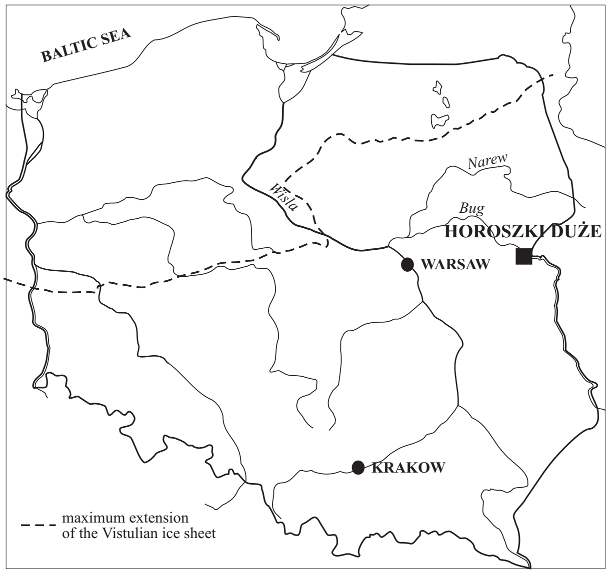

Fig. 2. Detailed map of the studied area

Andersen (1961) was the first one to draw the attention to two maxima of non arboreal (NAP) pollen which appear in Bitner's diagram above the Eemian part, separated by high AP values. He suggested a correlation with the Early Vistulian, i.e. Amersfoort and Brörup interstadials. Mamakowa (1989), recalculated Bitner's data and obtained a new version of the pollen diagram containing two Early Vistulian interstadials, i.e. Brörup including the part that been correlated by Andersen (1961) with Amersfoort in the Netherlands and Odderade. Mamakowa (op. cit.) also emphasized that it was essential to investigate the 9 m thick layer fine-grained sediments overlaying the Eemian-Early Vistulian part, and which had not been earlier studied.

SITE DESCRIPTION

The palaeolake in which drilling was carried out lies some 600 m west of the road from Janów Podlaski to Sarnaki, at the height of the village of Horoszki Duże in eastern Poland (Figs 1, 2). According to the physical-geographical division of Kondracki (1994), this region belongs to the mesoregion of the Podlasie Gorge of the Bug river (Podlaski Przełom Bugu), which spans the part of the Bug river valley between Polesie and the central Masovian Plain (Nizina Środkowomazowiecka). The ravined section of the Bug valley is the result of erosion of areas between Serpelice and Mielnik, which are constantly being elevated as a result of neotectonic movements (Nitychoruk 1995). This author assumes that the foundations of this section of the Bug valley derive from the period of the disappearance of the last ice sheet, and through the similarity of the geomorphological situation of the sediments at Horoszki to other sites in the Czyżówka valley the possibility that deposits occur representing one of the older interglacials is suggested.

The site is located in the elongated flat hollow in the source section of the Czyżówka river. The lake basin is today used as a meadow and the drilling site was determined on the basis of materials by Rühle and Zwierz (1961), who made a geological transect of the Bug river with ravines, near Mielnik. The stratigraphy unequivocally place the fine-grained sediments from Horoszki Duże in the stratigraphic position of the Eemian interglacial.

CORING AND SEDIMENT DESCRIPTION

The coring was carried out by double coring using a geological drill with a diameter of 11.2 cm and 13.2 cm. The sequence drilled was 24 metres long. The core obtained was placed in PVC tubes, wrapped in plastic foil and transported to the cold room of W. Szafer Institute of Botany, Polish Academy of Sciences in Kraków, where samples for pollen and macrofossil analyses were taken.

The bottom part of the lake sediments contains sand with gravel and pebbles, (up to 7 cm in diameter – till?) overlain by a series of sand and silty layers. From a depth of about 16 metres below surface there are biogenic sediments – calcareous gyttja, bituminous shales, peat, and silt (Tab. 1). This series is covered by ca. one metre of sand.

The lithology is described using the method of Troels-Smith (1955), and Wasylikowa (1973). It was only carried out for the section of the profile which had been studied palaeobotanically, and given in Table 1. The sediment colour was determined using Munsell Soil Color Charts (1954).

The organic matter content in the sediment was determined as the loss on ignition at +550°C for 2 hours. The $CaCO_3$ content was obtained by ignition of the residual material at +925°C for 4 hours (Bengtsson & Enel 1986).

Granulometric analysis of the sediment was made using the Fritsch Analysette 22 model of laser. Four grain size categories have been distinguished i.e. (in mm): 0.1–0.06, 0.06–0.02, 0.02–0.004, and below 0.0004. The results of the analysis are presented in Fig. 3.

MATERIAL AND METHODS

POLLEN ANALYSIS

Over 400 samples for pollen analysis, were taken from the core at 5 cm intervals or more frequently where needed, for instance around sediment boundaries. The samples were taken using a sampler $1cm^3$ in volume, and kept in a refrigerator. In order to establish the absolute concentration of sporomorphs in the sediment, two *Lycopodium* indicator tablets were

Table 1. Description of sediment according to Troels-Smith (1955)

Depth in m	Lithology / Sediment description
1.05 – 2.39	**peaty silt with clay and sand, dark olive grey;** Ag3, As0.5, Th/Tb0.5, Ga+ [Gg$_{(maj)}$+]; struc.: homogeneous, with plant detritus; nigr.2+, strf.0, elas.0, sicc.2, lim.sup.0
2.39 – 2.50	**peaty silt slightly clayey with sand and gravels, black;** Ag2.5, As0.5, Th0.5, Tb0.5, Sh+, Ga+, [Gg$_{(maj)}$+]; struc.: homogeneous, with fine plant detritus and grevel up to 3 cm; nig.2+, strf.0, elas 0, sicc.2, lim.sup.0
2.50 – 3.17	**peaty silt slightly clayey with sand, very dark grey;** Ag2.5, As0.5, Th0.5, Tb0.5, Sh+, Dg+, Ga+; struc.: homogeneous, with fine plant detritus; nig.2+, strf.0, elas.0, sicc.2, lim.sup.0,,
3.17 – 3.92	**silt slightly clayey with sand, very dark grey;** Ag3, As0.5, Sh0.5, Th/Tb+, Dg+, Ga+; struc.: homogeneous, plant detritus in some places; nig.2+, strf.0, elas.0, sicc.2, lim.sup.0
3.92 – 5.10	**silty gyttja, slightly clayey with traces of sand, olive grey;** Ag2.5, As0.5, Ld1, Sh+, Ga+; struc.: homogeneous, vivianite, more sandy at the top; nig.2, strf.0, elas.0, sicc.2, lim.sup.0
5.10 – 5.80	**silt slightly clayey with traces of sand, olive gray;** Ag3.5, As0.5, Ga+, Ld+; struc.: very homogeneous, mica.; nig.2+, strf.0, elas.0, sicc.2, lim.sup.0
5.80 – 6.89	**silt slightly clayey with traces of sand and gravel at the bottom, dark olive gray;** Ag3.5, As0.5, Sh+, Ga+ [Gg$_{(maj)}$+ at the very bottom, a pebble 5cm); struc.: homogeneous, with mica; nig.2+, strf.0, elas.0, sicc.2, lim.sup.0
6.89 – 7.70	**gyttja silty – sandy, very dark greyish brown;** Ld^{0}2, Ag/As2, Dg+ Ga+++; struc.: heterogenous, mica,, nig.2+, strf.0, elas.0, sicc.2, lim.sup.?
7.70 – 8.70	**organic silt, slightly clayey with traces of sand, black;** Ag3, As0.5, Sh0.5, Th+, Tb+, Ga+; struc.: very homogeneous, mica; nig.3, strf.0, elas.0, sicc.2, lim.sup.0
8.70 – 9.10	**organic silt with traces of sand, black;** Ag2.5, As0.5, Th/Tb0.5, Sh0.5, Ga+; struc.: very homogeneous; nig.3, strf.0, elas.0, sicc.2, lim.sup.0
9.10 – 9.50	**peat with traces of sand, black;** Th^{3}1, Tb^{3}1, Dg1, Sh1, Ga+; struc.: homogeneous, fine detritus visible, mica; nig.3, strf.0/3, elas.0, sicc.2, lim.sup.0
9.50 – 9.60	**substantia humosa with small admixture of gyttja and traces of sand, black;** Sh2, Ag/As1, Ld0.5, Th0.5, Tb+, Ga+; struc.: homogeneous, when dry peels, fine detritus, mica; nig.3, strf.0/3, elas.0, sicc.2, lim.sup.0
9.60 – 9.66	**clayey gyttja, silt with traces of sand and gravel, very dark grey;** Ag2.5, As0.5, Gg$_{(min)}$0.5, Ld^{0}0.5, Th/Tb+, Ga+; struc.: heterogeneous, gravel, mica; nig.2+, strf.0, elas.0, sicc.2, lim.sup.1
9.66 – 10.40	**clayey gyttja silt with traces of sand, very dark grey;** Ag3, As0.5, Ld^{0}0.5, Tb/Th+, Ga+; struc.: homogeneous, mica, heated with NaOH yellow; nig.2+, strf.0, elas.0, sicc.0, lim.sup.0
10.40 – 10.80	**silty peat with traces of sand, black;** Th^{2}1, Tb^{2}1, Dg0.5, Ag1,5, Ga+; struc.: homogeneous (vey fine detrituosus); nig.3+, strf.0, elas.0, sicc.0, lim.sup.0
10.80 – 11.40	**slightly silty peat, black;** Th^{1}2, Tb1, Sh0.5, Ag/As0.5, Ga+; struc.: homogeneous, very compact, (coarse detrituosus); nig.3+, strf.0/4, elas.0, sicc.0, lim.sup.2
disturbed while drilling	
11.81 – 11.86	**substantia humosa with traces of sand, very dark grey;** Sh2, Tb/Th1, As/Ag1, G+; struc.: heterogeneous, fragments of very fine detritus; nig.3, strf.0/3, elas.0, sicc.0, lim.sup.?
11.86 – 11.93	**peat, slightly clayey with traces of sand, black;** Tb21.5, Th11, Sh1, As/Ag0.5, Ga+; struc.: heterogeneous; nig.3+, strf.0/4, elas.0, sicc.0, lim.sup.2
11.93 – 12.02	**peat, when fresh brownish yellow, dried reddish black;** Tb$^{2\text{-}3}$4; struc.: homogeneous, loose; nig.2 (when dried 3), strf.0, elas.1, sicc.2, lim.sup.2
12.02-12.20	**substantia humosa with sand, black;** Sh4, Ga++; struc.: homogeneous, mica; nig.3, strf.0/4, elas.0, sicc.2, lim.sup.1
12.20 – 12.50	**sandy – silty gyttja, black;** Ag2, Ld1, Sh0.5, Ga0.5; struc.: homogeneous, mica; nig.3+, strf.0/3, elas.0, sicc.2, lim.sup.0
12.50 – 12.60	**substantia humosa with traces of sand, black;** Sh4, Th+, Ga+; struc.: homogeneous, very compact, mica; nig.3+, strf.0/4, elas.0, sicc.2, lim.sup.2
12.60 – 12.63	**peat, dark reddish brown;** Tb^{1}3.5, Th^{1}0.5;

Table 1. Continued

Depth in m	Lithology / Sediment description
	struc.: felty with fine tissue fragmetns, very compact; nig.3+, strf.0/3, elas.0, sicc.2, lim.sup.3
12.63 – 12.84	**substantia humosa with clay and traces of sand, black;** Sh3, Ag/As1, Tb+, Ga+; struc.: homogeneous, very compact, peels, mica; nig.3+, strf.0/4, elas.0, sicc.2, lim.sup.2
12.84 – 12.98	**sandy silt, black;** Ag2, Sh1.5, Ga0.5 struc.:homogeneous, mica; nig.3, strf.0/3, elas.0, sicc.2, lim.sup.2
12.98 – 13.11	**clayey silt with traces of sand and gravel, very dark grey;** Ag2.5, As0.5, Sh1, Ga+, $Gg_{(min)}$+; struc.: heterogeneous with gravel; nig.3, strf.0, elas.0, sicc.2, lim.sup.1
13.11 – 13.48	**clayey silt with gravel, very dark grey;** Ag3, As0.5, Sh0.5, Ga+, $Gg_{(maj)}$+; struc.: homogeneous at the bottom, heterogeneous at the top with gravel; nig.3, strf.0, elas.0, sicc.2, lim.sup.1
13.48 – 13.52	**substantia humosa with silt and traces of sand, black;** Sh2.5, Ag1.5, As+, Ga+; struc.: homogeneous, compact, mica; nig.3+, strf.0/4, elas.0, sicc.2, lim.sup.3
13.52 – 13.60	**substantia humosa with silt and traces of sand, very dark grey;** Sh3, Ag1, Ga+; struc.: homogeneous, compact; nig.3, strf.0/3, elas.0, sicc.2, lim.sup.2
13.60 – 14.02	**substantia humosa, sandy with traces of $CaCO_3$, black;** Sh3.5, Ga0.5, Lc+; struc.: homogeneous, very compact, mica, sand (in places), HCl+; nig.3+, strf.0/4, elas.0, sicc.2, lim.sup.2
14.02 – 14.30	**silty, calcareous gyttja, very dark greyish brown;** Lc1-2, Sh2-1, Ag1; struc.: homogeneous, compact, mica, HCl++; nig.2, strf.0/3, elas.0, sicc.2, lim.sup.2
14.30 – 14.70	**organic silt with traces of $CaCO_3$, black;** Sh1.5, Ag2.5, Lc++, Ga+; struc.: homogeneous, very compact, when dried peels, mica, HCl+; nig.3+, strf.0/4, elas.0, sicc.2, lim.sup.? disturbed while drilling
14.97 – 15.33	**organic silt with admixture of calcareous gyttja, sandy, very dark grey;** Ag1.5, Sh1.5, Lc0.5, Ga0.5, $Gg_{(min)}$+; struc.: homogeneous, very sandy, gravel at depth 15,10 m, HCl+ nig.2+, strf.0, elas.0. sicc.2, lim.sup.?
15.33 – 15.75	**silty calcareous gyttja sandy at top, with single gravel, dark gray;** Lc1, Sh0.5, Ag2, Ga0.5, $Gg_{(min)}$+ – at top; Lc2, Sh0.5, Ag1.5, Ga+ – at bottom; struc.: homogeneous, very fragile, plant detritus (at 15,59 m), silica grains (at 15,44 m) and gravel (at 15,34m), sandy towards the top, HCl+++; nig.3, strf.0, elas.0. sicc.2, lim.sup.?
15.75 – 15.90	**calcareous silt with gyttja, clayey, dark olive gray;** Lc1, Ag3, As+, Sh+; struc.: homogeneous, HCl+++; nig.2, strf.0, elas.0, sicc.2, lim.sup.3

added to each sample prior to maceration (Stockmarr 1971, Berglund & Jasiewiczowa 1986).

After adding the *Lycopodium* tablets, the sediment was covered with HCl to remove calcium carbonates, rinsed with water, and boiled in 10% KOH. After rinsing again with water and centrifugation the sample was covered with HF and boiled for ten minutes. After centrifugation it was treated with 10% boiling HCL in order to remove the siliceous material, rinsed twice with water, and covered with glacial acetic acid and subjected to acetolysis by Erdtman's (1960) method. The remaining sediment was rinsed with glacial acetic acid followed by 10% KOH. It was then rinsed twice with water and once with a mixture of water and ethanol. After centrifugation the sediment was covered with warm glycerine.

All pollen and spores were identified in two slides from each level analysed. Algal colonies (*Pediastrum*, *Botryococcus*) and spores of Bryales (Musci excl. *Sphagnum*) were only counted in half a slide; AP + NAP, specimens of algae and spores of Bryales subtotalled. After finishing to count the whole spectrum, values of *Pediastrum*, *Botryococcus* and Bryales were estimated from the ratio of the sum AP+ NAP obtained on half a slide to the final AP + NAP sum.

The pollen diagrams were drawn using the computer program POLPAL (Walanus & Nalepka 1996). The basic sum used for the percentage calculations consists of pollen from trees, shrubs and herbaceous terrestrial plants. The proportions of aquatic plant pollen and of spores were calculated in relation to the basic sum adding the number of the separate component. The same procedure was used for redeposited Tertiary pollen and spores, and colonies of *Pediastrum* and *Botryococcus*.

The taxa in the percentage pollen diagram (Fig. 3) are arranged according to habitat, and within the individual group the taxa are presented in a stratigraphic order.

PREPARATION AND ANALYSIS OF MACROSCOPIC REMAINS

Each sample for analysis of macroscopic remains corresponds to two palynological samples. 50 cm^3 of sediment was taken for each sample. In order to disintegrate the sediment, it was boiled in a 10% KOH solution for 1–2 hours. Samples containing highly compacted organic matter (bituminous shale) were boiled in a weak solution of $Na_2S0_4.10H_2O$ (Janczyk-Kopikowa 1966). The sediment was then rinsed in sieves with 0.5 and 0.2 mm mesh diameter; the macroscopic remains were picked out and determined under a stereoscopic microscope.

The results of macroscopic analysis are presented in a diagram (Fig. 4) as the total number of specimens per sample (50 cm^3 of sediment). The abundance of moss remains is given as a three-degree scale. All the macroscopic plant remains are housed at the Palaeobotanical Museum of W. Szafer Institute of Botany Polish Academy of Sciences (number of the collection: KRAM-P Q-132).

THE FOSSIL FLORA OF HOROSZKI DUŻE

FLORISTIC LIST

The fossil flora of Horoszki Duże comprises taxa determined on the basis of pollen, spores, fruits, seeds and vegetative remains. The names of vascular plants follow Mirek et al. (1995). The term “type” indicates that more than two species or genera have the same morphological type of pollen or spores (Birks 1973). The exception is the *Pinus cembra* type, in which only pollen grains of *P. cembra* and *P. sibirica* are included by the present author. The abbreviation “undiff.” indicates that within a given family or genus lower taxa have also been determined.

The floristic list contains all the taxa considered by the author to be autochthonous in the flora of Horoszki Duże. Where, in certain strata, some of these are considered to be redeposited, or partially redeposited, this has been indicated in Table 2.

At the determination of pollen and spores the following literature was used: Faegri & Iversen (1989), Beug (1961), Erdtman et al. (1961, 1963), Moore et al. (1991) and Reille (1992). An unpublished key for the identification of European sporomorphs, elaborated by Demske (1991) was also used. The primary source used, however, was the comprehensive collection of reference slides at the Department of Palaeobotany of the W. Szafer Institute of Botany, Polish Academy of Sciences in Kraków.

The following keys and atlases were used in determination of macroscopic plant remains: Beijerinck (1947), Berggren (1981), Kats et al. (1965), and Nilsson & Hjelmquist (1967). The reference collection of fruits and seeds of the W. Szafer Institute of Botany of the Polish Academy of Sciences in Kraków was a valuable tool at the identifications of plant macrofossils.

Taxa of Charophyta and Bryopsida were determined by Professor Kazimierz Karczmarz (The Maria Curie-Skłodowska University, Lublin) and the endocarps of *Potamogeton* by Professor Felix Yu.Velichkevich (Minsk, Belarus).

TAXONOMICAL NOTES

The following comments apply only to those taxa which, in the author’s opinion, need to be discussed in greater detail, or are for the first time identified from the Late Pleistocene in Poland.

A. Pollen and spores

Sellaginellaceae

Selaginella helvetica (Pl. 1, figs 1, 2). Spores with a distinct trilete mark, verrucate. *S. helvetica* and *S. denticulata* are combined into one type by Stafford (1991). According to whom, the spores of *S. helvetica* can be distinguished by having a thinner exine than *S. denticulata*. At Horoszki only spores with a thinner exine occurred, so they were counted as *S. helvetica*.

Apiaceae

All taxa within this family were distinguished on the basis of Punt’s key (1984).

Betulaceae

Alnus viridis (Pl. 1, fig. 4). Pollen grains < 20 μm with at least five pores, and with no arci visible.

Betula nana (Pl. 1, fig. 3). In determination, the morphology of the grain was taken into account (flat vestibulum), grain diameter < 21 μm, and thickness of the exine (Praglowski 1962, Andersen 1979).

Campanulaceae

In distinguishing between taxa within this family, grain size was the criterion used.

Triporate grains < 30 μm were included in

Fig. 3. Percentage pollen diagram from Horoszki Duże.
Lithology: **Ag** – *Argilla granosa*; **As** – *A. steatodes*; **Ld** – *Limus detrituosus*; **Lc** – *L. calcareus*; **Sh** – *Substantia humosa*; **Tb** – *Turfa bryophytica*; **Th** – *T. herbacea*; **Dg** – *Detritus granosus*; **Ga** – *Grana arenosa*; **Gg** – *G. glareosa*

Fig. 4. Macrofossil diagram from Horoszki Duże.
Names of plants without additional explanations mean the presence of reproductive bodies. Explanations of abbreviations: **cx** – calyx; **ds** – dwarf stem; **fs** – fruit scale; **n** – needle; **os** – oospores, oogonia; **pr** – perianthum; **w** – wood.
Lithology as in Fig. 3

Table 2. The flora list from Horoszki Duże.
Abbreviations used: **+** – presence of *Pediastrum* and *Botryococcus* colonies, *Cenococcum* and fragments of sporangia of Filicales Monolete (= Polypodiaceae s. l.); **O** – oospores, oogonia; **VR** – remains of bryophyte gametophytes; **Sp** – spores; **MISp** – microspores; **MAS** – macrospores; **P** – pollen; **L** – leaves; **S** – seeds; **W** – wood; **F** – fruit; **FS -** fruit scales; **CX** – calyx; **H** – hairs; **DS** – dwarf stem; **PR** – perianthum; **SN** – spine; **/ /**, – redeposited, partly redeposited, or, from long distance transport; **‡** – extinct species; **LGW** – Late Glacial of the Wartanian glaciation; **EEM** – Eemian interglacial; **EV** – Early Vistulian; **PV** – Plenivistulian

TAXON	**LG W**	**EEM**	**EV**	**PV**
CHLOROPHYTA				
Hydrodictyaceae				
Pediastrum Meyen	+	+	+	+
Botryococcaceae				
Botryococcus Kütz.	+	+	+	+
CHAROPHYTA				
Characeae				
Chara contraria A. Br. ex Kütz.	.	O	O	.
Ch. vulgaris L.	.	.	.	O
Nitellaceae				
Nitella capitata (Nees) Ag.	.	.	O	.
N. gracilis (Sm.) Ag.	.	.	.	O
N. mucronata (A.Br.) Miq.	.	O	.	O
N. syncarpa (Thuill.) Chev.	O	O	O	O
MYCOTA				
Hyphomycetes				
Cenococcum graniformae (Sow.) Ferd. & Winge [= *C. geophilum* Fr.]	.	+	+	+
HEPATICOPSIDA				
Ricciaceae				
Riccia L.	.	.	Sp	.
BRYOPSIDA				
Amblystegiaceae				
Amblystegium humile (P.Beauv.) Crundw.	.	.	.	VR
A. serpens (Hedw.) B.S.G.	.	.	VR	.
A. varium (Hedw.) Lindb.	.	.	.	VR
Calliergon trifarium (Web. & Mohr) Kindb.	VR	.	VR	VR
C. turgescens (Th.Jens.) Kindb.	.	.	VR	VR
Campylium elodes (Lindb.) Kindb.	.	.	.	VR
Cratoneuron commutatum (Hedw.) Roth. [=*Palustriella commutata* (Hedw.) Ochyra]	.	.	.	VR
Drepanocladus aduncus (Hedw.) Warnst.	.	VR	VR	VR
D. fluitans (Hedw.) Warnst.	.	.	VR	VR
D. polycarpos (Voit) Warnst.	.	VR	.	.
D. revolvens (Sw.) Warnst.	.	VR	VR	VR
D. lycopodioides (Schwaegr.) Warnst.	.	.	VR	.
D. exannulatus (B., S. and G.) Warnst.	.	.	VR	VR
D. sendtneri (Schimp. ex H.Müll.) Warnst.	.	.	VR	.
D. vernicosus (Lindb.) Warnst.	.	.	VR	.
Mniaceae				
Cinclidium stygium Sw.	.	.	.	VR
Meesiaceae				
Meesia triquetra (Richter) Angstr.	.	.	VR	VR
Bryaceae				
Bryum neodamense Itzigs.	.	.	.	VR
B. bimum (Brid.) Turn.	.	.	VR	.
B. pseudotriquetrum (Hedw.) Schwaegr.	.	.	.	VR
Sphagnaceae				
Sphagnum palustre L.	.	VR	.	VR
S. subsecundum Nees	.	.	VR	VR

Table 2. Continued

TAXON	LG W	EEM	EV	PV
Sphagnum Ehrh. sp. div.	.	.	VR	VR
Sphagnum Ehrh.	Sp	Sp	Sp	Sp
Bryales [=Musci excl. *Sphagnum*]	Sp	Sp	Sp	Sp
LYCOPSIDA				
Lycopodiaceae				
Diphasiastrum alpinum (L.) Holub [=*Lycopodium alpinum* L.]	Sp	Sp	Sp	Sp
Lycopodiella inundata (L.) Holub [=*Lycopodium inundatum* L.]	.	Sp	.	.
Lycopodium annotinum L.	.	Sp	Sp	Sp
L. clavatum L.	.	.	.	Sp
Lycopodium L. undiff.	Sp	Sp	Sp	Sp
Huperziaceae				
Huperzia selago (L.) Bernh. ex Schrank & Mart. [=*Lycopodium selago* L.]	.	.	.	Sp
ISOTOPSIDA				
Isoëtaceae				
Isoëtes L.	.	.	Sp	Sp
SELAGINELLOPSIDA				
Selaginellaceae				
Selaginella selaginoides (L.) P.Beauv. ex Schrank & Mart.	.	MISp	MISp, MASp	MISp
Selaginella helvetica (L.) Spring	.	.	MISp	MISp
SPHENOPSIDA				
Equisetaceae				
Equisetum L.	Sp	Sp	Sp	Sp
PTEROPSIDA				
Aspidiaceae				
Dryopoteris filix-mas (L.) Schott type	.	Sp	.	.
Ophioglossaceae				
Ophioglossum L.	.	Sp	.	.
Botrychium lunaria (L.) Sw. type	.	Sp	Sp	Sp
B. boreale Milde type	.	.	.	Sp
Osmundaceae				
Osmunda claytoniana L. type	.	Sp	.	.
O. cinnamomea L. type	.	.	Sp	Sp
Osmunda L. undiff.	.	.	Sp	Sp
Polypodiaceae				
Polypodium vulgare L.	.	Sp	.	Sp
Thelypteridiaceae				
Thelypteris palustris Schott	.	Sp	.	.
Hypolepidaceae				
Pteridium aquilinum (L.) Kuhn	.	Sp	Sp	Sp
Filicales monolete [=Polypodiaceae s.l.] – sporangia	.	+	.	.
Filicales monolete [=Polypodiaceae s.l.]	Sp	Sp	Sp	Sp
GYMNOSPERMAE				
Ephedraceae				
Ephedra distachya L. type	.	.	P	P
E. fragilis Desf. type	.	.	P	P
Taxaceae				
Taxus baccata L.	.	P	.	.
Pinaceae				
Abies alba Mill.	.	P	/P/	/P/
Larix Mill.	P.	P, L	P, L, S	P, L
Larix Mill. vel *Picea* Dietr.	.	.	W, S	.
Picea abies (L.) H.Karst. type	P	P	P	/P/
Picea abies (L.) H.Karst.	.	.	S	.

Table 2. Continued

TAXON	**LG W**	**EEM**	**EV**	**PV**
Picea Dietr.	.	S, L	S	.
Pinus cembra L. type	P	/P/	P	/P/
P. cembra L.	.	.	L	.
P. sylvestris L. type	/P/	P	P	/P/
P. sylvestris L.	.	S	S, L	.
Pinus L.	.	.	W	/W/
cf. *Pinus* L.	.	DS	S	.
Cupressaceae				
Juniperus L.	P	P	P	P
ANGIOSPERMAE				
Aceraceae				
Acer L.	.	W, P	.	/P/
Alismataceae				
Alisma plantago-aquatica L.	.	.	S	S
Alisma L.	.	P	P	.
Sagittaria L.	.	.	.	P
Apiaceae [=Umbelliferae]				
Astrantia major L. type	.	P	P	.
Bupleurum L.	.	.	P	P
Cicuta virosa L.	.	.	F	.
C. virosa L. type	.	.	P	P
Conium maculatum L. type	.	.	P	P
Hydrocotyle vulgaris L.	.	.	P	P
Oenanthe fistulosa L. type	.	P	.	P
Pastinaca L. type	.	.	P	P
Peucedanum palustre (L.) Moench type	.	P	.	.
Pimpinella major (L.) Huds. type	.	P	P	P
Pleurospermum austriacum (L.) Hoffm.	.	.	P	P
Apiaceae undiff. [=Umbelliferae undiff.]	P	P	P	P
Aquifoliaceae				
Ilex aquifolium L. type	.	P	/P/	/P/
Araliaceae				
Hedera helix L.	.	P	.	.
Asteraceae				
Achillea L. type	.	P	P	P
Ambrosia L. type	.	.	.	P
Artemisia cf. *vulgaris* L.	.	.	S	.
Artemisia L.	P	P	P	P
Aster L. type	.	P	P	P
Bellis L. type	.	P	P	P
Bidens tripartita L.	.	.	S	.
Bidens L.	.	.	S	.
Bidens L. type	.	P	P	P
Centaurea jacea L. type	.	.	.	P
C. nigra L. type	P	P	.	P
C. scabiosa L. type	.	.	P	P
Cirsium Mill. / *Carduus* L.	.	P	P	P
Echinops L. type	.	.	.	P
cf. *Jurinea* Cass.	.	.	P	.
Saussurea DC. type	.	P	P	.
Senecio L. type	.	.	P	P
Serratula L. type	.	.	P	.
Asteraceae sp.	.	.	F	.
A. undiff.	P	P	P	P
Betulaceae				
Alnus glutinosa (L.) Gaertn. type	/P/	P	P	/P/

Table 2. Continued

TAXON	LG W	EEM	EV	PV
A. glutinosa (L.) Gaertn.	.	F	.	.
A. viridis (Chaix) DC. type		P	P	P
Alnus Mill.	.	.	.	/W/
Betula alba type [=*B.* sect. *Albae*]	P	P	P	P
B. sect. *Albae*	.	F, FS	F, FS	F, FS
B. cf. *pubescens* Ehrh.	.	FS	FS	.
B. pendula Roth [=*B. verrucosa* Ehrh.]	.	.	FS	.
B. cf. *humilis* Schrank	.	.	F	F
B. nana L.	P	P	P, F, FS	P
Betula			FS	
Carpinus betulus L.	.	F	.	.
Carpinus L.	/P/	P	/P/	/P/
Corylus avellana L.	/P/	P	/P/	/P/
Boraginaceae				
Pulmonaria officinalis L. type	.	P	.	.
Symphytum L.	.	.	.	P
Brassicaceae [=Cruciferae]				
Rorippa palustris (L.) Besser	.	.	S	S
Brassicaceae [=Cruciferae]	P	P	P, S	P
Buxaceae				
Buxus sempervirens L.	.	P	.	.
Callitrichaceae				
Callitriche L.	.	.	F	F
Campanulaceae				
Campanula L.	.	.	P	P
Jasione L.	.	.	.	P
cf. *Phyteuma* L.	.	.	P	P
Cannabaceae				
Humulus lupulus L.	/P/	P	P	P
Caprifoliaceae				
Sambucus nigra L.	.	S	.	.
S. cf. *nigra* L.	P	P	P	P
S. cf. *racemosa* L.	.	.	P	P
Viburnum opulus L. type	.	P	.	.
Viburnum L. undiff.	.	P	.	/P/
Caryophyllaceae [= Silenaceae]				
Arenaria L. type	.	P	P	P
Cerastium L. type	.	.	P	P
Cerastium cf. *alpinum* L.	.	.	P	P
Dianthus L. type	.	P	P	P
Gypsophila fastigiata L. type	.	.	P	P
Herniaria L. type	.	P	P	P
Illecebrum verticillatum L.	.	.	.	P
Lychnis L. undiff.	.	.	P	P
L. flos-cuculi L. vel *Viscaria vulgaris* Röhl.	.	.	.	S
Sagina L. type	.	.	P	P
Scleranthus annuus L.	.	.	P	P, CX
S. perennis L.	.	.	P	P
Silene cf. *vulgaris* (Moench) Garcke [=*S.* cf. *inflata* (Salisb.) Sm.]	.	.	.	S
S. conica L. type	.	.	.	P
S. dioica (L.) Clairv. type [=*Melandrium rubrum* (Weigel) Garcke] type	.	P	P	P
S. vulgaris (Moench) Garcke type	.	.	P	P
Spergularia Presl type	.	.	P	P
Stellaria holostea L.	.	.	P	P

Table 2. Continued

TAXON	LG W	EEM	EV	PV
S. nemorum L.	.	P	.	.
S. palustris Retz.	.	.	S	.
Stellaria L.	.	.	S	.
Viscaria vulgaris Röhl type [=*Lychnis viscaria* L. type]	.	.	P	P
Caryophyllaceae	.	.	S	.
Caryophyllaceae undiff.	.	P	P	P
Ceratophyllaceae				
Ceratophyllum demersum L.	.	.	F	.
C. submersum L.	.	.	F	.
Ceratophyllum L.	.	H	H, S	H
Chenopodiaceae	P	P	P	P
Cichoriaceae	.	P	P	P
Taraxacum Zinn	.	.	.	F
Cistaceae				
Helianthemum alpestre (Jacq.) DC. type	.	.	P	P
H. nummularium (L.) Mill. type	P	P	P	P
Helianthemum undiff.	.	P	.	P
Crassulaceae				
Sedum L.	.	.	P	.
Sempervivum L.	.	.	.	P
Cyperaceae				
Carex elata All.	.	F	F	.
C. cf. *elongata* L.	.	.	.	F
C. rostrata Stokes vel *C. vesicaria* L.	.	.	F	F
Carex sp. div.	.	F	F	F
Eleocharis ovata (Roth) Roem. & Schult.	.	.	F	.
E. palustris (L.) Roem. & Schult.	.	.	F	.
Scirpus L.	.	F	.	.
Cyperaceae	P	P	P	P
Dipsacaceae				
Knautia L.	.	.	.	P
Succisa pratensis Moench	.	.	.	P
Droseraceae				
Drosera L	.	.	.	P
Elatinaceae				
Elatine hydropiper L.em.Oeder	.	.	S	S
cf. *Elatine* L.	.	.	P	.
Eleagnaceae				
Hippophaë rhamnoides L.	P	.	.	P
Empetraceae				
Empetrum L.	.	P	P	P
Ericaceae				
Andromeda polifolia L.	.	.	S	.
Andromeda L.	.	.	.	P
Arctostaphylos L.	.	.	P	P
Bruckenthalia spiculifolia (Salisb.) Reichenb.	.	.	P	P
Calluna vulgaris (L.) Hull	P	P	P	P
Chamaedaphne calyculata (L.) Moench	.	.	S	.
Ledum L.	.	P	P	P
Vaccinium L. type	.	P	P	P
Ericaceae undiff.	P	P	P	P
Euphorbiaceae				
Euphorbia L.	.	.	.	P
Mercurialis L.	.	.	.	P

Table 2. Continued

TAXON	LG W	EEM	EV	PV
Fabaceae [=Papilionaceae]				
Astragalus alpinus L.	.	.	.	P
A. danicus Retz. type	.	.	P	P
Astragalus L. undiff.	.	.	.	P
Cytisus L.	.	.	P	P
Genista L. type	.	.	.	P
Hedysarum L.	.	.	.	P
Lathyrus L. type	.	.	.	P
Lotus L.	.	.	P	P
Onobrychis Mill. type	.	.	P	P
Ononis L. type	.	.	.	P
Oxytropis cf. *lapponica* (Wahlenb.) Gay	.	.	.	P
Trifolium L. type	.	.	P	p
Vicia L. type	.	.	.	P
Fabaceae [=Papilionaceae]	.	.	.	PR
Fabaceae undiff. [=Papilionaceae undiff.]	.	.	P	P
Fagaceae				
Fagus L.	/P/	P	.	.
Quercus L.	/P/	P	/P/	/P/
Gentianaceae				
Gentiana campestris L. type [=*Gentianella campestris* (L.) Börner type]	.	.	P	P
G. pneumonanthe L. type	.	P	P	P
Gentianella tenella (Rottb.) Börner type	.	.	.	P
Gentiana L. undiff.	.	.	.	P
Swertia perennis L.	.	.	.	P
Geraniacaceae				
Geranium L.	.	P	.	P
Haloragaceae				
Myriophyllum alterniflorum DC. [=*M.alternifolium* DC.]	.	P	F, P	P
M. spicatum L.	.	P	P	P
M. verticillatum L.	.	P	P	P
‡ *M.* cf. *microcarpum* Dorof.	.	.	F	.
Hydrocharitaceae				
Stratiotes L.	.	.	SN	.
Hypericaceae				
Hypericum L.	.	.	P	P
Iridaceae				
Iris pseudoacorus L. type	.	P	P	P
Lamiaceae [=Labiatae]				
Lycopus europaeus L.	.	.	F	.
Mentha cf. *aquatica* L.	.	.	F	.
Mentha L.	.	.	F	F
Mentha L. type	.	P	P	P
Prunella L. type	.	.	.	P
Stachys palustris L.	.	.	F	.
Stachys L. type	.	P	.	P
Lemnaceae				
Lemna L.	.	.	.	P
Lentibulariaceae				
Utricularia L.	.	.	P	.
Liliaceae				
Tofieldia Huds.	.	.	.	P
cf. *Veratrum* L.	.	.	.	P
Liliaceae undiff.	.	.	P	P

Table 2. Continued

TAXON	LG W	EEM	EV	PV
Linaceae				
Linum austriacum L. type	.	.	P	P
L. catharticum L. type	.	.	.	P
Lobeliaceae				
Lobelia L.	.	.	P	P
Loranthaceae				
Viscum L.	.	P	.	.
Lythraceae				
Lythrum L.	.	.	P	P
Peplis L.	.	P	.	.
Menyanthaceae				
Menyanthes trifoliata L.	.	P.	P, S	P.
Myricaceae				
Myrica gale L. type	.	.	P	P
Najadaceae				
Najas flexilis (Willd.) Rostk. & W.L.E. Schmidt	.	F	F	.
N. marina L.	.	F	F	.
N. minor All.	.	F	.	.
Nymphaeaceae				
Nuphar pumila (Timm) DC.	.	.	S	.
Nuphar Sm.	.	P	S, P	P
Nymphaea alba L. type	.	P	P	P
Oenotheraceae				
cf. *Chamaenerion* Scop.	.	.	P	P
Epilobium L.	.	.	.	P
Trapa L.	.	P	.	.
Oleaceae				
Fraxinus L.	/P/	P	/P/	/P/
Papaveraceae				
Papaver radicatum Rottb. type	.	.	P	P
P. rhoeas L. type	.	.	P	P
Plantaginaceae				
Littorella Berg.	.	.	P	.
Plantago lanceolata L.	.	P	P	P
P. major L.	.	P	P	P
P. major L. / *media* L.	.	.	P	P
P. maritima L. s. str.	.	P	P	P
P. maritima L. s. l.	.	.	.	P
P. media L.	.	P	P	P
Plumbaginaceae				
Armeria maritima (Mill.) Willd. type A	.	.	P	P
Armeria maritima (Mill.) Willd. type B	.	.	P	P
Poaceae [=Gramineae]				
Phragmites Adans. type	P	P	P	P
cf. *Phragmites* Adans.	.	F	F	.
Poaceae sp. div. [=Gramineae sp. div.]	.	F	F	F
Poaceae undiff. [=Gramineae undiff.]	P	P	P	P
Polemoniaceae				
Polemonium L.	.	.	P	P
Polygonaceae				
cf. *Oxyria digyna* (L.) Hill	.	.	P	P
Polygonum amphibium L.	.	.	P	P
P. aviculare L. type	.	P	P	P
P. bistorta L. vel *viviparum* L.	P	P	P	P
P. persicaria L. type	.	P	P	P
Rumex acetosa L. type	.	P	P	P

Table 2. Continued

TAXON	LG W	EEM	EV	PV
R. acetosella L.	.	P	F, P	P
R. aquaticus L. type	.	P	P	P
R. longifolius DC. type	.	P	P	P
R. maritimus L.	.	.	F, PR	F, PR
Rumex L.	.	.	F	.
Potamogetonaceae				
Potamogeton cf. *friesii* Rupr.	.	.	F	.
P. filiformis Pers.	.	.	F	.
P. cf. *lucens* L.	.	.	F	.
P. natans L.	.	.	F	.
P. obtusifolius Mert. & W.D.J. Koch	.	.	F	.
P. cf. *obtusifolius* Mert. & W.D.J. Koch	.	.	F	.
P. perfoliatus L.	.	.	F	.
P. praelongus Wulfen	.	.	F	F
P. pusillus L.	.	.	F	F
‡*P. sukaczevii* Wieliczk.	.	.	F	.
P. vaginatus Turcz.	.	.	.	F
Potamogeton L. sp. div.	.	.	F	F
P. sect. *Coleogeton*	.	P	P	P
P. sect. *Eupotamogeton*	P	P	P	P
Primulaceae				
Lysimachia nemorum L.	.	.	P	P
L. thyrsiflora L.	P	.	P	P
L. vulgaris L.	.	P	P	.
Lysimachia L. undiff.	.	.	P	P
Trientalis europaea L.	.	.	P	.
Pyrolaceae				
Chimaphila umbellata (L.) W.P.C. Barton	.	P	.	P
Pyrola L. type	.	.	.	P
Ranunculaceae				
Aconitum L.	.	.	P	.
Anemone L. type	.	.	P	P
Batrachium S.F.Gray	.	F	F	F
Caltha L. type	P	P	P	P
Ficaria Adans.	.	.	.	P
Helleborus cf. *purpurascens* W.K.	.	.	P	.
Pulsatilla Mill.	.	.	P	P
Ranunculus acris L. type	.	.	P	P
R. flammula L.	.	.	F	.
R. flammula L. type	P	P	P	P
R. sceleratus L.	.	.	F	F
R. trichophyllus Chaix type [= *Batrachium trichophyllum* (Chaix) Bosch]	.	P	P	P
Thalictrum L.	P	P	P	P
Trollius L.	P	.	P	P
Rhamnaceae	/P/	.	.	.
Frangula Mill.	/P/	P	/P/	/P/
Rhamnus cathartica L.	.	.	/P/	.
Rosaceae				
Alchemilla L. type	.	P	P	.
Cotoneaster Med.	.	.	P	P
Comarum palustre L.	.	P	F, P	P
Dryas L.	.	.	P	.
Filipendula cf. *vulgaris* Moench [=*F.* cf. *hexapetala* Gilib.]	.	.	.	F
Filipendula Mill.	P	P	P	P

Table 2. Continued

TAXON	**LG W**	**EEM**	**EV**	**PV**
Fragaria L.	.	.	F	.
Geum L.	.	.	P	P
Potentilla anserina L.	.	.	F	.
P. supina L.	.	.	F	.
Potentilla L. sp. div.	.	F	F	F
Potentilla L. type	.	P	P	P
Rubus chamaemorus L.	.	.	.	P
R. cf. *arcticus* L.	.	.	P	P
Rubus L. undiff.	.	P	P	P
Rosa L.	.	P	P	P
Sanguisorba officinalis L. 2n=28	.	P	P	P
S. officinalis L. 2n=56	.	.	P	P
Sorbus cf. *aucuparia* L. em. Hedl.	.	.	.	P
Sorbus L. undiff.	.	.	P	P
Spiraea L.	.	P	.	.
Rosaceae undiff.	P	P	P	P
Rubiaceae	.	P	P	P
Salicaceae				
Populus L.	.	P	P, W	P
Salix L. undiff.	P	P	P	P
S. polaris Wahlenb. type	P	.	P	P
Saxifragaceae				
Chrysosplenium L.	.	.	P	P
Parnassia palustris L.	.	.	.	P
Ribes alpinum L. type	.	.	P	P
Saxifraga cernua L. type	.	.	P	.
S. hirculus L. type	.	.	P	P
S. oppositifolia L. type	.	P	P	P
S. stellaris L. type	.	.	P	P
Scheuchzeriaceae				
Scheuchzeria palustris L.	.	P	P, S	.
Scrophulariaceae				
Euphrasia L.	.	.	.	P
Melampyrum L.	.	P	.	P
Pedicularis palustris L. type	.	.	.	P
Rhinanthus L. type	.	P	P	P
Veronica L.	P	.	P	P
Solanaceae				
Solanum dulcamara L.	.	P	P	P
S. nigrum L. em. Mill.	.	.	.	P
Sparganiaceae				
Sparganium L. type	P	P	P	P
Tamaricaceae				
Myricaria germanica (L.) Desv.	.	.	P	P
Tiliaceae				
Tilia cordata Mill. type	/P/	P	/P/	/P/
T. cf. *platyphyllos* Scop./ *tomentosa* Moench	.	F	.	.
T. platyphyllos Scop. type	.	P	.	.
T. tomentosa Moench.	.	F	.	.
T. tomentosa Moench. type	.	P	.	.
Typhaceae	.	F	.	.
Typha latifolia L.	.	.	P	P
Typha L.	.	S	S	S
Ulmaceae				
Ulmus L.	/P/	P	/P/	/P/

Table 2. Continued

TAXON	**LG W**	**EEM**	**EV**	**PV**
Urticaceae				
Urtica dioica L.	.	.	F	.
Urtica L.	.	P	P	P
Valerianaceae				
Valeriana dioica L. type	.	.	P	.
V. officinalis L. type	.	P	P	P
Violaceae				
cf. *Viola* L.	.	S	.	.
Viola palustris L. type	.	P	P	P
Vitaceae				
Vitis sylvestris (C.C. Gmelin) type [=*V. vinifera* L. subsp. *sylvestris* (C.C. Gmelin) Hegi type]	.	P	.	.
Zannichelliaceae				
Z. palustris L. subsp. *pedicellata* (Wahlenb. & Rosén) Hegi [=*Zannichellia pedicellata* Wahlenb. & Rosén) Fr.]	.	.	.	F

Jasione, bigger ones in *Campanula*. Grains > 40 μm, sometimes tetraporate with spines larger than in the above-mentioned genera, were included in cf. *Phyteuma*.

Caryophyllaceae (= Silenaceae)

Illecebrum verticillatum and *Cerastium* cf. *alpinum* (Pl. 4, figs 7, 8) were determined by comparison with reference slides. For identification of other taxa within the family, the key of Moore et al. (1991) was used. Of the taxa determined the following are shown: *Scleranthus perennis* (Pl. 4, figs 13, 14), *S. annuus* (Pl. 4, figs 11–12), *Silene conica* type (Pl. 4, figs 9, 10) and *Gypsophila fastigiata* type (Pl. 4, figs 15, 16).

Cistaceae

Morphological criteria given by Wasylikowa (1964) were used to distinguish *Helianthemum alpestre* type and *H. nummularium* type, (Pl. 4, figs 5, 6).

Dipsacaceae

Knautia and *Succisa pratensis* were identified on the basis of the description given by Mamakowa (1989).

Ericaceae

Bruckenthalia spiculifolia (Pl. 3, figs 6–9). Pollen grains are tricolporate and psilate. It differs from grains of *Frangula alnus*, with which it used to be confused (Andersen 1973a, Menke 1976) in lacking a vestibulum in a polar position (op. cit., see also the illustrations ibid.). All the grains occurring in the material from Horoszki fully corresponded to the reference material and to the descriptions given by the above authors.

Fabaceae

In determining the pollen from this family, primarily the reference slides were used, and the unpublished key to the Papilionaceae by Faegri (1956). Some taxa were determined, of which *Genista* type (Pl. 2, figs 16, 17), *Hedysarum* (Pl. 2, fig. 15), *Ononis* type (Pl. 2, figs 13, 14), and *Oxytropis* cf. *lapponica* (Pl. 2, figs 11, 12) were documented photographically.

Plantaginaceae

Plantago maritima sensu stricto. Periporate pollen grains with pores lacking an annulus. On the basis of the statistical study carried out by Andersen (1961) most of the pollen grains lacking an annulus around the pores belong to *P. maritima* L.

P. maritima sensu lato. Pollen grains with pores which have an annulus. According to Andersen (op. cit.) such pollen grains are statistically more frequent in alpine species of *Plantago* (*P. alpina*, *P. serpentina* and *P. carinata*).

Primulaceae

Trientalis europaea. This species has dimorphic pollen (Punt et al. 1974). In the material from Horoszki Duże only type A pollen grain was found, tricolporate with a microreticulum. This is the first time pollen of *T. europaea* has been identified in sediments deposited during the Pleistocene in Poland.

Ranunculaceae

The key of Fegri and Iversen (1989) was used to determine the Ranunculaceae family, supplemented by the extensive work by Clarke et al. (1991).

Ficaria and *Pulsatilla* (Pl. 2, figs 3, 4). Determination was based on the description of Clarke et al. (1991) and comparison with reference material.

Helleborus cf. *purpurascens* (Pl. 3, figs 1–3). One grain was noted in the Early Vistulian sediments. The pollen grain is tetracolpate and reticulate, and with a diameter of about 65 µm. In the reference collection tricolpate grains dominate. This taxon was identified for the first time from the Pleistocene sediments in Poland.

Ranunculus trichophyllus type contains the most typical grains of the former genus *Batrachium*.

Rosaceae

Spiraea. One pollen grain was identified in the Eemian interglacial sediments by comparison with reference slides. The grain is striate with slight vallae, and perforations visible. Tricolporate with intectate operculum.

Tiliaceae

Tilia tomentosa type. Distinguished on the basis of the description by Mamakowa (1989). Determination of pollen type supported by the presence of macroscopic remains.

Valerianaceae

Morphological characteristics described in the key of Clarke and Jones (1977) were used. On their basis, *Valeriana dioica* type (Pl. 2, figs 9–10) and *V. officinalis* type were identified.

B. Macroscopic plant remains

Haloragaceae

Myriophyllum cf. *microcarpum* (Pl. 6, fig. 4). Extinct species described by Dorofeev (1963). The taxon differs from contemporary European species of *Myriophyllum* in size, shape, and the character of the nodules (Velichkevich 1982). The size of the specimen from Horoszki are 0.9 mm long × 0.6 mm wide, which is within the range of *M. microcarpum* which is 0.7–1.0 mm × 0.4–0.5 mm given by Velichkevich (op. cit.). The fruits of this species clearly differ from those of modern species of *Myriophyllum*, including *M. alterniflorum* (Pl. 6, fig. 9), the nuts of which are larger, lacking ridges and with a distinctly granular ventral side (op. cit.)

Nymphaeaceae

Nuphar pumila (Pl. 6, fig. 5). Seeds were found in the Early Vistulian layer. The features which make it possible to distinguish between *N. pumila* and *N. lutea* are given by Velichkevich (1973). The specimens from Horoszki fitted the descriptions of this author.

Table 3 summarizes the features enabling discrimination between the seeds of these two species (Velichkevich 1973, and pers. comm.)

Potamogetonaceae

Potamogeton sukaczevii (Pl. 5, figs 21, 22). Extinct species described by Velichkevich (1982), which in the structure of its endocarp is most like *P. maackianus* A. Benn. Endocarps of the fossil species are large (2.5–3.1 × 2.0–2.6 mm) broadly ovate, and massive. A precise morphological description of this species is found in the paper of Velichkevich and Granoszewski (1996). This taxon was identified for the first time from the Pleistocene sediments in Poland.

Tiliaceae

Tilia tomentosa Moench (Pl. 5, figs 18–20). One complete nut was removed from the sediment, identified to taxon and then split into carpels. The surface of these is uniformly covered with round, nodulous processes of varying size. This feature distinguishes *Tilia tomentosa* from *T. platyphyllos*. The surface of the carpel of this latter species is covered by

Table 3. Morphological features of *Nuphar pumila* and *N. lutea* seeds

species feature	***Nuphar pumila***	***Nuphar lutea***
size	3.0–4.0 × 1.8–2.7mm	3.6–6.0 × 2.4–4.7mm
shape	± ovate	± pear-shaped (pyriform)
apical opening	large, constituting 1/2 to 2/3 of the widest part of the seed	small; <1/2 of the broadest part of the seed
epidermis	thicker in section than that of *N. luteum*	thinner in section than in *N. pumila*
epidermis cells	smaller cells, more per unit of surface	larger cells, fewer per unit of area
colour	greysh-brown with brown tint, matt	yellowish-brown, with shiny lustre

nodules very irregularly, or is somewhat ribbed (Velichkevich 1973). This nut of *T. tomentosa* was the first one to be found in Pleistocene deposits in Poland.

Zannichelliaceae

Zannichellia palustris L. subsp. *pedicellata* (Wahlenb. & Rosén) Hegi (Pl. 6, fig. 13). All fruits found at Horoszki had complete or fragmentary stalks, which made it possible to unequivocally assign these to this subspecies.

LATE PLEISTOCENE HISTORY OF *BRUCKENTHALIA SPICULIFOLIA* AND *POTAMOGETON SUKACZEVII*

The thickness of the Eemian-Vistulian lake sediments at Horoszki Duże, the high frequency of sporomorphs and their good state of preservation made very detailed pollen analysis possible. Together with an analysis of macroscopic plant remains, this made it possible to determine species hitherto not reported from the Late Pleistocene in Poland.

Bruckenthalia spiculifolia

One of the interesting species is *Bruckenthalia spiculifolia* (Salisb.) Reichenb., the pollen of which was found in the Early and Middle Vistulian part of core from Horoszki. This ericaceous dwarf shrub has earlier been noted in the floras of Great Britain and Germany (Whittington 1994) as early as the Pliocene and onwards. In northern and western Finland it was already growing towards the end of the Eemian and in the Early Vistulian (Peltoniemi et al. 1989, Eriksson 1993, Saarnisto et al. 1999). Pollen of *B. spiculifolia* was also noted in Early Vistulian interstadial deposits in Sweden (Robertsson 1988, García Ambrosiani & Robertsson 1992, Granoszewski & Robertsson 1999) and in Denmark (Andersen 1973a). From Poland it has up to now only been reported from the Masovian floras in Kaliłów and Woskrzenica in Podlasie (Bińka & Nitychoruk 1995, 1996). In western and northern Europe it occurs most frequently during the early phase of the last glaciation. De Beaulieu and Reille (1992) consider the presence of *Bruckenthalia* pollen to be a characteristic feature of Early Vistulian deposits at sites in western Europe. The Early Vistulian distribution of this plant must therefore have been much wider to the north-west beyond its present occurrence (Fig. 5).

Bruckenthalia is a monotypic genus (Andersen 1973a), a Balkan, subalpine species occurring between (700) 1500 and 2000 (–2500) m above sea level (Boratyński et al. 1992). Its present range in Europe is restricted to the high montane regions of the continental part of Greece, Romania (Eastern and Southern Carpathians), and the mountain regions of Bulgaria, Macedonia and Yugoslavia (Serbia), and in Asia as far as the Pontic region of Asia Minor (Hall 1978). It is a calcifuge species and occurs as a component of three different phytosociological assemblages (Whittington 1994):

– in high mountain shrub communities, where it may dominate together with *Juniperus communis* subsp. *nana*, *Deschampsia flexuosa*, *Bellardiochloa violacea*, *Vaccinium vitis-idaea*, *V. myrtillus*, *Genista tinctoria*, and *Arctostaphyllos uva-ursi*

– in forest clearings with *Fagus sylvatica*, *Vaccinium* spp., *Erica carnea*, *Homogyne alpina*, *Juniperus communis*, and with *Abies alba*, *Picea abies*, *Pinus sylvestris*, *P. peuce*, and *P. nigra*

– in peat bogs formed of *Sphagnum*, accompanied by *Vaccinium uliginosum* (op. cit).

The present distribution area of *Brucken-*

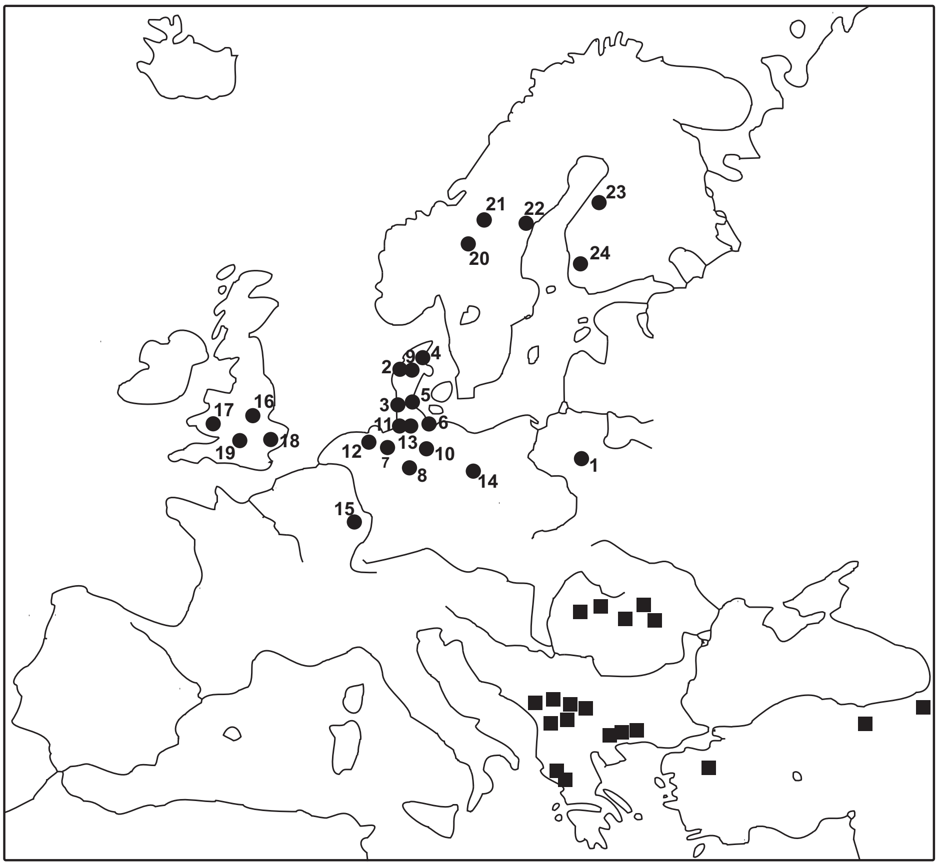

Fig. 5. Distribution of *Bruckenthalia spiculifolia* in the Early Vistulian (circles), and its contemporary range (squares) (Meusel et al., 1978)

1 – Horoszki Duże; **2** – Brörup (Andersen 1973a); **3** – Odderade (Averdieck 1967); **4** – Hollerup (Andersen 1973a); **5** – Keller (Menke 1970); **6** – Fahrenkrug (Averdieck 1962); **7** – Osterwanna (Behre 1974); **8** – Oerel (Behre & Lade 1986); **9** – Nřrbřlling (Andersen 1961); **10** – Quakenbrück (Hahne et al., 1994); **11** – Gross Todtshorn (Caspers 1997); **12** – Neuenhaus-Veldhausen (Freund 1997); **13** – Barendorf (Freund et al., 1997); **14** – Dell-Grund (Freund & Caspers 1997); **15** – La Grande Pile (Beaulieu & Reille 1992); **16** – Wretton (West et al., 1974); **17** – Four Ashes (Andrew & West 1977); **18** – Beetley (Phillips 1976); **19** – Wing (Hall 1980); **20** – Brovalltjärnen (Granoszewski & Robertsson 1999); **21** Pilgrimstad – (Robertsson 1988); **22** – Härnösand (García Ambrosiani & Robertsson 1992); **23** – Marjamurto (Peltoniemi et. al., 1989); **24** – Harrinkangas (Gibbard et al., 1989)

thalia spiculifolia is characterized by a continental climate with a high annual temperature amplitude. In Rodopy in Bulgaria, the mean temperature of January is -2.6°C, that of July being +16°C. The winter minima range from -24× to -29°C, summer maxima being +23° -35°C (Whittington 1994). This species thus can survive extreme temperature changes in winter and summer. This is consistent with various reconstructions of the palaeoclimate in the Early Vistulian in Europe.

The above data, both those on site and climatic requirements, show that *Bruckenthalia spiculifolia* may have been a significant component of the flora in Europe during the Early Vistulian. Unfortunately, this species has a very low pollen production (Birks & Ransom 1969), which results in low frequency in the pollen spectra.

Potamogeton sukaczevii

Potamogeton sukaczevii Wieliczk. is the second interesting species found in the flora from Horoszki Duże (Velichkevich & Granoszewski 1996). This is an extinct species found in Eemian – Vistulian sediments from the Cherikov site (Fig. 6) on the River Sozh in eastern Belarus (Velichkevich 1982). This species is most closely related to the modern far-eastern species *Potamogeton maackianus* A. Benn (Velichkevich 1973), which is today found on the Korean Peninsula, in Japan and the Russian Far East.

P. sukaczevii is the youngest species of the entire *Maackianus* phylogenetic group of *Potamogeton* and its stratigraphic range is so far restricted to the Eemian interglacial and the Early Vistulian (Velichkevich & Granoszewski

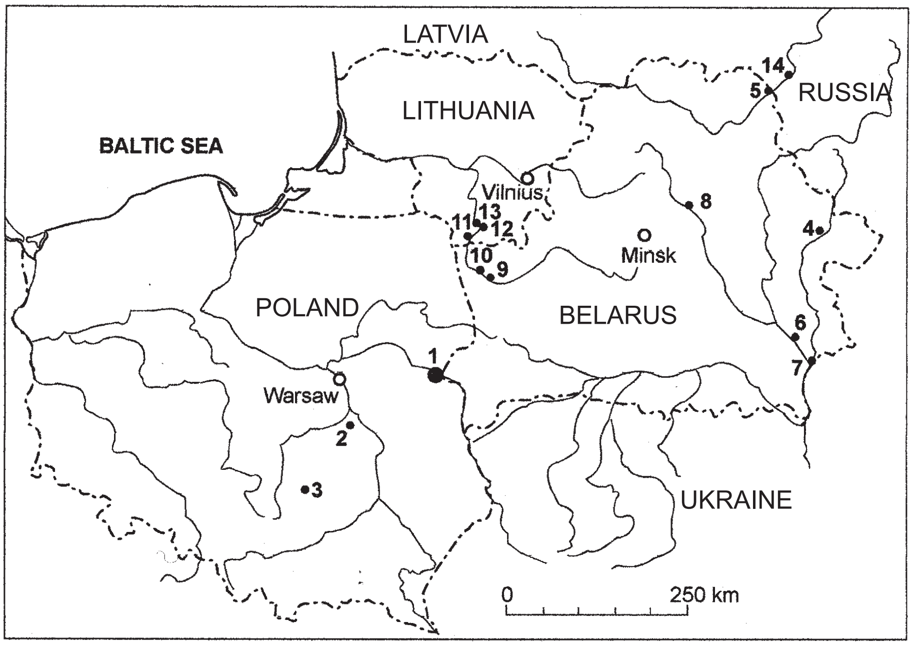

Fig. 6. Distribution of *Potamogeton sukaczevii* in Eemian-Vistulian floras (Velichkevich & Granoszewski 1996, supplemented)

1 – Horoszki Duże; **2** – Gołków; **3** – Bedlno **4** – Cherikov; **5** – Cherny Bereg; **6** – Borkhov Rov; **7** – Loyev; **8** – Murava; **9** – Knyazhevodtsy; **10** – Komotovo; **11** – Lishkyava; **12** Yanyonis; **13** – Nyatesos; **14** – Panfilovo

1996). The significance of the occurrence of *P. sukaczevii* at Horoszki lies not only in the first find of this species in Poland, but it also suggests a close floristic link between central Europe and far-eastern Asia during the last glaciation. This is supported by many other palaeobotanical data, which the present author discusses in the chapter concerning the history of the flora. During a taxonomic revision of reference material in the Palaeobotanical Museum of the W. Szafer Institute of Botany, Polish Academy of Sciences in Kraków endocarps of this species were also found in two other Eemian-Vistulian floras from Poland, i.e. from Gołków and Bedlno near Końskie (Velichkevich et al. 1998).

REDEPOSITED PRE-QUATERNARY SPOROMORPHS

Sporomorphs of pre-Quaternary age, mainly Tertiary, are fairly abundant in samples from a depth of 20.45 m, 17.85 m, 16.64 m, 16.39 m, and in the local pollen assemblage zone HD-1. They are accompanied by a moderate proportion of Dinoflagellate cysts and indeterminable sporomoromphs. Among the latter all four classes of damage distinguished by Cushing (1967) were found. Their coexistence with Tertiary sporomorphs makes it plausible that these too originate from redeposition and are probably of the same age. Low frequency of Tertiary pollen is also present in local pollen assemblage zones HD-2, HD-3, HD-4 and HD-9. The frequency of Tertiary taxa and an increase in their diversity is also observed in zones HD-21, HD-22, HD-25 – HD 27 and HD-31 – HD-39. In the percentage diagram (Fig. 3), all the pre-Quaternary sporomorphs determined are presented as a total "Tertiary sum" curve. A complete list of the redeposited sporomorphs identified included in this curve are given in Tab. 4.

The most probable source of the pre-Quaternary sporomorphs are silts of Odranian or Wartanian age, which constitute part of the moraine uplands of southern Podlasie and also occur in the marginal part of the basin at Horoszki Duże (Nitychoruk 1995).

POLLEN STRATIGRAPHY

The complete percentage pollen diagram (Fig. 3) is divided into 39 local pollen assemblages zones (L PAZ), which are numbered from the bottom upwards and preceded by the HD

Table 4. Redeposited Pre-Quaternary sporomorphs

Abies (metamorph.)
Acer (Tertiary type)
Anacardiaceae undiff.
Araliaceae
Carya
Castanea/Castanopsis
Celtis
Corylopsis
Cyrillaceae/Clethraceae
Engelhardtia
Ilex (Tertiary type)
Inaperturopollenites hiatus
Juglans
Leiotriletes wolffi
Liquidambar
Nyssa (Pl. 4 fig. 17)
Parthenocissus type (Pl. 4 fig. 18)
Picea (excl. *P. abies* type)
Pinus cf. *haploxylon* t. R.
Pinus haploxylon t. R.
Podocarpus
Quercus (Tertiary type)
Rhus type
Sciatopitys
Selaginella cf. *denticulata*
Selaginellisporis echinoides
Sequoia
Sporae (Tertiary types)
Symplocos
Taxodiaceae/Cupressaceae
Tertiary indeterminata
Tricolporopollenites fallax
T. edmundi
Tsuga diversifolia type
Tsuga undiff.
Vitis (Tertiary type)

index (Horoszki Duże). The zonation was made using the criteria described by West (1970), Birks (1973), and Janczyk-Kopikowa (1987, 1988). In general, when naming zones, only the genera name was used e.g. *Pinus* = *Pinus sylvestris* type, *Alnus* =*Alnus glutinosa* type, *Betula* = *Betula alba* type, *Picea* = *Picea abies* type, *Corylus* = *Corylus avellana* and *Taxus* = *Taxus baccata*. The exceptions are *Pinus cembra* type, *Salix polaris* type and *Ranunculus flammula* type.

The names of zones are given on the basis of the most characteristic taxa of a zone, or those represented in the greatest abundance.

HD-1, NAP–*Juniperus–Pinus* (15.89–15.79 m). The zone includes three samples. Sporomorph concentration is very low. The percentage proportions of AP are 50.4 – 71.1%, maximum NAP 49.6%. The highest proportions among AP being those of *Pinus sylvestris* type (40.7%), *Juniperus* (8.9%) and *Salix pentandra* type (8.1%). Pollen of *Betula nana* (2.3%) is present. In NAP the highest values are those of Poaceae undiff. (up to 15.9%), Cyperaceae (over 12%), *Artemisia* (10.7%), and Chenopodiaceae (6.1%). In this zone the proportion of Tertiary sporomorphs is up to 20%, and corroded pollen reaches over 10%. Dinoflagellate cysts are also present.

The upper boundary of this zone has been set above the distinct fall in the values of Poaceae undiff., *Artemisi*a, Cyperaceae, *Juniperus*, and *Salix polaris* type, and below the increase in AP value to 87.3%.

HD-2, *Betula–Pinus* (15.79–15.64 m). The zone spans three samples. Increase in share of AP to 90%. The lower part of this zone is dominated by the pollen of *Pinus sylvestris* type (max. 44.7%), the share of *Betula alba* pollen being 36.4% and that of *Artemisi*a up to 5.5%. In the middle and upper part of the zone, the pollen of *Betula alba* type dominates (max. 52.7%), pine reaching 33%. The pollen curve of *Populus* reaches a maximum of 2.5%. Pollen of *Betula nana* and *Juniperus* is still present. *Ulmus* and *Quercus* reach 2.2% and 1.1% respectively. The continuous curve of *Humulus lupulus* begins.

The upper boundary is designated above the slight fall in the value of *Betula alba* type pollen and before the increase in *Quercus* (1.1%).

HD-3, *Pinus–Betula–Quercus–Ulmus* (15.64– 15.49 m). The zone spans three samples. The highest values are that of *Pinus sylvestris* pollen (up to 40.6%) and *Betula alba* type (ca. 44%). The proportion of *Quercus* pollen increases from 4.3 to 23.7%. The values of *Ulmus* oscillate around 2.8%. In this zone the continuous curve of *Fraxinus* begins, reaching 2.8%. NAP values below 10%.

The upper boundary is designated above the drastic fall in the values of *Betula alba* type pollen and *Pinus sylvestris* type and below the increase in the values of *Quercus*.

HD-4, *Quercus–Fraxinus–Ulmus* (15.49–15.20 m). The zone spans six samples. At the bottom of the zone, the concentration of sporomorphs declines (Fig. 7). *Quercus* pollen dominates throughout, reaching 51.3%. Values of *Fraxinus* stable at first (about 8%), reaching a maximum in the uppermost layer of the zone (15.6%). The pine curve declines distinctly, to 9.3%. Constant presence of *Ulmus* pollen (2.8–5.6%). Pollen of *Taxus baccata* and *Hedera helix* occurs for the first time. In the upper part of the zone, values of *Corylus avellana* increase to 19.6%.

The upper boundary of the zone has been set where values of *Quercus* and *Fraxinus* fall and before an increase in values of *Corylus avellana*.

HD-5, *Corylus–Taxus–Ulmus* (*Quercus*) (15.20–15.00 m). The zone spans four samples. In the lower part of the zone, *Quercus* pollen dominates (to 26.1%), in the younger *Corylus avellana*, which holds the absolute maximum in this zone (72.1%). Maximum values are also reached by *Ulmus* (8.3%) and *Taxus baccata* (1.4%). Pollen of *Vitis sylvestris* type and *Hedera helix* are also present. *Viscum* pollen occurs for the first time. The values of *Alnus glutinosa* type, *Carpinus* and *Tilia cordata* type pollen increase slightly, and pollen of *T. platyphyllos* type and *T. tomentosa* type appears.

The upper boundary of the zone has been determined where a decrease in *Corylus avellana* occurs, and an increase in *Tilia cordata* type, *Alnus glutinosa* type and *Carpinus*.

HD-6, *Corylus–Tilia–Alnus* (15.00–14.60 m). The zone spans four samples. AP values are still very high (max. 99%). Values of *Corylus avellana* fall to about 56%, the proportion of *Alnus glutinosa* type pollen is rising to 13.3%, that of *Tilia cordata* type to 10.8% and that of *T. platyphyllos* type and *T. tomentosa* type to below 1%. The curve of *Carpinus* reaches 9.4%. *Hedera helix*, *Viscum* and *Trapa* pollen are present (Pl. 1, fig. 12).

The upper boundary of the zone has been set above the decline of *Corylus avellana* but, before the marked increase in *Carpinus* and *Tilia cordata* type

HD-7, *Carpinus–Corylus–Tilia* (*Alnus*) (14.60–14.33 m). The zone spans six samples. AP percentage values reach an absolute maximum of 99.5%. In the lower part of the zone *Corylus avellana* pollen dominates (41.2%), and *Carpinus* in the upper part (45.9%). The curve of *Tilia cordata* type reaches its absolute maximum in this zone (11.8%). Values of *Alnus glutinosa* type oscillate within the range of 14.1% to 10.8%. The *Quercus* and *Ulmus* curves do not exceed 2.8%. The continuous curve of *Picea abies* type reaches 1.1%. *Taxus baccata*, *Hedera helix* and *Viscum* occur with values of below 1%. In the topmost sample of the zone, pollen of *Buxus sempervirens* and *Ilex aquifolium* type appears.

The upper boundary of the zone has been set above the dramatic decline of *Corylus avellana* and before a successive rise in *Carpinus*.

HD-8, *Carpinus–Alnus–Picea* (14.33–14.04 m). The zone spans eight samples. *Carpinus* pollen dominates, reaching a maximum of 73%. *Alnus glutinosa* type pollen fluctuates from 9.8 to 13.1%. *Corylus avellana* decreases to 3.2%. *Tilia cordata* type and *Taxus baccata* have continuous curves under 1%. *Picea abies* type increases from 0.1% to 6.6%, the curve of *Abies alba* pollen also has an upward trend to 1.1%. Values of *Pinus sylvestris* type (6.5%), *Betula alba* type (3.7%) and *Quercus* (5.1%) rise. Single grains of the following pollen taxa are found: *Fagus*, *Hedera helix*, *Viscum* and *Buxus sempervirens*.

The upper boundary of the zone has been determined above the marked decline in the *Carpinus* pollen, and before an increase in pollen values of *Picea abies* type, *Pinus sylvestris* type and *Abies alba*.

HD-9, *Picea–Abies–Carpinus* (*Pinus*) (14.04–13.88 m). The zone comprises four samples. A characteristic feature is high frequency of *Picea abies* type (max. 17.7%) and a culmination of *Abies alba* at 2.5%. In the lower part of the zone, *Carpinus* pollen dominates, with a maximum of 49.2% and, in the upper part, the pollen of *Pinus sylvestris* type (max. 43.8%). The curves of *Betula alba* type (to 8.5%) and *Quercus* (to 10.3%) also show an upward trend. Pollen of *Fagus*, *Viscum* and *Buxus sempervirens* is present.

The upper boundary of the zone is set at the level of the decline or disappearance of the curves of: *Picea abies* type, *Abies alba, Carpinus*, *Alnus glutinosa* type, *Quercus*, *Corylus avellana*, and an increase in the curve of *Pinus sylvestris* type.

HD-10, *Pinus* (13.88–13.69 m). The zone spans five samples. The pollen of *Pinus sylvestris* type dominates absolutely, reaching a maximum of 85.5%. Of other trees, *Betula alba* type reaches 11.4%. The percentages of *Picea abies* type are below 0.5%. The continuous curves of *Betula nana* pollen and of *Juniperus* begin. The NAP proportion increases to 7% (Poaceae undiff. and Cyperaceae).

The upper boundary of the zone has been set at the level in which the *Pinus sylvestris* type curve falls while those of *Betula alba* type and *Picea abies* type increase.

HD-11, *Pinus–Betula–Picea* (13.69–13.59 m). This zone spans three samples. Pollen of *Pinus sylvestris* type continues to dominate, *Betula alba* type reaches 19.3%, and *Picea abies* type 3.4%. Pollen of *Juniperus* and *Larix* is present (Pl. 1, fig. 10), and that of *Betula nana*, with values below 1%.

The upper boundary of the zone is marked

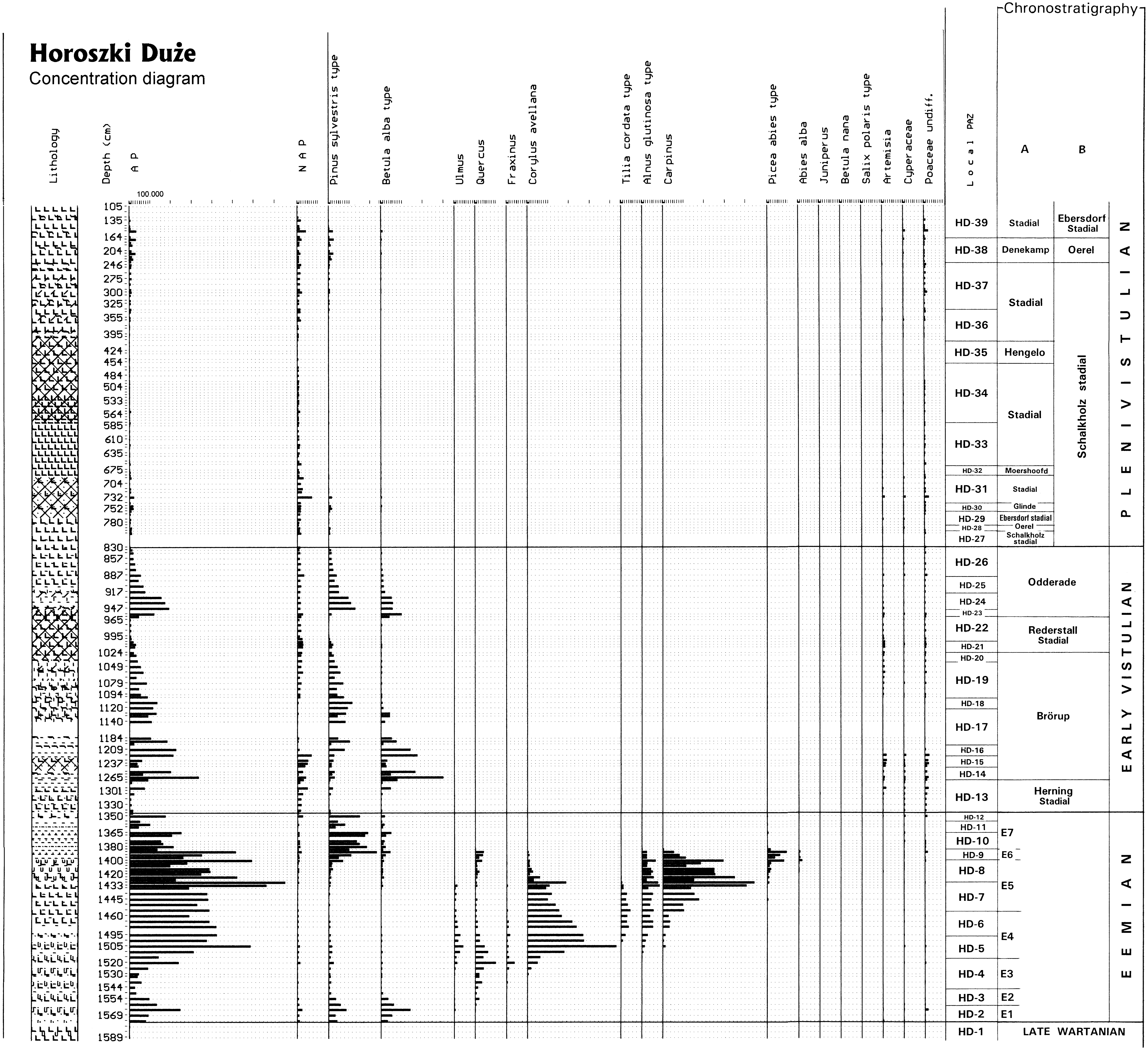

Fig. 7. Pollen concentration diagram of selected taxa.
Lithology as in Fig. 3

by a rise in *Pinus sylvestris* type pollen and a fall in those of *Betula alba* type and *Picea abies* type.

HD-12, *Pinus–Larix* (13.59–13.50 m). The zone spans two samples. Pollen of *Pinus sylvestris* type continues to dominate, increasing to 79.9%, as opposed to that of *Betula alba* type, the values of which fall to 8.5%. *Larix* pollen reaches a maximum of 1.6%. *Betula nana* and *Juniperus* pollen is present with values below a 1%. In the upper part of the zone, the proportion of NAP rises to 13.4%.

The upper boundary of the zone is marked by an increase in the NAP curve and a decrease in AP values.

HD-13, Poaceae–Cyperaceae–*Juniperus* (*Salix polaris* type) (13.50–12.81 m). The zone covers eight samples. It is characterized by an increase in NAP values to 69%. The highest pollen shares are those of Poaceae undiff. (33.4%), Cyperaceae (20.9%) and *Artemisia* (13.7%). Both *Juniperus* (max.7%) and *Salix polaris* type (max.2.8%) have constant and relatively high values. Values of *Betula nana* rise to 1.2%, those of *Alnus viridis* are below 1%. AP is represented chiefly by the curves of *Pinus sylvestris* type, whose values oscillate from 9.3 to 26.6% and by *Betula alba* type from 7.8 to 39.8%. Of other trees, values above 1% are reached by pollen of *Picea abies* type, *Pinus cembra* type (Pl. 1, fig. 5) and *Alnus glutinosa* type, *Larix* and *Populus* are present in this zone.

The upper boundary of the zone is determined by a decline of NAP and an increase of *Betula alba* type.

HD-14, *Betula* (12.81–12.53 m). The zone spans four samples. The pollen of *Betula alba* type dominates, with a maximum of 80%, *Pinus sylvestris* type reaching 24.1%. There are single pollen grains of *Populus, Larix, Pinus cembra* type, *Betula nana*, *Alnus viridis, Juniperus* and *Salix polaris* type. Values of NAP fall below 7%.

The upper boundary of the zone is determined by another increase in NAP values, and a fall in *Betula alba* type values.

HD-15, NAP–*Betula* (12.53–12.33 m). The zone spans 3 samples. Values of NAP increase to 58.3%; the highest proportions being those of Poaceae undiff. (23.3%), *Artemisia* (18.5%) and Cyperaceae 9.1%. Among AP, the curve of *Betula alba* type reaches a maximum of 32.5%, *Pinus sylvestris* type 20.3%, *P. cembra* type 2%. *Picea abies* type and *Larix* have values below 1%. Values of *Salix polaris* type, *Betula nana*, and *Juniperus* increase.

The upper boundary of the zone is determined by an increase in the curve of *Betula alba* type and a decline in NAP values.

HD-16, *Betula*–NAP (12.33–12.09 m). The zone spans 2 samples. AP values increase to 95.7%; the pollen of *Betula alba* type (63.2%) and *Pinus sylvestris* type (32.9%) dominates. Pollen of *Pinus cembra* type, *Larix* and *Betula nana* is present. NAP is represented by 24.4% in the lower spectrum, but decreases to 4.3%.

The upper boundary of the zone is marked by an increase in the curve of *Pinus sylvestris* type.

HD-17, *Pinus–Betula–Larix* (*Picea*) (12.09– 11.30 m). The zone spans 6 samples. The AP frequency are very high, reaching 96.5%. *Pinus sylvestris* type shows a distinct increase while *Betula alba* type falls. Continuous curves are present for *Pinus cembra* type (max.1.4%), *Larix* (max.2.8%), *Picea abies* type (max. 1.5%) and *Betula nana*.

The upper boundary of the zone is set at the depth at which the curves of *Pinus sylvestris* type and *P. cembra* type increase.

HD-18, *Pinus–Pinus cembra* type–*Picea* (11.30–11.09 m). The zone includes 2 samples. P values reach a maximum of 97.5%, dominated by *Pinus sylvestris* type. Of other trees, *P. cembra* type reaches 3.7%, *Larix* 2.7%, *Picea abies* type 1.8%, while the values of *Betula alba* type reach approximately 10%. *Betula nana* has a continuous curve.

The upper boundary of the zone is marked by a decrease in the proportion of *Pinus sylvestris* type and an increase in values of NAP, *Larix* and *Picea abies* type.

HD-19, *Pinus–Larix–Picea* (NAP) (11.09–10.49 m). The zone spans 7 samples. Arboreal pollen dominates throughout the zone, but decreases upwards. The highest values are reached by *Pinus sylvestris* type (72.1%), *Betula alba* type fluctuating under 8%. Of other trees, *Pinus cembra* type reaches 1.2%, *Larix* 5%, and *Picea abies* type 3.1%. Among NAP, the highest share is that of *Artemisia* pollen (13.6%) and Poaceae undiff. (9.5%). Taxonomic diversity increases among herbaceous plants.

The upper boundary of the zone is marked by a fall in the AP values (mainly *Pinus sylvestris* type) and an increase in NAP.

HD-20, *Pinus–Pinus cembra* type-NAP

(10.49–10.29 m). The zone spans two samples. Further decline in AP to 63.5%. Of arboreal pollen, *Pinus sylvestris* type continues to dominate. The values of the following taxa are relatively high: *Betula alba* type (7.9%), *Pinus cembra* type (6.4%), *Larix* (3%), and *Picea abies* type (1.2%). The curves of *Betula nana* and *Salix polaris* type are below 1%. NAP consists mainly of Poaceae undiff. (13%), *Artemisia* (14.5%), and Cyperaceae (6.2%), but the diversity of herbaceous taxa increases.

The upper boundary of the zone is marked by an increase in values of NAP and decline in AP.

HD-21, NAP–*Pinus-Pinus cembra* type (10.29–10.10 m). The zone spans 3 samples. A marked increase in the NAP values takes place (max.53.5%). *Artemisia*, Poaceae undiff. and Cyperaceae are dominant. The diversity of herbaceous plant taxa is large. Of AP the highest shares are those of *Pinus sylvestris* type, *Betula alba* type, and *Pinus cembra* type. *Larix* reaches 1.5%, and *Picea abies* type 1.1%. Continuous curves of *Betula nana* and *Salix polaris* type are present.

The upper limit of the zone has been set at the level at which the proportion of NAP, *Betula nana* and *Salix polaris* type increases and a decrease takes place in AP values.

HD-22, NAP–*Betula nana–Salix polaris* type–*Pinus cembra* type (10.10–9.65m). The zone spans 6 samples. The values of NAP reach 73.5%, the highest proportions being those of Poaceae undiff. (27.6%), *Artemisia* (24.4%), Cyperaceae (17.9%) and Chenopodiaceae (3%). There are many herbaceous taxa represented. The maximum values are reached by *Betula nana* 3%, *Salix polaris* type 2.1% and *Juniperus* below 1%. Of AP, the highest values are those of *Pinus sylvestris* type (20.2%), *Betula alba* type (18.3%) and *Pinus cembra* type (4.2%). *Larix* and *Picea abies* type occur with frequency below 1%.

The upper limit of the zone is marked by an increase in the AP curves and a decline in NAP.

HD-23, *Betula* (9.65–9.55 m). The zone spans two samples. Pollen of *Betula alba* type (68.7%) is absolutely dominant. The following pollen of other trees occurs: *Pinus sylvestris* type (max. 10%), *P. cembra* type (max. 2.1%), and *Picea abies* type (0.3%), NAP maximum 18.1%.

The upper boundary of the zone is marked by a decline in *Betula alba* type and an increase in *Pinus sylvestris* type.

HD-24, *Pinus–Betula–Pinus cembra* type (9.55–9.27 m). The zone spans 3 samples. AP (93.2%) dominates, with the maximum shares of *Pinus sylvestris* type at 63.3%, *Betula alba* type 31.5% and *Pinus cembra* type 1.8%. *Picea abies* type and *Betula nana* are present.

The upper boundary of the zone is marked by an increase in NAP values.

HD-25, *Pinus–Larix–Betula nana*–(NAP) (9.27–8.97 m). The zone spans 3 samples. The pollen of *Pinus sylvestris* type dominates. *Larix* and *Pinus cembra* type have continuous curves with a maximum of 2.4% and 1.7% respectively. *Betula nana* reaches 1.4%. In the NAP group, the highest proportions are those of: Poaceae undiff., *Artemisia* and Cyperaceae.

The upper boundary of the zone is marked by an increase of NAP.

HD-26, NAP–*Pinus–Larix–Salix polaris* type (8.97–8.38 m). The zone spans 6 samples. The proportion of NAP rises from 37.8 to 41.1% (max. Poaceae undiff. 20.2%, *Artemisia* 12.2% and Cyperaceae 10.1%). *Pinus sylvestris* type fluctuates around 45% while also showing a clear downward trend; likewise the curves of *Larix* (1.8–0.3%) and *Pinus cembra* type (2.5–0.4%). *Salix polaris* type, *Betula nana* and *Picea abies* type are present with continuous curves.

The upper boundary of the zone has been set below the dramatic increase in NAP values.

HD-27, Poaceae–*Pinus cembra* type (8.38–8.00 m). The zone spans two samples. NAP dominates in this zone (73.4%). The greatest share is that of Poaceae undiff. (39.6%), *Artemisia* (17.8%) and Cyperaceae (11.2%). *Pinus sylvestris* type (26%), *Betula alba* type (10.3%) and *Pinus cembra* type (4.1%) reach the highest values among the trees. *Larix*, *Picea abies* type, *Juniperus* and *Betula nana* are represented by values of under 1%. A high proportion of Bryales (=Musci excl. *Sphagnum*) spores is noted, with a maximum of 43.8%.

The upper boundary of the zone is marked by a slight increase in AP (mainly *Pinus sylvestris* type) and a decline in NAP.

HD-28, NAP–*Pinus-P. cembra* type (8.00–7.90 m). The zone spans two samples. The proportion of AP increases to 47.2%. *Pinus sylvestris* type reaches 38.1%, and *P. cembra* type 4.5%. *Larix*, *Picea abies* type and *Betula nana* pollen is present, with values below 1%.

The upper boundary of the zone is marked by a decline in the value of *Pinus sylvestris* type and an increase in NAP.

HD-29, Poaceae-Cyperaceae–*Artemisia*–*Pinus* (7.90–7.62 m). The zone spans 4 samples. A high NAP share with a maximum of 68%, including Poaceae undiff. 27.8%, Cyperaceae 20.8% and *Artemisia* 19.3%. *Betula nana* and *Salix polaris* type have continuous curves. The AP sum consists mainly of *Pinus sylvestris* type and *Betula alba* type.

The upper boundary of the zone is marked by an increase in AP and a decline in NAP.

HD-30, *Pinus*–NAP–*P. cembra* type (7.62–7.47 m). The zone spans three samples. The proportion of AP increases to 54.2%. The highest frequency is reached by *Pinus sylvestris* type (41.5%), *Betula alba* type (13.1%) and *Pinus cembra* type (3.7%). The main NAP taxa decrease: Poaceae undiff. to 16.4%, *Artemisia* to 6.4% and Cyperaceae to 8.8%.

The upper boundary of the zone is marked by the decreasing AP and NAP increasing again.

HD-31, Poaceae–*Juniperus*–*Ranunculus flammula* type (7.47–6.92 m). The zone spans six samples. NAP reaches approximately 75%. The highest proportions are those of Poaceae undiff. 31.4%, *Artemisia* 14.3%, Cyperaceae 15.9% and *Ranunculus flammula* type 22.1%. *Juniperus, Betula nana* have almost continuous curves and *Salix polaris* type shows a maximum of 0.7%. Pollen of *Larix*, *Pinus cembra* type and *Picea abies* type is present. The green algae *Pediastrum* has a maximum of 80%.

The upper boundary of the zone is set by a rise in the curve of AP.

HD-32, NAP–*Betula*–*B. nana* (*Pinus*) (6.92–6.75 m). The zone spans three samples. AP increases to 36%. The maximum proportion of *Betula alba* type is 15.1%, *Pinus sylvestris* type 17.3%, and *P. cembra* type 1.7%. *Betula nana* and *Salix polaris* type reach 2.9% and 2.2% respectively, *Juniperus* reaching 1.7%. Ericaceae undiff. is present with 4%. The NAP values continue to be high; dominated by Poaceae undiff., *Artemisia*, Cyperaceae and *Ranunculus flammula* type, which reaches 12.5% in the upper part of the zone.

The upper boundary of the zone has been set before AP values fall again.

HD-33, Poaceae–*Artemisia*–*Betula nana* (6.75–5.85 m). The zone spans ten samples. The values of NAP fluctuate between 72.7% and 78.5%. Poaceae undiff. dominates (44.8%), *Artemisia* (20.7%), and Cyperaceae (17.8%). Chenopodiaceae, *Betula nana* and *Salix polaris* type have continuous curves. AP is represented mainly by *Betula alba* type, *Pinus sylvestris* type, *P. cembra* type, and *Picea abies* type. *Larix*, *Populus* and *Abies alba* pollen are below 1%. Pollen of thermophilous trees is represented by *Alnus glutinosa* type, *Carpinus*, *Quercus*, *Fraxinus*, *Ulmus*, and *Corylus avellana*.

The upper boundary of the zone has been set after the decline in the values of Poaceae undiff. but before an increase in the values of *Pinus cembra* type.

HD-34, NAP–*Pinus cembra* type (5.85–4.64 m). The zone spans 19 samples. There is a slight increase in AP (max. 39.2%). Within NAP there is initially a decline in the values of Poaceae undiff. (min. 24.5%) but, in the top of the zone, an increase to 40.7%. The Cyperaceae curve fluctuates from 12 – 18%. The proportion of *Artemisia* is between 10 and 13% but with a maximum of 18,1% at the bottom of the zone. The pollen curve of *Pinus cembra* type reaches an absolute maximum (7.8%). Continuous curves are found for *Picea abies* type (max.1.8%) and *Betula nana* (max. 1.8%). Pollen of *Larix*, *Populus*, *Juniperus*, and *Salix polaris* type is present. Pollen of the thermophilous trees *Alnus glutinosa* type, *Carpinus*, *Quercus*, *Ulmus*, and *Corylus avellana* are noted.

The upper boundary of the zone is determined by another decline in the value of NAP and a slight increase in AP values (mainly *Pinus sylvestris* type).

HD-35, NAP–*Pinus*–*Pinus cembra type* (4.64–4.14 m). This zone spans 5 samples. The AP curve shows a slight increase (max. 43.1%). The most frequent tree pollen is *Pinus sylvestris* type, *Betula alba* type, and *Pinus cembra* type. *Betula nana* and *Salix polaris* type have continuous curves. Pollen of *Populus* and *Juniperus* occurs sporadically. NAP consists mainly of Poaceae undiff., Cyperaceae, and *Artemisia*. The continuous curve of Chenopodiaceae reaches 1.8%.

The upper boundary of the zone is determined by another slight decline in the proportion of AP.

HD-36, Cyperaceae–Poaceae–*Artemisia* (4.14–3.45 m). The zone spans 8 samples. An increase in NAP values occurs (max. 82.7%).

In the lower part of the zone, pollen of Cyperaceae (max. 35.6%) dominates, but in the upper part Poaceae undiff. (max. 38.2%) is dominating. *Artemisia* increases at the top of the zone to 13.1%. AP mainly consists of *Pinus sylvestris* type with a maximum of 19.1%, *Betula alba* type and *Pinus cembra* type. The curves of *Betula nana* and *Salix polaris* type are constant. Single pollen grains of *Picea abies* type, *Populus*, *Juniperus*, and *Alnus viridis* are found. As in the previous zone, pollen of thermophilous trees and *Corylus avellana* is present.

The upper boundary of this zone is set by a decline in the values of NAP and an increase in the proportion of *Pinus sylvestris* type.

HD-37, Poaceae–*Pinus* (3.45–2.46 m). The zone spans 11 samples. An increase in AP values to 45.9% takes place at the bottom of this zone and a decline to 33.8% in its upper part. AP is dominated by *Pinus sylvestris* type (max. 33.4%). The values of *Betula alba* type fluctuate around 10%. *P. cembra* type has a continuous curve. Pollen of *Larix*, *Picea abies* type, and *Populus* is present. Declines take place in the values of *Betula nana* (max. 1.2%) and *Salix polaris* type to below 1%. Poaceae undiff. with a maximum of 44.5% and Cyperaceae (max. 17.6%) comprise the bulk of NAP. *Artemisia* decreases from 10% at the bottom to 5% at the top of the zone. Pollen of thermophilous trees (*Ulmus*, *Quercus*, *Alnus glutinosa* type, *Carpinus*), and *Corylus avellana* occurs with values below 1%.

The upper boundary of the zone is marked by an increase in values of *Pinus sylvestris* type and a decline in the values of Poaceae undiff.

HD-38, *Pinus*–NAP (2.46–1.74 m). The zone spans 8 samples. AP increases to ca. 68%. Pollen of *Pinus sylvestris* type dominates (max. 53.6%). The curves of *Pinus cembra* type and *Betula alba* type are continuous. Pollen of *Larix*, *Picea abies* type, and *Populus* is present. *Betula nana* has a continuous curve. *Salix polaris* type and *Juniperus* show values below 1%. Pollen of thermophilous trees and of *Corylus avellana* present. NAP is dominated by Poaceae undiff., Cyperaceae, and *Artemisia*.

The upper boundary of the zone is determined by a decline in the values of AP and an increase in NAP.

HD-39, Poaceae–*Betula nana* (1.74–1.05 m). The zone spans 7 samples. An increase in NAP takes place, to max. 83.5% at the top of the zone. Pollen of Poaceae undiff. is dominant (up to 60.7%). Of other herbaceous plants, Cyperaceae and *Artemisia* are abundant. The curves of *Betula nana* and *Salix polaris* type show an upward. The AP curve at the base of the zone is formed mostly by *Pinus sylvestris* type and, at the top, *Betula alba* type. Pollen of *Pinus cembra* type (max. 2.2%) is present and also traces of *Picea abies* type and *Larix*. Pollen of thermophilous trees, and of *Corylus avellana* occur sporadically.

STRATIGRAPHY OF MACROSCOPIC REMAINS

13 local macrofossil assemblage zones (L MAZ) have been distinguished (Fig. 4). They are numbered from the bottom of the profile upwards HDM-1 – HDM-13 (HDM=Horoszki Duże Macrofossil). In distinguishing these, the feature used was the presence of taxa which are diagnostic for a given zone, or their abundance.

The correspondence of macrofossil assemblage zones to local pollen assemblage zones has been presented in Fig. 4.

HDM-1 (15.865–14.525 m). The zone includes 11 samples. The lower part of the zone is dominated by the remains of tree birches (Pl. 5, fig. 9). A few taxa was noted. The remains of *Phragmites* and *Typha* are present almost constantly. Among aquatic plants, there are *Najas marina* (Pl. 6, fig. 6), *N. flexilis* (Pl. 6, fig. 7), and *N. minor* (Pl. 6, fig. 8). Mosses are represented by four species, of which the only remains to occur regularly are those of *Drepanocladus revolvens*. There are traces of *Cenococcum graniformae*.

The upper boundary of the zone has been set below the appearance of the remains of *Tilia tomentosa* and *T.* cf. *platyphyllos*.

HDM-2 (14.525–13.980 m). The zone includes 7 samples. This zone is very poor in macroscopic remains. Remains of thermophilous trees are present, i.e. *Tilia tomentosa*, *T.* cf. *platyphyllos*, *Carpinus betulus* (Pl. 5, fig. 16), *Alnus glutinosa*, and *Acer*. *Larix* needles and seeds (Pl. 5, figs 5, 6) occur in this zone. Of mosses, only *Drepanocladus polycarpos* present.

The upper boundary of the zone is placed below the increase of *Betula* sect. *Albae* remains.

HDM-3 (13.980–13.630 m). The zone spans 5 samples. A characteristic feature of this zone is numerous remains of tree birches (*Betula* sect. *Albae*), e.g. *Betula pubescens* (Pl. 5, fig. 10). *Pinus sylvestris* seed (Pl. 5, fig. 2), and fragments of *Picea abies* needles (Pl. 5, figs 7, 8) also occur. A fruit stone of *Sambucus nigra* was found (Pl. 5, fig. 17). Mosses are represented by two species of *Drepanocladus*, i.e. *D. polycarpos* (abundant) and *D. revolvens*.

The upper boundary of the zone has been determined where *Larix* needles reappear.

HDM-4 (13.630–12.925 m). The zone spans 8 samples. *Larix* and *Betula* sect. *Albae* are present in comparatively great abundance. Of other trees, *Pinus sylvestris* occurs in low amounts. The diversity of herbaceous plants increases. *Carex rostrata/vesicaria*, *Potentilla sp. div.*, *Rorippa palustris* and, in somewhat greater numbers, *Ranunculus sceleratus* (Pl. 6, fig. 15) are present. Aquatic plants are represented by *Callitriche*, *Nitella syncarpa*, *Batrachium* (Pl. 6, fig. 21), *Stratiotes*, and several species of the genus *Potamogeton*. Endocarps of *Potamogeton sukaczevii* are present for the first time. The diversity of mosses increases, of which *Drepanocladus revolvens* is the most abundant.

The upper boundary has been set below the considerable increase in remains of *Betula* sect. *Albae*.

HDM-5 (12.925–11.860 m). The zone includes 13 samples. The most abundant remains are the nuts of tree birches. Fruit scales of *Betula pendula* are present (Pl. 5, fig. 11). Of other trees, *Pinus sylvestris* and *Larix* are infrequently represented. The group of herbaceous plants already present in the previous zone are increased, by *Fragaria* (Pl. 6, fig. 23), *Ranunculus flammula* (Pl. 6, fig. 14), and *Bidens tripartita* (Pl. 6, fig. 18). Aquatic plants noted were *Ceratophyllym demersum* (Pl. 6, fig. 10) and *Potamogeton praelongus* (Pl. 5, fig. 28). The remains of *Drepanocladus revolvens* still occur in the greatest abundance among mosses.

The upper boundary of the zone has been set at the point where *Najas flexilis* appears in great abundance.

HDM-6 (11.860–11.325 m). The zone covers 4 samples. This is the zone with the most abundant occurrence of *Najas flexilis*. The algae *Chara contraria* occurs for the first time in greater numbers. A few remains of *Larix* and *Betula* sect. *Albae* were identified.

The upper boundary of the zone has been set after a decline in *Najas flexilis* and an increase in the number of *Larix* needles.

HDM-7 (11.325–10.520 m). The zone spans 10 samples. *Larix* needles are most abundant in this zone out of the whole profile. Larch seeds are also present (Pl. 5, fig. 4), and wood of *Picea/Larix*. The genus *Pinus* is represented by needles of *P. sylvestris* (Pl. 5, fig. 2) and *P. cembra* (a fragment of a needle). In the upper part of the zone, remains of *Ranunculus sceleratus*, *Eleocharis ovata* (Pl. 6, fig. 16), *Callitriche,* and *Chara contraria* are abundant. The diversity of aquatic taxa increases. *Nuphar pumila*, *Myriophyllum alternifolium*, and 7 species of the genus *Potamogeton* are present, of which *P. sukaczevii*, *P. pusillus,* and *P. praelongus* are most abundant. Throughout the zone, *Drepanocladus revolvens* are the most frequent moss remains. *Meesia triquetra* and *Calliergon trifarium* are also present.

The upper boundary has been set after a decline in *Larix* and before the abundant appearance of *Nitella syncarpa*.

HDM-8 (10.520–9.725 m). The zone spans 7 samples. Rich abundance of *Nitella syncarpa*, *Chara contraria*, and *Batrachium*. *Callitriche* and *Najas flexilis* are relatively abundant. In the lowermost part of the zone *Larix* and *Picea abies* occur. Only in this zone *Betula nana* is present (Pl. 5, figs 12, 14–15). Among mosses, the most abundant is *Drepanocladus revolvens*. *Calliergon trifarium* is relatively common, while *Meesia triquetra* and *Calliergon turgescens* are sporadic.

The upper boundary is put above a decline in *Nitella syncarpa*, *Batrachium*, and *Callitriche* and before an increase of *Betula* sect. *Albae*.

HDM-9 (9.725–9.400 m). The zone includes 3 samples. The zone of the most abundant presence of tree birches nuts (*Betula* sect. *Albae*, Pl. 5, fig. 9). Wood of *Populus* is present. Remains of sedges are relatively abundant (*Carex* sp. div., *C. elata,* and *C. rostrata/vesicaria*). The most frequent remains are those of *Rumex maritimus* and *Potamogeton sukaczevii*. Mosses are only represented by *Drepanocladus revolvens* and *D. aduncus*.

The upper boundary of the zone is marked by a decrease in the quantity of *Betula* sect. *Albae* and an increase of *Nitella syncarpa*.

HDM-10 (9.400–8.300 m). The zone spans 12 samples. This is the zone in which the maximum quantity of *Nitella syncarpa* is found. This is the first time *Nitella gracilis* appears in great abundance (maximum). There are considerable amounts of *Batrachium* and *Callitriche* at the bottom of the zone. Macrofossils of tree birches and larch occur and are quite abundant at the bottom of the zone. *Myriophyllum* cf. *microcarpum* and *Ceratophyllum submersum* are present (Pl. 6, fig. 11). Mosses are represented by a few species of which, *Drepanocladus revolvens* and *D. aduncus* are the most abundant.

The upper boundary has been set above a decline in the abundance of *Nitella syncarpa* and an increase in *Callitriche* and *Batrachium*.

HDM-11 (8.300–7.450 m). The zone includes 6 samples. In this zone, mainly *Callitriche* and *Batrachium* are present as well as various mosses, but with no species clearly dominant. Low amounts of tree birches occur (*Betula* sect. *Albae*), as well as *Rorippa palustris, Elatine hydropiper,* and *Chamaedaphne calyculata* (Pl. 6, fig. 26).

The upper boundary of the zone has been set above the abundant occurrence of *Batrachium* and *Callitriche* remains and before a considerable increase in *Nitella syncarpa*.

HDM-12 (7.450–5.710 m). The zone spans 20 samples. Among aquatic plants, *Nitella syncarpa* occurs abundantly throughout the zone, *Callitriche* and *Batrachium* being less abundant. *Nitella gracilis* was found only in the upper part, sporadically also *Potamogeton pusillus* and *P. praelongus*. *Alnus* wood was identified in one sample. Of herbaceous land plants, *Scleranthus annuus* (Pl. 6, fig. 28), *Mentha* sp., and *Potentilla* sp. div. occur sporadically. Mosses are relatively diverse, especially in the lower part of the zone. *Drepanocladus revolvens* is the most abundant. *Amblystegium varium* occurs only in this zone.

The upper limit has been set above the abundant occurrence of *Nitella syncarpa* and *Batrachium* and before an increase in the remains of *Callitriche*.

HDM-13 (5.710–1.120 m). The zone spans 42 samples. *Callitriche* is the most abundant taxon in this zone, *Batrachium* and *Nitella syncarpa* less so. In the middle part of this zone, *Zannichellia palustris* subsp. *pedicellata* is relatively abundant. Remains of *Betula* sect. *Albae*, *Betula* cf. *humilis* (Pl. 5, fig. 13), *Larix*, and wood fragments of *Alnus* and *Alnus*/*Betula* are present in small quantities. Among herbaceous plants the following are present: *Filipendula* cf. *vulgaris* (Pl. 6, fig. 30), *Taraxacum* (Pl. 6, fig. 32), *Rumex maritimus* (Pl. 6, fig. 19), *Ranunculus sceleratus*, and *Carex* cf. *elongata*. Mosses are relatively diverse, especially in the upper part of the zone. Remains of *Calliergon trifarium*, *Drepanocladus aduncus*, and *D. revolvens* are most abundant. *Campylium elodes*, *Cinclidium stygium*, *Bryum pseutotriquetrum*, *B. neodamense*, *Amblystegium humile,* and *Cratoneuron commutatum* occur only in this zone.

CHRONOSTRATIGRAPHY

The pollen spectra of the sequence from Horoszki Duże have been divided into 39 local pollen assemblage zones (L PAZ), representing three different stages of the Pleistocene. Correlation of the local pollen assemblage zones with chronostratigraphic units is based on characteristic features in the vegetation succession, and presented in Table 5.

L PAZ HD-1 represents a treeless period. The L PAZ HD-2 to HD-12 document an interglacial plant succession. This succession is characterized by the spread of trees and hazel in the following order: *Betula–Pinus, Ulmus, Quercus, Fraxinus, Corylus, Alnus, Taxus, Tilia, Carpinus, Picea–Abies,* and *Pinus*. This vegetation succession can be correlated with the forest history at the Eemian interglacial stratotype site in Holland (Zagwijn 1961).

The local pollen assemblage zones from Horoszki were first correlated with the regional Eemian pollen assemblage zones R PAZ distinguished by Mamakowa (1989) for Poland (E1 – E7 R PAZ).

Since, no hiatus is observed in the profile from Horoszki below the Eemian sequence of local pollen assemblage zones, zone HD-1 represents the Late Glacial of the Wartanian (Saalian) Glaciation and the upper boundary of this level is at the same time the lower boundary of the Eemian interglacial.

The L PAZ HD-13 documents a treeless stadial phase, zones HD-14 to HD-20 represent an interstadial plant succession. Local zones HD-21 and HD-22 reflect the next cryomer period and L PAZ HD-23 to HD-26 correspond to the next succession of an interstadial character.

Table 5. Correlation of L PAZ from Horoszki with general chronostratigraphy. Two alternatives (A and B) of interpretation are given for the Plenivistulian. Oxygene isotope stages according to Pisias et al. (1984)

O^{18}	L PAZ	Chronostratygraphy		Stage	
		A	B		
2	HD-39 Poaceae–*Betula nana*; 1.74–1.05 m	Stadial (PV11)	Ebersdorf stadial (PV3)	MIDDLE	VISTULIAN
3	HD-38 *Pinus*–NAP; 2.46–1.74m	Denekamp interstadial (PV10)	Oerel interstadial (PV2)		
	HD-37 Poaceae–*Pinus*; 3.45–2.46 m	Stadial (PV9)	Schalkholz stadial (PV1)		
	HD36 Cyperaceae–Poaceae–*Artemisia*; 4.14–3.45 m				
	HD-35 Poaceae–Cyperaceae–*Pinus*; 4.64–4.14 m	Hengelo interstadial (PV8)			
	HD-34 NAP–*Pinus cembra* t.; 5.85–4.64 m	Stadial (PV7)			
	HD-33 Poaceae–*Artemisia*–*Betula nana*; 6.75–5.85 m				
	HD-32 NAP–*Betula*–*B. nana*–(*Pinus*); 6.92–6.75 m	Moershooft interstadial (PV6)			
	HD-31 Poaceae–*Juniperus*–*Ranunculus flammula* t.; 7.47–6.92 m	Stadial (PV5)			
	HD-30 *Pinus sylvestris*–NAP–*P. cembra* t.; 7.62–7.47m	Glinde interstadial (PV4)			
	HD-29 Poaceae–Cyperaceae–*Artemisia*–(*Pinus sylvestris*); 7.90–7.62 m	Ebersdorf stadial (PV3)			
	HD-28 NAP–*Pinus sylvestris*–(*P. cembra* t.); 8.00–7.90 m	Oerel interstadial (PV2)			
4	HD-27 Poaceae–*Pinus cembra* t.; 8.38–8.00 m	Schalkholz stadial (PV1)			
5a	HD-26 NAP–*Pinus*–*Larix*–(*Salix polaris* t.); 8.97–8.38 m	Odderade interstadial (EV4)		EARLY	
	HD-25 *Pinus*–*Larix*–*Betula nana*–(NAP); 9.27–8.97 m				
	HD-24 *Pinus*–*Betula*–*P. cembra* t.; 9.55–9.27 m				
	HD-23 *Betula*; 9.65–9.55 m				
5b	HD-22 NAP–*Betula nana*–*Salix polaris* t.–(*Pinus cembra* t.); 10.10–9.65 m	Rederstall stadial (EV3)			
	HD-21 NAP–*Pinus*–*P. cembra* t.; 10.29–10.10 m				
5c	HD-20 *Pinus*–*P. cembra* t.–NAP; 10.49–10.29 m	Brörup interstadial (EV2)			
	HD-19 *Pinus*–*Larix*–*Picea*–(NAP); 11.09–10.49 m				
	HD-18 *Pinus*–*P. cembra* t.–*Picea*; 11.30–11.09 m				
	HD-17 *Pinus*–*Betula*–*Larix*–(*Picea*); 12.09–11.30 m				
	HD-16 *Betula*–NAP; 12.33–12.09 m				
	HD-15 NAP–*Betula*; 12.53–12.33 m	cold oscillation			
	HD-14 *Betula*; 12.81–12.53 m				
5d	HD-13 Poaceae–Cyperaceae–*Juniperus*–(*Salix polaris* t.); 13.50–12.81 m	Herning stadial (EV1)			

Table 5. Continued

O^{18}	L PAZ	Chronostratygraphy		Stage
		A	B	
5e	HD-12 *Pinus–Larix*; 13.59–13.50 m	E-7		EEMIAN
	HD-11 *Pinus–Betula–Picea*; 13.69–13.59 m			
	HD-10 *Pinus*; 13.88–13.69 m			
	HD-9 *Picea–Abies–Carpinus–(Pinus)*; 14.04–13.88	E-6		
	HD-8 *Carpinus–Alnus–Picea*; 14.33–14.04 m	E-5		
	HD-7 *Carpinus–Corylus–Tilia–(Alnus)*; 14.60–14.33 m			
	HD-6 *Corylus–Tilia–Alnus*; 15.00–14.60 m	E-4		
	HD-5 *Corylus–Taxus–Ulmus–(Quercus)*; 15.20–15.00 m			
	HD-4 *Quercus–Fraxinus–Ulmus*; 15.49–15.20 m	E-3		
	HD-3 *Pinus–Betula–Quercus–(Ulmus)*; 15.64–15.49 m	E-2		
	HD-2 *Betula–Pinus*; 15.79–15.64 m	E-1		
6	HD-1 NAP–*Juniperus–Pinus*; 15.89–15.79 m	LATE WARTANIAN		

The continuous sedimentation above the Eemian sequence allows us to assume that L PAZ HD-13 to HD-26 represent the early glacial of the Vistulian Glaciation (= Early Vistulian), the lower boundary of zone HD-13 being also the upper boundary of the Eemian interglacial at Horoszki Duże. This makes it possible to correlate individual local pollen zones from Horoszki with chronostratigraphic units distinguished for Poland by Mamakowa (1989), and for north-western Europe by Behre and Lade (1986) and Behre (1989).

Zones HD-13, HD-21 and HD-22 correspond to regional pollen zones EV1 and EV3 respectively (Mamakowa 1989), representing the Herning and Rederstall interstadials in the stratigraphic scheme of Behre (1989).

Local pollen zones HD14 to HD-20 have been correlated with the Brörup interstadial (EV2). In the succession of this interstadial at Horoszki, two main phases can be distinguished. The first is the spread and dominance of birch forests (L PAZ HD-14 to HD-16). The second phase is characterized by the development and dominance of pine forest (*Pinus sylvestris*), including *Picea abies*, *Larix*, and *Pinus cembra/sibirica*. Initially, the proportion of tree birches (*Betula alba* type pollen) is relatively high in this phase (HD-17) but they decrease later, giving way to the spread of pine.

The birch phase of the Brörup interstadial at Horoszki Duże is tripartite. After a period of a dominance of tree birches (HD-14) the retreat of birch forests took place and open communities spread (HD-15). In the next zone (HD-16) the return of tree birches is registered. A similar picture of a tripartite birch phase of Brörup has been observed at other sites in western Europe (Zagwijn 1961, Menke & Tynni 1984, Behre 1989, Reille et al. 1992). This climatic oscillation is reflected also at the Zgierz-Rudunki site (Jastrzębska-Mamełka 1985) on the Łódź Upland (Wyżyna Łódzka). The birch phase of the Brörup interstadial from Horoszki corresponds to the Amersfoort interstadial (Zagwijn 1961), the pine phase can be correlated to the Brörup interstadial sensu Andersen (1961).

On the basis of plant succession, local pollen zones HD-23 to HD-26 were correlated with the younger interstadial of the Early Vistulian, Odderade (EV4). As in the Brörup interstadial, we can distinguish a shorter birch phase (HD-23) and a pine phase (HD-24 to HD26) with spruce, larch, and stone pine (*Pinus cembra*). In the vegetation succession from Horoszki Duże no climatic oscillation was found between these.

The upper boundary of zone HD-26 constitutes the upper boundary of the Early Vistulian. This is in agreement with the stratigraphic scheme of the Weichselian given by Behre (1989).

The remaining local pollen assemblage zones, HD-27 to HD-39, are supposed to represent sedimentation during the Plenivistulian.

The Early Vistulian part of the profile from Horoszki does not cause major difficulties in the identification of bio– and chronostratigraphic units and their correlation with other European sequences (Erd 1973, de Beaulieu & Reille 1984). To separate different chronostratigraphic units above the Early Vistulian (L PAZ HD-27 to HD-39) is, however, difficult.

A radiocarbon dating of 22 500 ±1000 carried out on peaty silt at a depth of 1.74 m, in L PAZ HD-38 is to some extent a fixing point. The peaty silt was dated after removal of rootlets, which are considered to be fresh. Nevertheless, contamination of the sediment in this zone is very high, and as stated by de Vries (1958, 1959 after Andersen 1961), a 1% admixture of young material is sufficient to make material 37 000 years old 5 000 years younger. The present author consider the date obtained from Horoszki to be a minimum age. In order to assess the significance of vegetation changes at Horoszki during the Plenivistulian on the basis of palaeobotanical investigation, it is crucial to date lower zones. This would be helpful in determining how late into the Plenivistulian the sedimentation continued. Because of lack of absolute dates there are present two alternative of chronostratigraphic interpretations of the Plenivistulian part of the Horoszki sequence.

Alternative A

In correlating separate local pollen zones with chronostratigraphic units of the Plenivistulian the slight increase in percentage AP values was the criterion of improvement in climatic conditions. These zones were correlated with interstadials, in contrast to decrease in AP values and increase in NAP being treated as a reaction of the plants to deteriorating climatic conditions and stadial conditions. Since nowhere in the Plenivistulian part of the profile do AP values substantiate the development of forest vegetation in the vicinity of the lake basin at Horoszki, the increases in arboreal pollen may reflect small shifts in the northern boundary of the forest, which ran far south of Horoszki. These shifts in a northerly direction may be reflected in the increase in relative AP values.

In this interpretation, five Plenivistulian interstadials have been distinguished and correlated with the north-west European – Oerel (HD-28), Glinde (HD-30), Moershooft (HD-32), Hengelo (HD-35) and Denekamp (HD-38) interstadials.

Alternative B

Bearing in mind the possibility of a too young radiocarbon date, an alternative interpretation of the chronostratigraphy of the Plenivistulian part of the profile is possible.

The small fluctuations of the AP curve may indicate that all L PAZ from HD-27 to HD-37 represent the first stadial of the Plenivistulian i.e. Schalkholz. In this alternative, the zone corresponding to the Orel interstadial is supposed to be HD-38, in which the increase in AP values reaches 68%, of which *Pinus sylvestris* type reaches 53%. The top zone, HD-39, would thus represent the second stadial phase of the Plenivistulian, Ebersdorf.

The correlation of all L PAZ with the Vistulian chronostratigraphic units distinguished and two alternatives of interpretation of the Plenivistulian part of the diagram is presented in Table 5.

VEGETATION HISTORY

LATE GLACIAL OF THE WARTANIAN GLACIATION

HD-1, NAP–*Juniperus-Pinus* L PAZ, the oldest part of HDM-1 L MAZ

A very high proportion of Tertiary and unidentifiable sporomorphs and the presence of Dinoflagellate cysts is indicative of erosion processes in a soil not fully stabilized by a continuous plant cover (cf. Mamakowa 1989).

Some of the sporomorphs common to both the Tertiary and Quaternary are associated with redeposition, especially pollen of thermophilous trees and shrubs (*Alnus glutinosa* type, *Corylus avellana*, *Fraxinus*, and *Carpinus*) as well as *Picea abies* type and *Pinus sylvestris* type. The shape of the curves of these taxa may be seen as evidence of redeposition, being very similar to that of Tertiary taxa, which are undoubtedly redeposited. Mamakowa (1989) drew attention to similar features in the Late Glacial of the Middle Poland Glaciation sensu lato at Imbramowice.

The very low frequency of all sporomorphs (Fig. 7) and a high probability that some of the *Pinus sylvestris* type pollen comes from long-distance transport show a very open type of vegetation in the vicinity of the lake. Moist habitats were occupied by sedge communities and those of shrub tundra with *Betula nana* and shrub willows (*Salix polaris* type). Most probably, *Polygonum bistorta/viviparum* also grew there, as did various representatives of Asteraceae undiff. The significant role played by mosses in the formation of the vegetation is confirmed by the huge amount of Bryales spores (=Musci excl. *Sphagnum*). More marshy regions (including those along watercourses) sustained tall herb communities, which were the likely source of the pollen of such taxa as *Thalictrum*, *Trollius*, *Filipendula*, *Lysimachia thyrsiflora*, *Rhinanthus* type, and *Veronica*. Remains of *Calliergon trifarium* and *Drepanocladus revolvens* and *Ophioglossum* spores should also be associated with this group of communities. In drier habitats, open (steppe?) grass communities spread, with a high proportion of *Artemisia*, Chenopodiaceae, *Juniperus*, and *Hippophaë rhamnoides*. Pollen of *Helianthemum nummularium* type, *Centaurea nigra* type, *Calluna vulgaris*, and spores of *Lycopodium alpinum* were probably associated with plants in these habitats. Despite the dominance of herbaceous plant communities we cannot rule out the possibility of the presence of single trees of *Pinus sylvestris*, *Picea abies*, *Larix*, willows and birches (*Salix* undiff. and *Betula alba* type).

Aquatic and littoral vegetation

It is difficult to find a single dominant element in the local vegetation, which consisted of Cyperaceae, *Phragmites* as well as *Sparganium* and *Typha* (?*angustifolia*). The belt of marginal reeds may also have included *Equisetum*. Aquatic vegetation is represented by pollen of *Potamogeton* sect. *Eupotamogeton*, *Nitella syncarpa*, and the algae genera *Pediastrum* and *Botryococcus*, which is not surprising bearing in mind the low level (below 3%) of organic matter in the sediment. The presence of *Nitella syncarpa* and a high carbonate content (21.5%) may be evidence of the presence of patches of a community similar to the modern *Nitelletum syncarpae* living in alkaline waters (Tomaszewicz 1979).

EEMIAN INTERGLACIAL

The changes in vegetation communities at Horoszki Duże during the Eemian interglacial are described on the basis of the L PAZ HD-2 to HD-12 and are correlated with the regional pollen zones (R PAZ) E1 to E7 distinguished by Mamakowa (1989) for Poland.

E1 *Pinus–Betula* R PAZ

HD-2, *Betula*–Pinus L PAZ, part of HDM-1 L MAZ

The local *Betula-Pinus* zone corresponds to the initial phase of the interglacial. With a weakening of periglacial processes and an improvement in climatic conditions, the plant cover becomes more diverse and the soils develop and stabilize (Iversen 1958, Tobolski 1976, Dzięciołowski & Tobolski 1982). A gradual increase also takes place in organic matter content in the sediment, to 11.2%, and in carbonates, to 40%. The absolute concentration of sporomorphs in the sediment increases significantly (Fig. 7).

Despite the increase in the pollen values of tree birches and pine, it seems that, especially in the older part of the zone, open communities of herbaceous plants played an important role in the landscape. The pollen of *Betula nana* (continuous curve) and *Salix polaris* type as well as spores of Bryales are evidence of patches of tundra vegetation. Damp areas continue to be occupied by communities of the wet meadow type. These were probably the source of the pollen of *Rumex acetosa* type, *Mentha* type, *Ranunculus flammula* type, *Stachys* type, *Valeriana officinalis* type, and *Thalictrum*. Dry areas on carbonate-rich soils might have been occupied by xerothermic grass communities with various species of *Artemisia* and other herbaceous plants and shrubs, represented by such taxa as *Helianthemum nummularium* type, *Saxifraga oppositifolia* type, *Achillea* type, *Rubus* undiff., and in part also by Rubiaceae and *Thalictrum*.

The continuing improvement in the climate, stabilization of soils and the openness of habitats alter the character of the vegetation, clearly transitional in the older part of the zone, into forest in the younger part. This is reflected in the doubling of the pollen concentration in the sediment. The development of pioneer birch-pine forests takes place, perhaps also of purely birch forest, as evidenced by numerous tree birch nuts and fruit scales. These must certainly have been scattered and sunlit stands in which birches probably dominated over pines, as indicated by the dominance of *Betula alba* type pollen over that of *Pinus sylvestris* type. Perhaps these were communities of the birch swamp wood type with *Betula pubescens*. Today, this community occurs in the more atlantic, north-western part of Europe (Matuszkiewicz 1981) and has its eastern limit in Poland. Its phytocoenoses occupy closed depressions in the ground moraine).

In the younger part of the zone, when the significance of birch had declined somewhat and the share of pine increased, fragments of moist pine forest may have developed. *Frangula* pollen can most probably be linked to such communities.

The very high proportion of *Populus* pollen and the presence of tree willow pollen (*Salix* undiff.) are evidence of the presence of poplar-willow floodplain forest in river valleys, with similarities to the present-day *Salici–Populetum* Meijer Drees 1936. *Solanum dulcamara* pollen and probably part of the *Mentha* type pollen derives from riverine communities. Very soon *Ulmus* and *Quercus* enter these communities, gradually changing them into elm riverine forests, in which *Humulus lupulus*, present from this zone on in the form of a continuous curve, had its habitats.

Aquatic and littoral vegetation

Phragmites type pollen and macroscopic remains of cf. *Phragmites* indicate the presence of littoral reedswamp communities of the *Phragmitetea* class. Seeds of *Typha* sp. suggest the development of communities with *Typha angustifolia* or *T. latifolia*, while spores of *Thelypteris palustris* would point to the occurrence, in the mosaic of the littoral flora, of patches reminiscent of the present-day *Thelypteridi–Phragmitetum*. In the deeper lake margins there was already vegetation characteristic of the class *Potamogetonetea*, represented by the pollen of *Potamogeton* sect. *Coleogeton* and *P.* sect. *Eupotamogeton*, hairs of *Ceratophyllum* sp., pollen of *Nuphar* (Pl. 1, fig. 9) and *Najas marina* fruit.

E2 *Pinus–Betula–Ulmus* R PAZ

HD-3, *Pinus-Betula-Quercus* (*Ulmus*) L PAZ, part of HDM-1 L MAZ

In this zone a further decline of open communities may be observed, both herbaceous and shrub. Only in the lower part of the zone does pollen of *Juniperus* and *Betula nana* occur. With the appearance of new tree species, the forest communities are transformed. Throughout the entire zone, birch-pine communities still seem to play a significant role in the landscape, as indicated by the presence of *Betula* sect. *Albae* macroscopic remains, but later *Pinus sylvestris* and tree birches gradually declined in significance in the upper part of the zone.

Riverine forests were also transformed and gained new species. Initially, these communities were reminiscent of present-day poplar-willow woods (*Salici–Populetum*) found beside regularly flooding rivers. The newly arrived tree species invaded these fertile sites. At first these were *Ulmus* and *Quercus*, joined in the younger part of the zone by *Fraxinus*. As a result of their expansion, a new multi-species elm-ash riverine forest was formed, reminiscent perhaps, in terms of site and habitat, of the modern *Ficario–Ulmetum campestris* Knapp 1942, dominated by oak, elm, and ash (Matuszkiewicz & Matuszkiewicz 1996). Tree willows (*Salix* undiff.) and *Humulus lupulus* continued to be constant elements of these communities, in which *Acer* also appeared.

Aquatic and littoral vegetation

On the basis of the plant remains determined it seems that the local vegetation did not undergo any significant change in this zone. Around the lake there was still a reedswamp belt with *Phragmites* (*Phragmites* type pollen and seeds of cf. *Phragmites*) and *Typha* (macrofossils). The presence of *Thelypteris palustris* spores suggests the persistence of communities of the *Thelypteridi–Phragmitetum* type.

The presence of *Scheuchzeria palustris* pollen, *Lycopodiella inundata* spores and macroremains of *Drepanocladus aduncus* may point to the presence of fragments of low-sedge swamps in the vicinity of the lake, perhaps corresponding to the modern communities of the *Scheuchzerietalia palustris* order. *Peplis* pollen suggests the presence of moist grassland with terrophytes in its marginal parts.

The following taxa were found in the lake: *Myriophyllum spicatum*, *M. alternifolium* (Pl. 1, fig. 9), *Nuphar*, *Nymphaea alba* (pollen *N. alba* type – Pl. 1, fig. 11), *Potamogeton* sect. *Eupotamogeton*, and *Ceratophyllum* (hairs). The presence of *Myriophyllum alternifolium* may be evidence of dystrophic conditions in the lake. Such a conclusion is also supported by a fall in organic matter in the sediment to 3.9%, with a decreasing, but still relatively high level of carbonates of 6.4% (Fig. 3).

E3 *Quercus–Fraxinus–Ulmus* R PAZ

HD-4, *Quercus–Fraxinus–Ulmus* L PAZ, part of HDM-1 L PAZ

Changes in the vegetation, which began in the previous zone, point to a bi-directional succession in forest communities. On one hand, there is the rapid retreat of pine-birch forest; on the other hand, with the expansion of *Ulmus, Quercu,s* and *Fraxinus* in the region of the modern Bug valley, there are successional changes in the communities from poplar-willow floodplain wood (of the *Salici–Populetum* type) to communities of elm-oak-ash floodplain wood, possibly like the modern *Ficario–Ulmetum* community.

The vegetation composition reflected on the basis of the percentage pollen diagram points to the dominant role of *Quercus* in the composition of the forests. As we already know, *Quercus*, along with genera such as *Betula*, *Pinus*, and *Alnus*, is over-represented in the pollen rain, while other trees are under-represented, e.g. *Tilia* and *Fraxinus*. Faegri and Iversen (1989) and Andersen (1973b) discuss this phenomenon and give the so-called correction factors which are used for trees in order to calculate the pollen spectra in a way that is more representative of their distribution. Andersen (1973b) also draws attention to the considerable over-representation of *Quercus* pollen in lake sediments. He suggests revision of the role played by *Quercus* in the postglacial and Holocene history of the flora.

In order to reproduce more reliable proportions of trees, the Eemian succession of plants from Horoszki has been presented in an additional, abbreviated diagram, adjusted using Andersen's correction factors (Fig. 8). In a diagram thus corrected, in zone HD-4 *Quercus–Fraxinus–Ulmus* the proportions of *Fraxinus* and *Ulmus* rise while those of *Pinus sylvestris* type, *Betula alba* type, and *Quercus* decrease. Such a picture seems a more accurate reflection of the quantitative relationships between the trees dominating communities of this time. In the corrected diagram the receding trend of pine-birch communities is obvious, while the importance of ash and elm has been enhanced. The percentage of oak pollen declined, which seems to give a truer picture of its presence in forest communities. It is still very high, despite the correction.

In the author's view it is very likely that the high proportion of oak pollen in this zone should be mainly associated with floodplain woods. In south Podlasie, this was the dominant forest community at this time, with elm, oak, and ash, perhaps corresponding to the modern *Ficario–Ulmetum campestris* Knapp 1942, or perhaps the west European riverine forest of the *Ulmo–Quercetum* type (Ellenberg 1988). Many modern sites of riverine forest in Germany, in which purely oak stands exist (Ellenberg 1988) permit the hypothesis that similar forest may also have occurred during the Eemian interglacial.

The high affinity of oak (*Quercus robur*) for riparian habitats was noticed a long time ago. Moor (1938) states that the alliance *Fraxino–Carpinion* Tx. 1936 spans "all the associations of the order *Fagetalia,* in which the tree stands are composed not of beech or fir, but of oak, ash, alder, maple and elm". Ellenberg also (1988, p. 281) lists *Quercus robur* among the trees of floodplain terraces. Dister (1980, after Ellenberg 1988) quotes an example where *Q. robur* was capable of surviving three-month summer floods of the Rhine unharmed. Despite the fact that the phytosociological concept

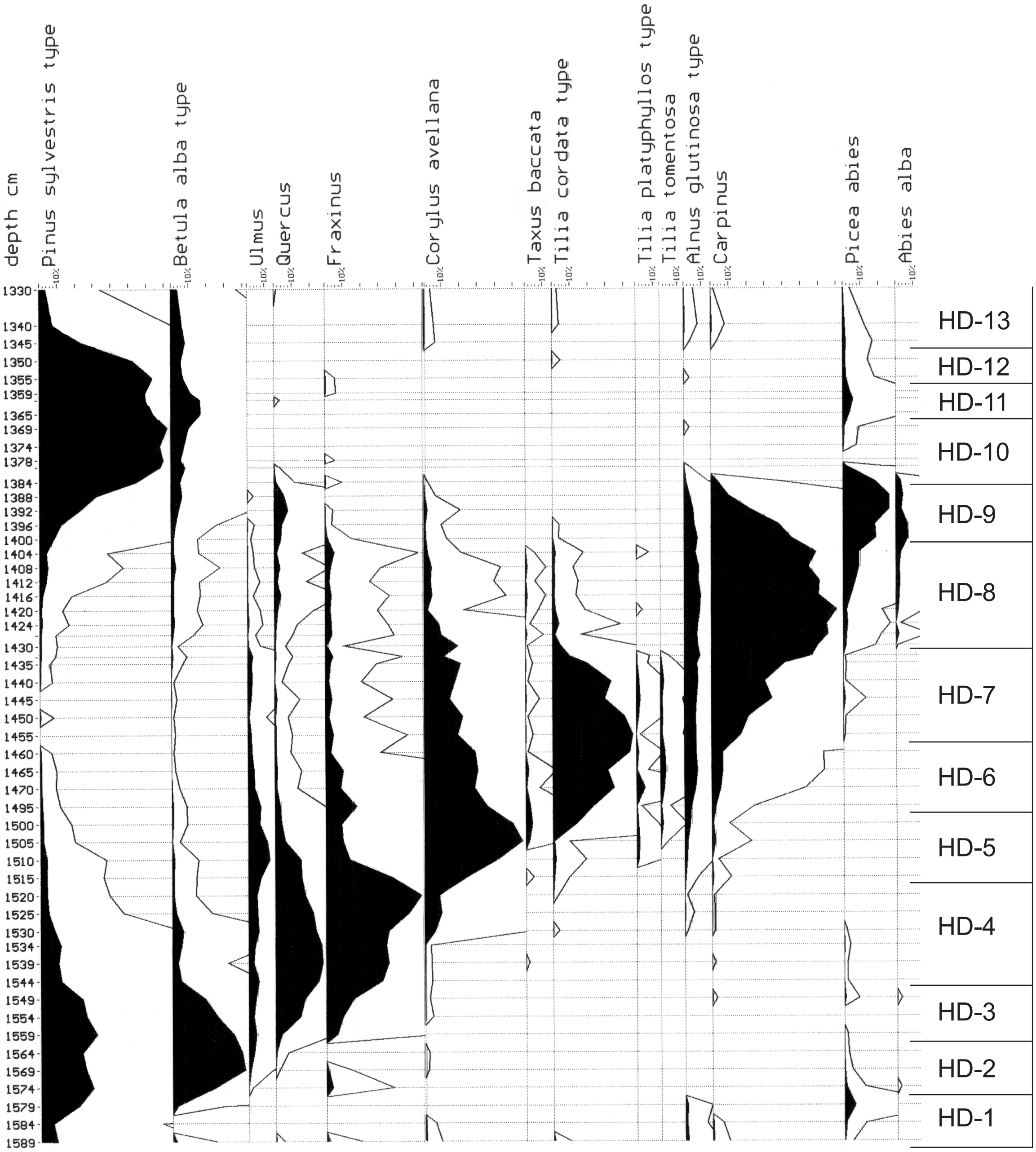

Fig. 8. Pollen diagram of the Eemian part of the Horoszki sequence with Andersen (1973b) correction factors applied

of riparian forests has changed many times (Matuszkiewicz & Borowik 1957, Medwecka-Kornaś 1972, Matuszkiewicz 1976, Matuszkiewicz 1981, Matuszkiewicz & Matuszkiewicz 1996) the fact remains that oak is still strongly associated with this type of community.

Elm-ash floodplain wood now occurs mainly in valleys of great rivers in places which are only occasionally flooded (lower terraces being occupied by poplar-willow wood) which another subassociation, *Ficario–Ulmetum campestris chrysosplenietosum* occurs beside small watercourses, in gullies with periodically running rainwater, in dips of the land and on the slopes of depressions, on terraces beside lakes (Matuszkiewicz 1976). Regardless of the relief of the terrain these are always very fertile sites including river muds, lake sediments, residual and boulder clays, as well as loesses and clays. The soils which form on these are very fertile and have a neutral or slightly alkaline pH (op. cit.). In communities which occur in the valleys of large rivers the fertilizing factor is the episodic flooding, while in sites which are not directly connected with rivers this function is performed by the runoff of precipitation, the movements of soil water and the tides of the lake waters (op. cit.).

The present conditions enable us to understand the high proportion of these communities in the *Quercus–Fraxinus–Ulmus* zone of the Eemian interglacial, both in the vicinity of Horoszki Duże and in Poland as a whole.

The dense network of rivers (Marks & Pochocka 1999), the great number of lakes in the region of central Europe and an abundance of carbonates in the soil (though the latter have been partially leached by pine-birch forests) seem to meet fully the conditions needed for the development of these communities during the so-called "oak phase" of the Eemian. An abundance of water and nutrients made these river valleys excellent migration routes for riparian species, making them the next, after pine and birch, to colonize during the Eemian succession.

The elm-ash floodplain community of the *Ficario–Ulmetum* type is thermophilous and its main contemporary centre of occurrence today lies in the south and south-eastern parts of central Europe, having its most north-easterly sites in Poland (Matuszkiewicz & Borowik 1957). From palaeobotanical and other data we know that the climate of the Eemian interglacial was warmer and more atlantic than that of the Holocene (Mamakowa 1989, Litt 1994, Zagwijn 1996, Aalbersberg & Litt 1998, Cheddadi et al. 1998, and others), so conditions particularly conducive to the development of these forests must have existed at this time. The range of these communities may have been much greater, and may have stretched much further north (Eriksson 1993, Eriksson et al. 1999, Robertsson 2000) and east (Shalaboda 2001). Perhaps this is the reason for which Eemian pollen diagrams from different areas of Europe (from the West Russian lowland to the lowlands of Western Europe) show such similarity and the "oak period" is so prominent in diagrams of complete succession. Naturally, local differences must be borne in mind, particularly in north-south direction where, it seems, the presence of mountains in the south of Europe may modify the presented picture somewhat, in connection with a greater diversity of sites, in which pine may have been retained for longer, or the presence of *Pinus mugo* in the dwarf mountain pine belt or *P. uliginosa* in mires for instance in Podhale Region and in the Sudety Mountains.

Preliminary analysis of the Polish Eemian pollen diagrams, e.g.: Główczyn (Niklewski 1968), Zgierz-Rudunki (Jastrzębska-Mamełka 1985), Imbramowice (Mamakowa 1989), Jóźwin (Tobolski 1991), Łomżyca (Niklewski & Krupiński 1992), Warszawa-Wawrzyszew (Krupiński & Morawski 1993), Proniewicze (Krupiński 1995) and Ruszkówek (Janczyk-Kopikowa 1997) shows a situation similar to Horoszki. At many sites (Imbramowice, Główczyn) in the oak zone, *Quercus* wood is also noted, which may also be evidence of the occurrence of this tree in wetland sites, close to lakes and water bodies.

In the light of the above discussion we can assume that the regional vegetation of this zone was dominated by elm-oak-ash floodplain wood, in which the proportion of *Quercus robur* was most likely to have been considerably higher than in Holocene floodplain forest. The appearance of the pollen of *Corylus avellana*, *Alnus glutinosa* type, *Acer* (?*A. campestre*), and *Carpinus* in the lower part of the zone suggests that they may have already been present in these communities as a minor admixture, or that they grew somewhere nearby. In he shrub layer grew *Sambucus nigra* and *Rosa*. Vines were represented by *Humulus lupulus* and *Hedera helix*. The understorey must have been complex and, among its plants may have occurred the taxa which were the source of the pollen of the following: *Artemisia* (?*A. vulgaris*), *Alchemilla* type, *Bidens* type (Pl. 3, fig. 11), *Mentha* type, *Pulmonaria officinalis* type, *Thalictrum*, *Caltha* type, *Urtica*, and the spores of *Dryopteris filix-mas* type. In more open, meadow-like places there were *Valeriana officinalis* type, *Sanguisorba officinalis*, *Filipendula* (?*F. ulmaria*), *Rumex acetosella* and *R. acetosa* type, and *Comarum palustre*.

From the percentage diagram, *Quercus* may be seen to have been the dominant element in the youngest portion of the zone, too. The recalculated diagram, taking into account Andersen's correction factors (Fig. 8), indicates a much greater role of ash at this time. A similar opinion about the role of ash in this part of the Eemian interglacial was also expressed by Mamakowa (1989). The *Fraxinus* curve has its maximum (15.6%) at Horoszki and after taking corrections into account it reaches over

50%. This may be evidence not only of the dominance of ash in mixed riverine forests of this part of zone HD-4 but perhaps also of the existence of riverine forests at this time, in which the prevalence of *Fraxinus* as the dominant forest tree species was considerable. Dister (1980, after Ellenberg 1988) attributes a strong competitive ability to ash in natural communities, which might explain its expansion in this zone.

Ash riverine forest (*Astrantio–Fraxinetum* Oberd. 1953) is known from Germany and in fragments from south-west Poland. Perhaps it is with such forests that the pollen of *Astrantia major* type should be associated (Pl. 4, fig. 3) in the profile from Horoszki. Another type of ash forest that may have developed in this period of the Eemian interglacial was a community similar to the modern *Carici remotae–Fraxinetum* Koch 1926. In Europe, this association occupies lowlands with an atlantic climate and areas of low mountains and foothills (Matuszkiewicz & Matuszkiewicz 1996). It may be assumed that in the Eemian, during which the climate was much more oceanic than in the Holocene (Zagwijn 1996 and others) this type of community must have reached much further east.

As mentioned earlier, Eemian riverine forests did not only occupy river valleys (as did those in the Holocene), but also floodplain terraces. Today, such places are (potentially, at least) occupied by any of a broad spectrum of lime-hornbeam woods which are the climax forest community of the Holocene and, as may be seen from palaeobotanical data, also of the Eemian. The modern communities of riverine forest, especially variants which grow in drier sites (ones that are not flooded) have a large share of species of the *Querco–Fagetea* class and the alliance *Carpionion* association. This proves that they are most like mesophilic deciduous forests of the lime-hornbeam type (Matuszkiewicz 1981, Matuszkiewicz & Borowik 1957). The appearance of *Corylus avellana* pollen in the younger part of zone HD-4 *Quercus–Fraxinus–Ulmus* marks the beginning of a general, large-scale reconstruction of forest communities in the direction of lime-hornbeam woods in the broadest sense.

The other type of forest community still persisting in the vicinity of Horoszki in the older part of zone HD-4 are moist pine woods, perhaps rather like the modern-day *Molinio–Pinetum*. Beside pine, birch (?*B. pubescens*), and spruce (*Picea abies*) formed the tree stands. *Juniperus* was found in the shrub layer. *Arctostaphylos* pollen should be associated with these forests, perhaps also *Helianthemum nummularium* type, *Polygonum aviculare* type, and *Pteridium* spores. This type of forest in the *Quercus–Fraxinus–Ulmus* zone is already a receding community, and ends in the next zone.

Aquatic and littoral vegetation

A decrease in organic matter to 3.8% is observed in the sediment, and downward trend in carbonate content is maintained, from 13.8 to 10.7%. The littoral and aquatic vegetation did not, however, change significantly; all the existing types of habitat and communities persisted. The macrophyte composition remained largely unchanged; only the fruit of *Najas marina* appeared again, while an increase in the pollen values of *Potamogeton* sect. *Eupotamogeton*, *Ranunculus trichophyllus* type, and hairs of *Ceratophyllum* suggests a greater proportion of pond-weed, *Ceratophyllum* and perhaps *Batrachium* (represented by *R. trichophyllus* type pollen). The very small proportion of *Pediastrum* is typical of very deep water in this lake basin.

E4 *Corylus–Quercus–Tilia* R PAZ

HD-5 and HD-6 L PAZ

HD-5, *Corylus–Taxus–Ulmus* (*Quercus*) L PAZ, part of HDM-1 L MAZ

In the oldest part of this zone, forests of the elm-ash floodplain type continued to be the dominant plant community with *Fraxinus*, *Quercus* and *Ulmus*. *Alnus glutinosa* type, *Carpinus*, *Tilia cordata* type, and *T. platyphyllos* type also occurred and these taxa may have grown as a small admixture in riverine forest. A few *Taxus baccata* pollen show that yew may have been present here, too. Tree willows and poplars were a small but constant element of these communities. Vines were represented by *Humulus lupulus*, which has its maximum in this zone, and by *Vitis sylvestris* (pollen of *V. sylvestris* type). Oberdorfer (1953) considers *V. sylvestris* to be a species characteristic of elm-ash floodplain forest in western Europe. This would support the opinion that the boundaries of elm-ash riverine forest in the pre-optimal stage of the Eemian interglacial was located much further to the east. The shrub layer consisted of *Sambucus nigra* and *Viburnum opulus*; *Hedera helix* was a frequent vine in these forests. The pollen of *Caltha* type, *Mentha* type, and *Rhinanthus* type was associated with the undergrowth layer.

The most important feature of the vegetation is the expansion of *Corylus avellana*. This is a pioneer species light demanding and thus with a high affinity for open spaces, although it can also grow in slight shade. It seems that such conditions existed in the initial stage of its expansion, since the existing riverine forest probably did not cover the ground completely. The presence of pollen of *Helianthemum nummularium* type, *Achillea* type, *Rumex acetosa* type, *R. acetosella*, *Thalictrum* or *Valeriana officinalis* is evidence of the occurrence of open communities in both dry and fresh habitats.

If we take into account the considerable ecological scope of the hazel and its preference for rich, eutrophic soils, such as those in already existing forest communities, we can assume that it also entered forests lying in drier places which were not flooded. Thriving also in moist sites (Neustadt 1953) it may have expanded into forests lying lower in river valleys.

In the succession of trees of the Eemian interglacial in central Europe, *Corylus avellana* arrives after the genera *Ulmus*, *Quercus*, and *Fraxinus*. In the next wave of immigrants it is the "advance guard" of the lime-hornbeam wood species. From its rapid spread of 5 do 7 km per annum – data calculated for the beginning of the Holocene by Firbas (1949) – *Corylus* overtook all the species of lime and hornbeam in the colonization of new areas. Since hazelnuts are heavy, Neustadt (1953) stresses the role of rivers and man in their dispersal at the beginning of the Holocene. The former may have also played a role in the Eemian. Undoubtedly animals also contributed to the seed dispersal of hazel. These conditions contributed to the rapid expansion of hazel, which in the older part of L PAZ HD-5 *Corylus*–*Taxus*–*Ulmus* (*Quercus*) reached a maximum distribution in the region of Horoszki. This level seems to be a crucial point in the development of vegetation not only in this part of Poland but also in the Eemian interglacial as a whole. The maximum spread of *Corylus avellana* marks the beginning of the climatic optimum of the interglacial. Not yet competing with broadleaved trees, which arrived after *Corylus*, it was for a time the dominant species. This is a characteristic feature of the Eemian succession. The period in which *Corylus* dominated in the Eemian was calculated to be about 700 years, on the basis of laminated lake sediments from Bispingen/Luhe in north-west Germany (Müller 1974).

In L PAZ HD-5 *Corylus*-*Taxus*-*Ulmus* (*Quercus*) at Horoszki there are already some lime-hornbeam wood species such as *Carpinus*, *Tilia cordata* type, *T. platyphyllos*, and *T. tomentosa* as well as *Alnus glutinosa*. *Taxus baccata* reached the maximum of its range at this time. Most probably it grew in mixed riverine forest under the canopy of taller trees, though with its wide ecological amplitude (Król 1975) and the more oceanic character of the contemporary climate we cannot exclude the possibility of the presence of yew in higher-lying places. Similar sites were invaded by the abovementioned species, forming the beginnings of a mixed thermophilous deciduous forest. Of the indicator species, *Viscum* appeared for the first time. *Acer* pollen is present throughout, which would suggest its occurrence in situ.

At the same time, the expansion of alder (*Alnus glutinosa* type) began in this area. Its spread should probably be associated with the most waterlogged sites. We can thus assume that the lowest-lying riverine communities gained a new component, and that *Alnus glutinosa* type pollen most probably represents the species *A. glutinosa*, especially in lowland areas (Środoń 1980).

As mentioned above, of all the riverine forests, the elm-ash ones are closest to mesophilous lime-hornbeam wood, on the other hand it shows affinities with alder carr communities, especially those growing within floodplain terraces. It seems, therefore, that sites of a wide range of elm-oak-ash forests were the starting point of two general lines of forest communities, i.e. lime-hornbeam wood and alder carr.

HD-6 *Corylus–Tilia–Alnus* L PAZ

On the basis of qualitative and quantitative changes observed in the pollen diagram, two general lines of succession may be distinguished in the forest communities in the region of Horoszki. The first, after a period of the dominance of *Corylus*, was associated primarily with the spread in these regions of new species of trees, mainly lime and hornbeam, and led to the formation of mixed broadleaved forests in the broad type of modern lime-hornbeam wood. From this time on this was a mesocratic climax forest community with a broad regional range. In this zone, hazel played a considerable part in the formation of forest communities. The diagram which takes into account Andersen's correction factors only slightly modifies its role in communities.

Lime pollen occurs in the pollen diagram in significant amounts after the maximum of *Corylus*, but culminates later. In Mamakowa's classification (1989) this is the so-called "late lime" in the region of Poland. In the *Corylus–Tilia–Alnus* zone, its role increases very quickly in the region of Horoszki. The genus *Tilia* is represented here by three species: *T. cordata* (pollen) *T. platyphyllos*, and *T. tomentosa* (pollen and macroremains). This last species is alien to the contemporary Polish flora. *Tilia cordata* is the most important tree in the area at this time. Its real contribution in the formation of forest communities is better reflected by a pollen diagram which uses Andersen's correction factors (Fig. 8). The more rapid expansion of lime before hornbeam may be the result of it having a very strong tendency to form suckers (Faliński & Pawlaczyk 1991). These authors point to the phenomenon of the regeneration of primeval lime-hornbeam wood communities in the Białowieża Forest (Puszcza Białowieska), where lime is the first to be renewed in a sudden waves. It is only with the limes that hornbeam and maple return in the process of regeneration. The development of the lime population is vital to this process (op. cit.). This example shows the pioneer character of the lime and may explain its more rapid rate of expansion than that of the hornbeam during the succession of the Eemian interglacial. The positive effect of lime forest on the soil it covers can also be considered a pioneer characteristic. The more numerous occurrence of lime in lime-hornbeam woods causes a local change in the soil pH from slightly acid to neutral or slightly alkaline, and a general improvement in soil fertility. The lime leaf litter has twice as much calcium as that of hornbeam, 2.5 times as much as oak leaves as six times as much as pine needles (Faliński & Pawlaczyk 1991). The same is true of potassium and magnesium (1991). Despite the fact that today lime trees seldom form independent stands, throughout zone HD-6 it seems to be the dominant species in the formation of a multispecies forest, and it may also have formed independent communities at this time. The proportion of hornbeam in these stands was still relatively small. Hornbeam may have occupied riverine sites and together with elm and ash formed transitional communities tending towards lime-hornbeam wood or may have occupied drier sites within riverine forest, much as is the case at present (Faliński & Pawlaczyk). The other trees in these communities were *Quercus*, *Fraxinus*, *Ulmus*, *Acer*, and *Taxus baccata*.

The co-occurrence of *Tilia platyphyllos*, *Acer* and *Ulmus* pollen in this zone and the next may suggest the occurrence of lime forests with elm (?*Aceri–Tilietum* Faber 1936). Today this community occurs mainly in the south of Poland on hillsides with moist soils. Northward, the phytocoenoses of this community become poorer floristically, in particular *Tilia platyphyllos* disappears (Matuszkiewicz 1981). In the Eemian interglacial both *Tilia platyphyllos*, *Acer* and *Ulmus* were present throughout zones HD-6 and HD-7 in the region of Horoszki.

The second direction of succession, alongside that to lime-hornbeam wood, is associated with the expansion of alder and the consequent alteration of riverine forest communities, perhaps in the direction of communities reminiscent of modern alder carr. Palaeobotanical data permit the assumption that both in the Eemian interglacial and in the Holocene the alder (*Alnus glutinosa*) was a species associated with lowlands (Środoń 1980). Alder had already been present in the region of Horoszki during the previous zone, but only in zone HD-6 did the curve of *Alnus glutinosa* type reach significant values, and was from there maintained at a virtually unchanged level throughout the entire period during which alders occur. Of course, it is easiest to imagine that it found the most suitable habitats in river valleys, where the level of groundwater suited it. Thus it became a component of riverine forests, initially slowly and then rapidly in zone HD-6, forming, together with trees already established in these habitats (mainly *Fraxinus* and *Ulmus*) another type of riverine forest, ash-alder riverine forest (similar, perhaps, to the modern *Circaeo–Alne-*

tum Oberd. 1953, or its western variant *Pruno–Fraxinetum* Oberd. 1953). The ash-alder floodplain forest community, *Pruno–Fraxinetum*, (current name *Alno–Fraxinetum*) is, according to Ellenberg (1988) associated with streams, but in central Europe occupies large areas outside stream or river valleys. According to Matuszkiewicz (1981) this community occurs in habitats which are slightly swampy, intermediate between typically floodplain and alder carr ones. Today in Poland, outside the mountains, it is a constituent of the most important potential communities in the landscape (Matuszkiewicz & Matuszkiewicz 1996). This is evidence of its wide distribution and persistence in the Holocene. Values of ash pollen which are still high at Horoszki together with high values of alder may be seen as evidence of a similar community. This picture is reinforced by the diagram which takes into account Andersen's correction factors (Fig. 8). Tree willows (pollen of *Salix* undiff.), *Populus*, *Picea abies,* and *Frangula* as well as *Humulus lupulus*, grew in these forests in the region of Horoszki. The presence of *Bidens* type pollen, *Stellaria nemorum*, remains of *Drepanocladus revolvens*, and *D. polycorpos* is associated with the undergrowth of these forests.

Aquatic and littoral vegetation

Reedswamp communities persisted in the marginal zone of the basin, as shown by the presence of macroremains of *Phragmites*, *Sparganium*, and *Typha*. *Alisma* pollen occurs in this zone, probably also from patches of vegetation of the *Phragmitetea* class. The presence of *Alisma* points to eutrophic, or at least mesotrophic conditions in the lake (Podbielkowski & Tomaszewicz 1996). In shallower places, communities of the modern *Thelypteridi–Phragmitetum* type may have developed, as evidenced by the presence of *Thelypteris palustris* spores. In reedswamp and sedge-swamp communities the following taxa most probably found their habitats: *Menyanthes trifoliata* (pollen), *Iris pseudoacorus* as well as *Drepanocladus revolvens* and *Cratoneuron commutatum*. The presence of vegetative remains of *Sphagnum palustre* is evidence of the presence of peat-forming communities.

The development at this time of macrophyte communities of the *Potamogetonetea* class is indicated by the presence of pollen of the *Potamogeton* sect. *Eupotamogeton* and *Coleogeton*, *Myriophyllum verticillatum*, and *M. spicatum*. In areas dominated by this last species the constant elements were *Ceratophyllum* (hairs present), most likely various representatives of the genus *Batrachium* (pollen of *Ranunculus trichophyllus* type) and *Trapa*, present in zone HD-6. Its presence is evidence of a good level of oxygenation in the lake (Podbielkowski & Tomaszewicz 1996). The find of the fruits of *Najas marina*, *N. flexilis*, and *N. minor* may suggest communities close to the modern association *Parvopotamogetoneto–zannichellietum*, for which *Najas* species are characteristic species (op. cit.).

E5 *Carpinus–Corylus–Alnus* R PAZ

HD-7 and HD-8 L PAZ

HD-7, *Carpinus–Corylus–Tilia* (*Alnus*) L PAZ, the youngest part of HDM-1 and part of HDM-2 L MAZ

A characteristic feature of vegetation from this zone is a considerable increase in the proportion of hornbeam in the forest communities of the region of Horoszki. From this point, *Carpinus* was the main community-forming tree in the area. Together with lime (*Tilia cordata*) it constituted the basis of communities of a multi-species broadleaved forest which, on the basis of the species composition of the trees, and their proportion in tree stands can be compared to modern lime-hornbeam wood (?*Tilio–Carpinetum* Tracz. 1962) in its typical variant. Macroscopic remains of *Tilia platyphyllos* and *T. tomentosa* (nuts), and *Carpinus betulus* (fruit) were found in the sediments representing this zone. Other components of these forests were *Acer*, *Quercus*, *Ulmus*, *Fraxinus*, *Taxus*, *Larix*, and *Picea abies*. The presence of this last-named in the vicinity is demonstrated by a seed fragment while that of larch by a fragment of a needle despite the absence of *Larix* pollen, which does not appear till the next zone. Pollen diagrams (Figs 4, 9) show *Corylus* to have been an important constituent of these forests, in which it may have been both the understorey and growing on the edges of the forest, forming edge communities. The continuing high proportion of hazel pollen, despite the assumption that it occurred in the understorey might have been affected by the fact that it flowers before the forest breaks into leaf. Thus its pollen may have been freely carried above the crowns of the trees, which, combined with its rich pollen production, may have been reflected in the spectra. With time, its proportion in communities declined; perhaps it was gradually eliminated by hornbeam underwood, as having the greater demand for light. In the understorey layer *Ilex* (pollen of *I. aquifolium* type) also grew, which points to a more westerly type of lime-hornbeam forest than at present. *Hedera helix* (continuous pollen curve) and *Viscum* were still found in these forests.

In the forest communities of the younger part of the zone the proportion of lime decreases, while that of hornbeam rises. The reason for this may be sought both in the life strategies of these trees, in the changes in soil conditions and perhaps in the order of succession itself, and general climatic changes. Both lime and hornbeam show a strong tendency to produce offshoots, but the hornbeam combines many types of biological strategy, which gives it a competitive edge over other trees in the lime-hornbeam wood (Faliński & Pawlaczyk 1993). Ellenberg (1988) also describes its high competitive capacity. The elimination of lime by hornbeam may have also been affected by a greater tolerance of hornbeam to soil acidification (Mamakowa 1989). Moreover the signs of an increasing wetness of the climate, which may be noted in this zone (continuous *Picea* curve + macroremains), may have affected the recession of lime. Today in Poland's lime-hornbeam wood communities the proportion of lime increases with an increasingly continental type of climate, i.e. from south-west to north-east (Faliński & Pawlaczyk 1991). Meanwhile in the younger part of the *Carpinus–Corylus–Tilia* (*Alnus*) zone the presence of *Ilex aquifolium* is evidence of a more westerly type of lime-hornbeam wood, which grew at this time in the region of Horoszki and thus also of a more oceanic climate at the time. Perhaps, among other factors, the increase in the oceanic character of the climate contributed to the recession of lime.

Alnus glutinosa was one tree which, despite the strong expansion of *Carpinus*, did not decline in significance in this zone and must have formed separate communities. Together with *Fraxinus* it formed ash-alder riverine forests in the less boggy areas, though the decline in the values of ash pollen in this zone may be evidence of its smaller share in these communities. We cannot rule out the possibility that the decline in values of *Fraxinus* pollen is a statistical artefact in the picture presented by the pollen diagram due to the very high proportions of the pollen of other trees, especially hornbeam. The diagram with correction factors applied (Fig. 8) would point to a still significant proportion of ash, primarily to its continuous presence in riverine communities, both throughout zone HD-7 *Carpinus–Corylus–Tilia* (*Alnus*) and in the next zone. Part of the ash pollen should probably be associated with patches of forest lying at the transition of lime-hornbeam wood communities with riverine ones and also with ash-alder floodplain forest (?*Circaeo–Alnetum*). In turn, very swampy habitats were the site of the alder. It may have formed communities resembling modern alder carrs (formerly characterized as *Carici elongate–Alnetum*); however, the true nature of these communities is difficult to assess on the basis of palynological data. Due to the absence of data on the presence of characteristic species, it is difficult to say anything of their character in the categories of phytosociology and the geographic distribution of their various forms in the Eemian interglacial. Being, as they are now, par excellence an azonal community in the Eemian, they must likewise have shown a considerable resemblance throughout their entire range (Ellenberg 1988).

Around Horoszki, *Picea abies* (seeds), willow trees (pollen *Salix* undiff.), and *Populus* (pollen) may also have been components of alder carrs. It is also with these communities that pollen of *Humulus lupulus*, *Filipendula*, *Urtica*, perhaps part of pollen of *Aster* type, and Apiaceae undiff. should most probably be associated.

A tiny proportion of herbaceous plant pollen shows the dominance of dense forest communities in the landscape around Horoszki.

HD-8, *Carpinus–Alnus–Picea* L PAZ

During this zone significant changes may be observed, even though mixed deciduous forests remained the dominant formation. With an increase in hornbeam and a distinct decline in lime and elm values, an increase may be observed in the proportions of pine, birch, oak, spruce, and the appearance of *Abies*.

A consistent increase in proportions of spruce and the presence of fir in tree stands may be evidence of the environment becoming wetter, probably an increase in precipitation, which may have initiated soil degradation associated with their leaching and acidification (Iversen 1958, Andersen 1969). Changes in the composition of the sediment in the lake basin at Horoszki also suggest increased precipitation. In zone HD-8, there is sand in the silty gyttja, which may be the result of runoff into the lake (Fig. 3). The presence of *Coenococcum graniformae* is also evidence of soil erosion. Niklewski (1968) described a similar phenomenon during the hornbeam period in sediments from Główczyn, as did Mamakowa (1989) from Imbramowice and other sites from Poland and western Europe. The increasingly oceanic climate is also expressed by a continuous, rising curve of *Calluna vulgaris*. The presence of *Buxus*, *Viscum*, and *Hedera helix* pollen shows that an increase in moisture was not accompanied by a strong shift to glacial climate, as was suggested in the work of Field et al. (1994). Neither was this hypothesis supported in a paper based on a reconstruction of the climate in the Eemian interglacial by the method of modern pollen spectra analogues used for several Eemian profiles from France and Poland (Cheddadi et al. 1998). Neither do Aaby and Tauber (1995) agree with a cooling of the climate in this period of the Eemian interglacial, basing their opinion on the presence in this period of such classic indicators of high temperatures as *Hedera helix* and *Ilex aquifolium*. On the basis of palaeobotanical data, also Litt et al. (1996) and Zagwijn (1996) do not point to any major fall in temperature in this period of the Eemian interglacial.

In the *Carpinus–Alnus–Picea* zone, the dominant forest community in the region of Horoszki was lime-hornbeam wood, in which hornbeam was the absolutely dominant tree. Being less demanding than other broadleaved trees with respect to edaphic conditions it spread rapidly and was for a long time the dominant species. The picture presented by the pollen diagram would point to the occurrence of almost pure hornbeam stands in the older part of the zone. A similar situation is known in sites of Eemian from e.g. Główczyn near Wyszogród (Niklewski 1968) and Józefów (Sobolewska 1966) on the Łódź Upland (Wyżyna Łódzka). Most probably, it filled all the layers of the forest stand, successfully displacing hazel from the understorey. Spruce was also a component of these forests, as is the case in lime-hornbeam wood communities of the Holocene in eastern and north-eastern Poland. From the palynological data presented by Środoń (1983) and supplemented by Mamakowa (1989) it may be deduced that the range of *Abies alba* in the Eemian extended further north and east than at present (cf. Kondratiene 1996, Kalnina 2001). This was also confirmed in the material from Horoszki were, fir was an element of the tree stands.

Beside hornbeam, spruce, and fir, *Tilia cordata*, and *Acer* were components of the forests, and, in their more moist variants also, *Taxus baccata* grew. The deterioration in soils must have affected the role of *Quercus* in oak-hornbeam forest. *Hedera helix* and *Viscum* still occurred in this zone.

The pollen of *Fagus sylvatica* also appeared in the hornbeam zone of the sediments from Horoszki. The possible presence of beech (*Fagus sylvatica*) in the Eemian interglacial in Poland is a very interesting topic, which has been widely discussed in the literature (Niklewski 1968 Środoń 1985, 1990a, Mamakowa 1989, Krupiński 1995, Kuszell 1997, Gerlach at al. 1997). According to Środoń (1985), *Fagus* was not present in the Quaternary in Poland until the Holocene, and the presence of its pollen in Eemian diagrams is explained by him in terms of redeposition or long-distance transport. On the basis of *Fagus sylvatica* pollen found in Eemian deposits from Główczyn, Niklewski (1968) suggests that beech was present during the Eemian in Poland. In his opinion, it may have been a rare element of the forests. Also the compilation by Mamakowa (1989) of Eemian sites in which beech pollen was noted sporadically would seem to support this hypothesis. *Fagus* always appears in the R PAZ E5 (*Carpinus–Corylus–Alnus*), and is not accompanied by other sporomorphs that could unequivocally be described as redeposited, which would seem to support the exclusion of redeposition. This is a period in interglacial succession which is more or less analogous to the period of beech expansion in the Holocene. It is difficult to accept that, in a period of close forest cover, beech pollen which is heavy and not readily airborne, would have been transported from a long distance. The presence of this tree in the Eemian, however, remains open until macroscopic remains are found.

Beside hornbeam, alder probably also played a considerable part in the formation of forest communities in zone HD-8 *Carpinus–Alnus–Picea*. The course of the *Alnus glutinosa* type curve shows that despite the enormous proportion of *Carpinus* pollen, the community-forming role of the alder did not decline in this zone, but was similar to that of the previous zone. Alder carrs most probably constituted, as did lime-hornbeam woods, an equally important element of the forest landscape of the region of Horoszki. Beside the alder, there also grew tree birches (?*B. pubescens*); an increase in the curve of *Betula alba* type pollen and also the presence of tree birch macroremains provides evidence of their return to the vicinity of the lake basin at Horoszki. The spores of *Osmunda claytoniana* type and *Equisetum* should be associated with the undergrowth of alder carrs.

The continuous curves of *Fraxinus* and *Ulmus* may be evidence of the presence of ash-elm riverine forest, but their distribution in the area was not as large as in older zones. Relatively high values of *Fraxinus* (especially in the diagram using Andersen's factors – Fig. 8), with relatively high values of *Alnus glutinosa* type pollen would indicate the continued presence of ash-elm riverine forest in the vicinity of the lake at Horoszki. After Zaręba (1971) fir may also have occurred in these communities, as pointed to by contemporary fir stands in the ash-alder riverine woods in the Kozienice Forest (Puszcza Kozienicka). Perhaps such stands were intermediate sites in the northward and eastward spread of the fir, from where it spread into much more favourable lime-hornbeam wood habitats. Ash-elm floodplain forests would certainly have formed ecotone belts with alder carrs on one side and lime-hornbeam wood on the other. Besides the ash and alder it is with these that the occurrence of *Viburnum opulus* and *Humulus lupulus* most probably were associated, and in part also that of *Taxus baccata* and *Acer*. The pollen of *Populus* and *Salix* undiff. may be evidence of the local presence of poplar-willow riverine forests, but these trees may equally well have been components of both ash-alder riverine forest and alder carr (*Salix*). Boggy, open places may have included meadow communities and a source of the pollen of *Gentiana pneumonanthe* type, *Lysimachia vulgaris* type, *Peplis*, *Potentilla* type, *Ranunculus acris* type, *R. flammula* type, *Rumex acetosa* type, as well as *Menyanthes trifoliata*, *Thalictrum*, and Apiaceae undiff.

Besides fertile, moist sites, sustaining lime-hornbeam climax wood, there were probably also drier habitats, in which xerothermic vegetation may have occurred on higher ground where it received more light. These sites may have been occupied by forest scrub communities formed by trees "returning" in this zone, *Quercus* and *Pinus sylvestris*. Unfortunately, we cannot establish by pollen analysis which species of oak (and whether only one) constituted the *Quercus* curve in this zone. *Buxus* pollen, present here, should most probably be associated with communities of the abovementioned type. *Buxus sempervirens* today grows in xerothermic communities in the Mediterranean area and is considered an oceanic element in the European flora (Ellenberg et. al. 1992), while Matthews (1955) considers this element in the British Isles to be transitional between a southerly continental element and a southerly oceanic one.

At present, in the centre of its occurrence, the box forms the shrub layer in mixed oak forests with *Quercus pubescens* and is a component of xerothermic scrub *Buxo–Quercetum* communities of the order *Quercetalia pubescentis* (Ellenberg 1988). This scrub is under constant anthropogenic pressure, that is, oak is maintained only at the underwood stage and, left without human interference, these communities rapidly revert to the form of tall forest (op. cit.). In the British Isles, *Buxus sempervirens* is a native element of the flora, and grows in beech forest and scrub on lime substrate (Clapham et al. 1952). It also forms scrub on the limestone slopes of the Swiss Jura. Jessen et al. (1959) and Sobolewska (1977) are of the opinion that the box avoids too a dry climate, finding the most suitable conditions in an area where annual precipitation exceeds 1000 mm and the annual isotherm reaches 10°C. It seems that it may have encountered precisely such conditions during the Eemian interglacial at Horoszki and other sites in Poland (Niklewski 1968, Krupiński 1995, Kuszell 1997). In Eemian diagrams from Poland, *Buxus* appears in the hornbeam period and is still present in the spruce period. Considering its modern requirements we can suppose that it grew in thermophilous oak forests on dry calcareous soils. We cannot rule out the presence of *Quercus pubescens* in the Eemian interglacial in Poland (though this has not been confirmed). This species is closely related to *Quercus petrea* (=*sessiliflora*), with which it may form a number of intermediate hybrid forms (Ellenberg 1988). At present *Q. pubescens* or rather, its hybrids (Staszkiewicz 1977) only occurs in one site (Bielinek) in Poland by the lower Oder (Odra), forming perhaps a borderland form of the *Lithospermo–Quercetum* community (Matuszkiewicz & Matuszkiewicz 1996) which is widespread in southern Germany, Austria, and the Czech Republic. This location, in Bielinek by the lower Oder, is quite markedly separated from the main range of *Q. pubescens*, being 500 km to the north-east and some authors have suggested that it is of anthropogenic origin (Celiński & Filipek 1958). If, however, the site in Bielinek is a relict of the Atlantic period, then in the much more oceanic climate of the Eemian interglacial the presence of *Q. pubescens* in eastern central Europe would be probable.

A different interpretation is possible of the presence of *Buxus* in the Eemian interglacial in central Europe. If the hypothesis concerning the presence of forests with *Quercus pubescens* is not correct, *Q. petrea* is more likely to have occurred in this zone, which in its ecological requirements is more like beech than *Q. robur*. *Q. petrea* prefers a milder (more oceanic) climate, it is less resistant to harsh winters and late frosts and, like the beech, it avoids floodplain terraces almost completely, as opposed to *Q. robur* (Ellenberg 1988). If this assumption is made, the rise in the *Quercus* curve in zones HD-8 and HD-9 should be associated more with *Q. petraea* than *Q. robur*.

Aquatic and littoral vegetation

This zone is very poor both in macroscopic remains and in pollen of aquatic plants. At this time, organic silts and calcareous-organic gyttja were deposited in the lake, which is evidence of favourable trophic conditions. Carbonates also increased to over 30% (Fig. 3).

Since no major changes are observed in the composition of the local flora in relation to the previous zone, it may be assumed that in the vicinity of the lake and in the lake itself all the types of phytocoenoses existing in the previous zone persisted. In the reedswamp vegetation two new taxa appeared: (macroremains) of *Scirpus* and *Viola* cf. *palustris*.

E6 *Picea–Abies–Alnus* R PAZ

HD-9, *Picea-Abies-Carpinus* (*Pinus*) L PAZ, the upper part of HDM-2 and the lower one of HDM-3 L MAZ

In this zone, besides the increased wetness of the climate, a change took place to lower temperature. These two factors made their mark in a thinning of the forest cover, thus enabling the return and formation of communities of more open areas, as shown by the continuous increase in the NAP curve.

The climatic change, the diversity of habitats and soil types, and the large-scale mobilization of regressive succession, led to the development of a greater diversity of forest communities. The general trend of changes in forest communities was directed towards a broad range of mixed forest. This stage of climatic-edaphic changes marks the beginning of the closing phase of the glacial-interglacial cycle.

Zone HD-9 *Picea–Abies–Carpinus* (*Pinus*) at Horoszki clearly splits into two subzones – the older, *Carpinus* and the younger *Pinus*, which have their analogues in the regional biostratigraphic division (Mamakowa 1989). A noteworthy feature of forest communities of this zone is the maximum spread of spruce and fir, the latter having had its maximum proportion in communities before the maximum spread of the spruce.

In the older part of the zone lime-hornbeam woods still occurred, with a dominance of hornbeam and a considerable share of oak. Fir and spruce were significant components of these communities (macroremains). Mesotrophic lime-hornbeam habitats were probably conducive to the spread of fir. At present, within the range of the fir, hornbeam forests with a high proportion of fir are known in eastern Poland; for instance, Zaręba (1971) reports a fir lime-hornbeam wood from the Kozienice Forest (Puszcza Kozienicka). In the highland belt and the Roztocze it is an almost constant component of lime-hornbeam woods, in parts dominating the tree stands. An analogous situation probably existed in the Eemian, though the ranges of fir and spruce overlapped in north-eastern Poland, hence the simultaneous presence of these species in lime-hornbeam wood. Fir is also a frequent component of lime-hornbeam woods in north-eastern Poland (Faliński & Pawlaczyk 1993). In these lime-hornbeam woods the maple also occurred, and small-leaved lime, while hazel and elder was present in the understorey. Mistletoe should also be associated with these.

In this period, changes also took place in the composition of riverine forests and alder carrs. More demanding trees such *Fraxinus* and *Ulmus* retreated almost entirely from the area. A decreasing tendency of *Alnus glutinosa* may also be noted through the older part of the zone, to its almost total recession at the upper boundary. It is most likely that habitats of the alder were gradually taken over by spruce.

The progressive deterioration of the climate, the leaching of soils, the opening up of the forest, created conditions for the return of light demanding, light-seeded trees e.g. *Pinus sylvestris* and *Betula* sect. *Albae*. Both genera are also represented by macroremains; a scale of *Betula pubescens* was found. These trees formed birch-pine forests, perhaps with the participation of oak, as is the case today in the northern parts of central Europe within the area affected by oceanic climate. In a more oceanic climate these communities are mainly formed by birch and oak (?*Betulo–Quercetum*) and with progression towards the zone influenced by a continental climate, the proportion of pine increases (Ellenberg 1988). At present, these communities occur only in the north-western part of the country (Matuszkiewicz & Matuszkiewicz 1996) and are the habitat equivalent of pine forest. Spores of *Pteridium aquilinum* (continuous curve) was most probably associated with pine-birch communities.

In the younger part of the zone, in the *Pinus* subzone, all the above changes in forest communities became more distinct. Lime-hornbeam woods became increasingly poor, their main component beside hornbeam being fir, oak, and spruce. Pine forests most probably increased in significance in various combinations with the tree species already present. Soils became increasingly leached, the openness of vegetation increased and communities of open spaces appeared in the landscape. Not only the increase in the NAP curve, but also the increase in the diversity of herbaceous plant taxa is evidence of this change.

The expansion of spruce in the younger part of the zone led to a strong acidification of the substrate, which, beside climatic factors, may have been the cause of the decline in the role of the fir in lime-hornbeam woods. Also, the leached soils favoured oak more than hornbeam.

In the latter part of the zone practically all the tree species with greater climatic requirements, including spruce, disappeared. Boreal pine-spruce woods with a proportion of birch (?*Betula pubescens*) were the dominant plant formation, with a local admixture of willows and poplar.

An increasing role was played in the landscape by herbaceous communities of open areas. A continuous, rising presence of *Calluna vulgaris* is evidence of the spread of oligotrophic habitats. Open acidophilic communities of the meadow type also occurred, and these most probably were the source of the pollen of such taxa as *Centaurea nigra* type, *Herniaria* type, *Plantago media* or *Pimpinella major* type. Meadow communities developed in boggy places, represented by the pollen of *Cirsium/Carduus*, *Peucedanum palustre* type, *Plantago lanceolata*, *P. major*, *Ranunculus flammula* type, *Rumex acetosa* type, *Thalictrum*, *Urtica*, and Apiaceae undiff. The first signs of *Betula nana* (pollen) and *Sphagnum* towards the end of the zone and the presence of remains of the mosses *Drepanocladus revolvens* and *D. polycarpos* reflect the occurrence of peat bogs or boggy meadows.

Aquatic and littoral vegetation

This zone is scarce in remains of local flora. A very high proportion of organic matter in the sediment (max. 54.1%) is an indication of eutrophication of the lake. The low amount of macroscopic remains may be explained by the central positioning of the profile in the basin and the high water level. Field (pers. comm.) has recently conducted drillings in the transect from the edge to the centre of the lake and demonstrated that the quantity of macroscopic plant remains decreases with distance from the shore of the basin, to their almost complete disappearance in its central part. At this level macroscopic tree remains are more abundant than those of aquatic and littoral vegetation. This may be evidence of the immediate presence of forest in the environs of the basin, which restricted the development of littoral communities.

Reedswamp communities still occurred, as demonstrated by the presence of the pollen of *Phragmites* type. The disappearance of *Thelypteris palustris* spores may indicate its recession from the region of the basin, and thus the disappearance of phytocoenoses of the *Thelypteridi–Phragmitetum* type. Maybe this was a consequence of the deterioration of the climate. A new component of reedswamp vegetation appeared, represented by the pollen of *Oenanthe fistulosa* type.

Most probably, significant changes did not occur in the composition of macrophyte communities in relation to those of the previous zone. Three species of *Najas* continued to be present (find of fruits), *Myriophyllum spicatum*, *Potamogeton* sect., *Eupotamogeton*, and *Coleogeton* pollen.

E7 *Pinus* R PAZ

HD-10, HD-11 and HD-12 L PAZ

HD-10, *Pinus* L PAZ, part of HDM-3 and part of HDM-4 L MAZ

The vegetation of this zone reflects the strengthening of climatic trends initiated during zone HD-8 and HD-9, namely increasing precipitation and, more importantly, a general cooling of the climate. The landscape of the region of Horoszki in zone HD-10 *Pinus* was dominated by pine forest. Beside *Pinus sylvestris* (macroremains), which was the main forest-forming species, there grew tree birches (macroremains of *Betula alba* type) while spruce persisted in the older part of the zone (macroremains); *Populus* and tree birches (*Salix* undiff.) were also present.

Pine forests were perhaps like the modern suboceanic *Leucobryo–Pinetum* Mat. (1962) 1973. This is a tall pine forest within the range of oceanic climate in central and eastern Central Europe (Matuszkiewicz & Matuszkiewicz 1973), in which birch and spruce locally constitute an admixture. The presence of *Calluna vulgaris* and *Melampyrum* pollen is associated with the undergrowth of these forests. In lower areas (peatlands) a local admixture of spruce may have been greater or perhaps even spruce-pine boreal forest (?*Sphagno–Piceetum*) occurred there, as might be indicated by the continuous and increasing presence of *Sphagnum* spores. *Pinus sylvestris* and *Betula pubescens* may have occurred in these communities, and sometimes alder and aspen, as is the case in the present (Matuszkiewicz 1977).

Due to the spread of coniferous forest, in which there is little shade, the significance of communities of open spaces increased further. Drier forest habitats were perhaps occupied by patches of heath, as indicated by the continuous curve of *Calluna vulgaris* pollen. The pollen of *Herniaria* type, *Plantago media*, *Dianthus* type, and *Rumex acetosella* probably comes from drier, sandy habitats. The greatest diversity of herbaceous plant taxa, however, was associated with moist and boggy habitats, which probably dominated at the time in the landscape of the vicinity of Horoszki. Their increasing role is evidenced by the rising NAP curve, due mainly to an increase in the pollen of Poaceae undiff. and Cyperaceae. The grasses were possibly associated with the local, boggy form of pine forest. The existence and expansion of meadow communities in open places is evidenced by taxa such as: *Pimpinella major* type, *Plantago major*, *P. maritima*, *Polygonum bistorta/viviparum*, *Potentilla* type, *Rhinanthus* type, Rubiaceae, *Rumex acetosa* type, *Sanguisorba officinalis* type, *Saxifraga oppositifolia* type, Apiaceae undiff., *Viola palustris* type, and the spores of *Selaginella selaginoides*, appearing for the first time. The presence of such taxa as *Peucedanum palustre* type and *Solanum dulcamara*, which are characteristic of the ground cover of alder carrs, may indicate that the dominance of pine forest communities is a relatively recent fact. The conservatism of the original undergrowth long after the change in the tree species is known in contemporary phytosociology.

Betula nana is a notable element of the flora of the communities of this zone, which highlights the implications, in terms of flora and climate, of the changes described above. This species reappeared in the region of Horoszki following an interglacial absence from the older part of level HD-3 (*Pinups-Betula-Quercus* (*Ulmus*) L PAZ). *Betula nana* together with *Sphagnum* prove the presence of extremely acidophilic and oligotrophic communities of peat bogs (*Oxycocco–Sphagnetea* Class).

HD-11, *Pinus–Betula–Picea* L PAZ

This (probably short) period of time was marked by the slight recession of pine and an increase in the proportion of tree birches (pollen of *Betula alba* type), *Picea abies* as well as the appearance of *Larix* (pollen and needles). A similar phenomenon, though somewhat more pronounced, is found at a site of Eemian deposits at Machnacz (Kupryjanowicz 1994) in the Knyszyn Forest (Puszcza Knyszyńska), some 100 km north of Horoszki. At Machnacz, these changes are additionally accompanied by an increase in the proportion of Cyperaceae pollen. The author suggests the occurrence of a short-lived cold oscillation. As at Machnacz (Kupryjanowicz 1994) there are indications of surface runoff in the sediment at Horoszki, in the form of sand and gravel up to 3 mm. It seems highly likely that this zone reflects some sudden climatic change in the direction of wetness, and cooling. At Horoszki this is reflected in a loosening of the forest cover, which consists more in the local spread of birch and larch than an increase in the significance of herbaceous vegetation. A similar picture, though less pronounced than at Horoszki and Machnacz, may be seen in the pine zone in the material compiled by Mamakowa (1989). It is seen in the diagram from Konopki Leśne and Szwajcaria 1 (Borówko-Dłużakowa & Halicki 1957), but it is also observed at the sites Nakło (Noryśkiewicz 1978) and Imbramowice (Mamakowa 1989). Perhaps this phenomenon was more clearly reflected in diagrams from north and northwest Poland.

The birch, probably *B. pubescens* (macroremains in zone HD-9) may have formed local stands (?*Betuletum pubescentis*) in boggy former sites of alder carr communities, acidified by spruce. According to Matuszkiewicz & Matuszkiewicz (1996) this community is now widely found in northern Germany and central and western Pomerania (Pomorze Zachodnie). Among other trees, *Pinus sylvestris* and *Picea abies* grew there. In the understorey *Frangula* may have occurred, while it is with the undergrowth that the pollen of *Empetrum*, *Vaccinium*, and spores of *Lycopodium annotinum* should be associated. Despite the temporary increase in the significance of birch it seems that pine-spruce forests with some larch constituted the core of contemporary forest communities. The pollen of *Chimaphilla umbellata* most probably comes from the undergrowth of these communities.

Communities of open habitats continued to exist, both on drier soils (*Herniaria* type) and on wetter ones (*Silene dioica* type, *Polygonum aviculare*, *P. persicaria*, *Caltha palustris* type, and others already present in the previous zone). Peatland communities did not decline in significance, as indicated by the continuous and increasing proportion of *Sphagnum* and *Betula nana*. *Alnus viridis* also appears. The decrease in forest cover may also be suggested by the increasing role of *Juniperus*, which had already appeared in the younger part of the previous zone. Also, the trace quantities of *Pinus* cf. *cembra* pollen may prove that the tree stands were in the region around the lake was already so poor that pollen may have found its way into the sediment, most likely by long distance transport.

HD-12, *Pinus–Larix* L PAZ

After an oscillation caused most probably by a temporary deterioration in the climate, pine returned to places occupied for a time by birch. It is hard to say whether this return had a climatic cause, or whether it was a reflection of local relationships of competition and regressive succession, caused by habitat conditions. Kupryjanowicz (1994) explains this change by an improvement in the climate. However, the general tendency of the vegetation succession would point to continuous deterioration of the climate. In the profile from Horoszki this is supported by a decrease in organic matter from ca. 40% to ca. 10% (Fig. 3) and a decreasing trend in the concentration of the sporomorphs of land plants (Fig. 7) and an increase in the proportion of NAP.

The forest communities in the older part of the zone were composed of *Pinus sylvestris*, *Betula* spp., *Larix*, and *Picea abies*. The low frequency of thermophilous tree pollen probably represent long-distance transport or redeposition from older sediment. *Juniperus* and *Alnus viridis* were found in these light and loose forests. The pine forest was boreal in nature and in the upper part of this zone even had features of forest tundra, perhaps similar to the modern subzone of the forest tundra (Norin 1961) and were clearly in retreat. The improving light conditions were conducive to the development of heath communities, of which the increase in proportions of *Calluna* *vulgaris* is an expression (cf. Behre 1989). The striking increase in *Sphagnum* shows the occurrence of oligotrophic peatland habitats with widespread dwarf birch (*Betula nana*), as well as *Drepanocladus revolvens* and *Calliergon trifarium*. The pollen of *Ledum*, *Empetrum*, and *Vaccinium* type comes from these habitats, and probably some of that of Cyperaceae. A marked loosening of the forest cover is also supported by the manifold increase in the share of Bryales spores.

The relatively high proportions of Poaceae undiff. pollen, *Artemisia*, Chenopodiaceae, and the presence of such forms as *Arenaria* type, Cichoriaceae, *Cerastium* type, *Helianthemum nummularium* type, *Herniaria* type, *Spergularia* type, *Saussurea* type, and *Rumex acetosella* indicates the presence at this time, not far from the lake, of light-demanding communities of sand grassland. Such taxa as *Geranium*, *Polygonum bistorta/viviparum*, *Thalictrum*, *Solanum dulcamara*, *Filipendula*, Brassicaceae, *Achillea* type, *Aster* type, *Ranunculus acris* type, *R. flammula* type, *Valeriana officinalis* type, and *Rumex acetosa* type may be associated with the wetter and more fertile meadow habitats.

Aquatic and littoral vegetation

In the sediment, the proportion of the organic fraction is still high, though it declines towards the end of the zone. At the edges of the basin there still remained reed and tall sedge communities of the *Phragmitetea* class, as indicated by the presence of *Phragmites* pollen and the nuts of *Carex elata*. *Menyanthes trifoliata* and *Batrachium* (pollen of *Ranunculus trichophyllus* type) were also a component of the reedswamp communities. In the basin macrophyte communities developed with *Myriophyllum alternifolium*, *M. spicatum*, and *Ceratophyllum* (hairs) as well as *Najas flexilis*. Among algae, the proportions of *Botryococcus* colonies increased.

EARLY VISTULIAN

An intensification in climatic changes towards cooling finally brought about the thinning and retreat of compact forest communities from the area of Horoszki Duże and an increased spread of pioneer plant communities of open areas. This process is reflected in the pollen diagram, in a very marked increase in herbaceous plant pollen, which marks the boundary between the interglacial and glacial succession of vegetation at Horoszki.

The changes in plant communities at Horoszki during the early Vistulian were described on the basis of local pollen zones HD-13 to HD-26 and given in relation to the regional pollen zones EV1 – EV5 distinguished by Mamakowa (1989).

Herning stadial

EV-1, Gramineae–*Artemisia–Betula nana* R PAZ

HD-13, Poaceae–Cyperaceae–*Juniperus* (*Salix polaris* type) L PAZ, part of HDM-4 and the oldest part of HDM-5 L MAZ

The most characteristic feature of the first post-Eemian section of the Vistulian is the prevalence of open communities of herbaceous vegetation over forest communities, as indicated by the high NAP values, reaching 69% of the total pollen sum of land plants. A confirmation of this is a drop in the concentration of pollen of trees and shrubs, especially in the lower part of the zone, and an increase in the concentration of herbaceous plant pollen (Fig. 7). However, the presence of macroscopic remains of tree birches (*Betula* sect. *Albae*, *B.* cf. *pubescens*), larch needles and a fragment of a seed (*Larix/Picea*) indicates the presence of these trees in the vicinity of the lake. Low percentages of *Pinus sylvestris* type pollen and an absence of pine macroremains may point to its complete withdrawal from the vicinity of Horoszki at this time. The pollen of thermophilous broadleaved trees most probably derives from long-distance transport and its presence in spectra would be indicative of an open landscape (Środoń 1960, Granoszewski & Robertsson 1996) rather than the presence of these trees nearby. These data thus suggest the continuous presence of single specimens of tree birches and larch in the vicinity of Horoszki during the first stadial of the Vistulian and, in the younger part of the stadial, even forest tundra with birch.

The vegetation of the older part of the stadial was dominated by species of the families Poaceae, Cyperaceae, and various species of *Artemisia* and Chenopodiaceae. The continuous and high proportion of *Sphagnum* spores is evidence of the widespread presence of peat bogs in the region of Horoszki. It is these that formed habitats suitable for shrub tundra communities with *Betula nana* and *Salix polaris* type In this zone the pollen of *Bruckenthalia spiculifolia*, a plant which was most probably a component of mire communities (cf. p. 20) appears for the first time. The almost continuous curve of *Alnus viridis* suggests the presence of this species.

The great diversity of pollen taxa is evidence of different plant communities in the landscape of the lake at Horoszki. Beside peatland there existed other types of wetland habitats. They were undoubtedly the source of pollen of Cyperaceae, abundant in this zone. Both its abundance and ubiquitous presence in many other sites of this age (Krupiński 1992, Kupryjanowicz 1994) provides evidence of the regional nature of this fact and the wide distribution of sedge communities at the time. In this kind of community there grew plants which were the source of the pollen of such taxa as *Bidens* type, *Cirsium/Carduus*, Cichoriaceae, *Conium maculatum* type, Brassicaceae, *Filipendula*, *Lotus*, *Rumex maritimus* (macroremains) *Thalictrum*, *Trollius*, *Viola palustris* type, *Ranunculus flammula* type, *Solanum dulcamara*, *Polygonum persicaria*, and many others. In general, on the basis of the palynological picture of this zone, it seems that the pollen flora reflects wetland communities. This is also evidenced by the presence of macroscopic moss remains: *Calliergon trifarium* (now considered a glacial relict in Poland's flora) *Drepanocladus revolvens*, *D. aduncus*, *Bryum bimum*, *Sphagnum* sp., and a very high proportion of Bryales spores, which probably grew in profusion in the undergrowth of dwarf shrub tundra.

Among the pollen taxa of herbaceous plants there are many which point to a rich vegetation of the meadow type. These habitats were most probably the source of the pollen of *Gentiana campestris* type (Pl. 4, fig. 4), *Hypericum*, *Lythrum*, cf. *Oxyria digyna*, *Papaver rhoeas* type, *Plantago major* type, *P. media*, *Polygonum aviculare* type, *P. bistorta/viviparum*, *Ranunculus acris* type, *R. sceleratus* (macroremains) *Trifolium* type, and *Valeriana officinalis* type.

On higher ground or in areas with better drainage on leached sandy soils there occurred vegetation composed by plants with different ecophysiological requirements. It is there that juniper scrub occurred. The presence of plant communities associated with a sandy, acidic substrate may be indicated by the pollen of *Arenaria* type, *Gypsophila fastigiata* type, *Helianthemum alpestre* type, *H. nummularium* type, *Hypericum*, *Jasione*, *Scleranthus annuus*, *S. perennis*, and others. Pollen of *Ephedra fragilis* type, *Artemisia*, and Chenopodiaceae points to a high degree of openness of the landscape and of the occurrence of steppe communities.

The great diversity of the pollen flora described makes it possible to infer that the vegetation of the region of Horoszki in the first stadial of the Early Vistulian must have been characterized not only by a considerable diversity of taxa but also a great diversity of habitat conditions and phytosociological relations, which are difficult to reproduce (cf. Birks 1986).

In the younger part of the stadial there was a gradual increase of tree birches in the flora (*Betula alba* type pollen), which reflects the expansion of birch forest.

Aquatic and littoral vegetation

In the first stadial of the Vistulian a change took place from a strongly organic sediment to a more mineral one (silt) as expressed in the very distinct decrease in the amount of organic matter in the sediment (cf. Fig. 3).

The high curve of *Phragmites* type, and the presence of *Sparganium* type, *Typha*, *Alisma*, and spores of *Equisetum* prove the presence of reedswamp communities in the surroundings of the lake. In turn the nuts of. *Carex rostrata/vesicaria*, and the pollen of *Lysimachia thyrsiflora*, *Menyanthes trifoliata*, and *Rumex aquaticus* type are evidence of the development of tall sedge reeds. Also, remains of the mosses *Drepanocladus revolvens*, *D. aduncus*, *Calliergon trifarium*, and *Sphagnum palustre* most probably come from reedy habitats. The presence of *Rumex maritima* macroremains and *Elatine* pollen in more eutrophic, shallow spots indicates the presence of these communities. Macrophyte communities are represented by endocarps of the pondweeds *Potamogeton sukaczevii* and *P. pussilus* (Pl. 6, fig. 2), and the pollen of *Myriophyllum spicatum* and *M. verticillatum*. In shallow water, in spots sheltered from rippling, communities including *Stratiotes* and *Callitriche* developed. The abundant occurrence of *Pediastrum* and *Nitella syncarpa* would indicate meso– or even eutrophic conditions prevailing in the lake (Tołpa 1961, Podbielkowski & Tomaszewicz 1996).

Brörup interstadial

EV2, *Betula–Pinus* R PAZ

HD-14 – HD-20 L PAZ, HDM-5 – the oldest part of HDM-8

HD-14, *Betula* L PAZ

The expansion of tree birches begun towards the end of the first stadial, and reached its maximum at the beginning of the Brörup interstadial represented by L PAZ HD-14. Birch forest developed at this time in the vicinity of Horoszki. Not only the high proportions of *Betula alba* type pollen but also the abundant presence or macroscopic remains (scales and nuts of *Betula* sect. *Albae*) provide evidence for its presence in the immediate vicinity of the basin. Birch was undoubtedly the most important tree in communities of this time (?*B. pubescens*). The development of similar forests of this age is observed at many other sites in this period from Poland (Jastrzębska-Mamełka 1985, Mamakowa 1989, Tobolski 1991, Kupryjanowicz 1994). This shows the regional extent of this phenomenon, so it can be linked with a general improvement in climatic conditions. *Pinus sylvestris* occurred in the vicinity of Horoszki (seed found), as well as *Larix*, *Populus*, and probably *Picea abies*. These communities can be compared with the present east-European taiga forest tundra in the Komi Republic (Katenin 1972). In the undergrowth in these forests, there occur *Betula nana*, *Juniperus sibirica*, and many members of the Ericaceae family, (such as *Vaccinium myrtillus*, *V. uliginosum*, *V. vitis–idaea*, *Ledum palustre*, and *Empetrum hermaphroditum*). In more open areas, the undergrowth of these forests at Horoszki *Fragaria* can most probably be associated. *Alnus viridis*, *Juniperus*, and *Rosa* constituted the understorey. Many of the taxa found in deposits of this age indicate patches of dwarf shrub tundra with *Betula nana*, and *Salix polaris* type. The area around Horoszki was probably never completely covered by forest during the Brörup interstadial. Such taxa as *Herniaria* type, *Jasione*, and *Helianthemum alpestre* type show the continuing presence of the communities of open spaces, with the character of steppe or grassland in sandy areas. Meadow communities on wet sites are reflected by *Filipendula*, *Geum* type, *Lotus*, *Plantago major*, *Pleurospermum austriacum*, *Potentilla* type, Rubiaceae, *Rumex acetosa* type, *Thalictrum*, *Valeriana dioica* type, and Apiaceae undiff. The marked decrease in the proportion of *Sphagnum* spores suggests a different conclusion may be drawn; namely, a change in hydrological conditions in the direction of decreasing wetness and a decrease in the area occupied by tundra and birch forest.

Cold intra-Brörup oscillation

HD-15, NAP–*Betula* L PAZ

The expansion of birch forest after the first stadial of the Early Vistulian most probably, did not last too long. Climatic conditions deteriorated again, birch woods retreated, and communities of open areas expanded. A similar picture in the development of the vegetation of this section of the Vistulian was registered in many diagrams from continuous profiles not only in Poland (Jastrzębska-Mamełka 1985, Mamakowa 1989, Kupryjanowicz 1994) but also in profiles from the area of Germany (Erd 1973, Behre 1989, Hahne et al. 1994, Müller et al. 2003), France (Reille et al. 1992) and even in central Sweden (Robertsson 1988).

At Horoszki, this cooling was reflected in a spread of the area of shrub tundra, as seen by the increase in the curves of *Betula nana* and *Salix polaris* type. Moreover, *Alnus viridis* and *Juniperus* were a constant, element of shrub communities of this time, probably forming single small stands. *Myricaria germanica* grew in habitats along streams. In this period, larger areas were probably occupied by dry habitats than during the first stadial of the Early Vistulian (HD-13). This is indicated by the proportion of *Artemisia* pollen, which is doubled, and the lower percentages of Cyperaceae pollen. Negligible amounts of *Sphagnum* spores are evidence of the fact that peat bog communities did not play a significant role in the surrounding vegetation, though the presence of *Andromeda polifolia* seeds points to its presence in the vicinity of the lake.

A very high proportion of the genus *Artemisia* (probably different species), and of species from the families Poaceae and Chenopodiaceae indicates the existence of steppe communities. Plants represented by the following taxa were most probably also constituents of these communities: *Achillea* type, *Aster* type, Asteraceae undiff., Cichoriaceae, Rubiaceae, *Rumex acetosella*, *Arenaria* type, *Cerastium* type, *Herniaria* type, *Lychnis viscaria* type, *Pulsatilla* type, *Ranunculus acris* type, and *Scleranthus perennis*.

The continuing presence of tree birch macroremains is noteworthy, but may suggest that patches of birch forest tundra persisted, but undoubtedly with a higher proportion of herbaceous communities. This is indicated both by the low percentages and the low concentration of *Betula alba* type pollen. The presence of *Pinus sylvestris* cannot be ruled out and *Larix* was one of the trees growing in the region of Horoszki as reflected by pollen showing its presence *in situ*. The presence of spruce (maybe *Picea obovata*) is also quite likely. The occurrence of *Pinus cembra* pollen should, owing to the openness of the landscape in this zone, most probably be associated with long-distance transport, though its presence at not too a great distance was possible. The boreal species *Trientalis europaea* was associated with the forest undergrowth.

The occurrence of the macroremains of *Rumex maritimus*, *Potentilla supina* (Pl. 6, fig. 24) *Ranunculus sceleratus*, *R. flammula*, and *Carex* nuts shows that the vegetation cover was mosaic and composed of different communities.

HD-16 – HD-20 L PAZ

After a cool episode there was an improvement in climatic conditions, which made the spread of forest possible again, this time with a greater variety of trees.

On the basis of the pollen diagram, the second part of the vegetation succession of the Brörup interstadial following the cooling can be divided into two parts. First, birch forests spread again (zone HD-16), later transformed into pine-birch communities (zone HD-17), which turned into pine communities with the participation of larch, spruce, and stone pine (zone HD-18). A characteristic feature of the vegetation of the final part of the Brörup interstadial is the increasing proportion of open communities, including Poaceae undiff., *Artemisia*, Cyperaceae, Chenopodiaceae, and an increasing diversity of herbaceous plant taxa (zones HD-19 – HD-20).

HD-16, *Betula*–NAP, HD-17, *Pinus–Betula–Larix* (*Picea*) and HD-18, *Pinus–P. cembra* type–*Picea* L PAZ

Following the period of intra-Brörup cooling, tree birches spread fast (*Betula alba* type pollen and macroscopic remains, including *B. pendula*) followed by the Scots pine, *Pinus sylvestris*. Its presence in this area is supported by macroscopic remains, already found at the beginning of this phase. Small percentage of *Larix* pollen, as well as macroscopic remains proves that larch occurred in the area from the beginning of the second part of the Brörup interstadial. Spruce was most probably present in situ, even though macroscopic remains appear a little later. These data show that the dominant community at this time in the region of Horoszki was a boreal birch-pine forest of a taiga character. Its undergrowth was most probably not very rich and changed in accordance with local habitat conditions. On dry, leached soils *Pteridium aquilinum* occurred, and in moist places, e.g. in river valleys, *Humulus lupulus*. This points more to a relatively mild boreal climate. Shrub of *Alnus viridis* occurred.

A very high proportion of AP (up to 98%) would support both the considerable compactness of these forests, and also the limited area occupied by non-forest communities. However, the constant presence of *Betula nana* (macroremains) and *Salix polaris* type shows that patches of shrub tundra still persisted in the area. In these communities, *Rubus arcticus*, *Empetrum*, *Equisetum*, and *Saxifraga stellaris* most probably occurred. It may thus be assumed that, at least locally, there were areas where these two formations were interspersed, forming an ecotone zone of forest tundra, with an increasing proportion of tundra communities to the north (Liivrand 1991, Satkunas & Grigiene 1997, Satkunas et. al. 1998, Lagerbäck & Robertsson 1988). Another factor indicating that the communities of birch-pine forests were most probably not too compact was the fact that both tree birches (*Betula alba* type) and *Pinus sylvestris*, being wind-pollinated plants, produce large amounts of pollen, and in consequence are frequently over-represented in the pollen flora. This is also supported by the occurrence of pollen of plants, which could represent communities of the same type as fresh meadows, i.e. *Sanguisorba officinalis*, *Pleurospermum austriacum*, *Filipendula*, *Plantago major*, *Ranunculus acris*, *R. sceleratus* (seeds), *Rumex acetosa* type, *Thalictrum* as well as Apiaceae undiff., and Compositae. The composition of the communities of these meadows and probably also those of peat bogs of the palsa type also included the mosses *Drepanocladus aduncus*, *D. revolvens*, *D. sendtneri*, *D. lycopodioides*, and *Sphagnum*. The presence of peat bogs of the aapa type may be indicated by abundant macroscopic remains of *Drepanocladus exannulatus* (Boch & Solonevich 1972, Kac 1975).

HD-19 *Pinus–Larix–Picea* (NAP) and HD-20 *Pinus–P. cembra* type–NAP L PAZ

After the maximum spread of birch and pine, the forest communities of the younger part of this interstadial underwent both quantitative and qualitative changes. The most important of these is the expansion of *Picea abies*, *Larix*, and *P. cembra* at the expense of tree birches, macroremains of the latter indicating their constant participation in forest communities in the vicinity of the lake at Horoszki. The dominant species was undoubtedly *Pinus sylvestris*, especially at the beginning of the younger (second) part of the interstadial.

Although it was not possible to establish which species of spruce was present in the material evidence from Horoszki, we cannot exclude *Picea obovata*. It is supported by the identification of macroremains of *P. obovata* in Early Vistulian and Eemian deposits from Lithuania (Riszkiene in Kondratiene 1996). In the material from Horoszki, not only the presence of *Pinus cembra* type pollen is important but also the fragment of a *Pinus cembra* needle, which confirms the presence of this species in the forest communities.

It would be interesting to determine the direction of the migration of *Pinus cembra* in the Early Vistulian into the lowland areas of central Europe. Unfortunately, this problem is difficult to solve at our present stage of our knowledge of the distribution of *Pinus cembra* during the last glaciation. The modern range of this species spans western and central Siberia as well as the Alps and Carpathians (Meusel et al. 1965); moreover, the subspecies *P. cembra* subsp. *sibirica* (Rupr.) Rupr. occurs in Asia. The European region of the present distribution of the stone pine is of a relict nature from the transition boundary of the Tertiary and Quaternary, when the Siberian stone pine, together with other plants of the taiga spanned central and western Europe (Szczepanek 1971a). Assuming the existence of these two distribution regions of the stone pine in the Eemian interglacial in more or less the same form, we can imagine two directions from which it may have migrated into the northern lowlands of eastern Europe in the Early Vistulian. The shortest migration route during the early glacial could have been from the Carpathians. At a time when the Early Vistulian climate became increasingly harsh and species of thermophilous trees retreated southward, conditions may have been favourable for the expansion of the stone pine not only into lower locations in the Carpathians but also further north.

Another alternative of the spread of stone pine in the Early Vistulian is also probable. During the post-interglacial cooling, when floristic and climatic zones moved in a southerly and southwesterly direction (Frenzel 1968), the Siberian stone pine could have reached central Europe (yet again in the Pleistocene?). A fact, which could possibly suggest an extension of the range of the Siberian pine at this time is the presence of *Picea obovata* in Lithuania during the Early Vistulian (Riszkiene in Kondratiene 1996). The modern ranges of this species (i.e. *Picea obovata* and *Pinus sibirica*) overlap to a considerable degree, though the range of the Siberian spruce (*Picea obovata*) reaches a lot further east and northwest, up to the northern part of the Scandinavian Peninsula (Meusel et. al. 1965). Unfortunately so far no palaeobotanical evidence is found confirming the presence of Siberian stone pine in the Early Vistulian to the east of Poland.

In pine–spruce–larch forest with stone pine, it seems that *Pinus sylvestris* was the main tree taxa while others occurred in admixture, although the few percent of *Larix* pollen would seem to support its considerable proportion in communities. Occasionally, perhaps in wetter sites, small stands of tree birches remained, together with single *Populus* trees. The ground layer was formed by dwarf shrubs: *Vaccinium* type and *Empetrum*, while in drier areas there occurred *Juniperus*, *Calluna vulgaris*, *Pteridium*, and *Lycopodium alpinum*.

During the transformation of forest communities and the spread of stone pine, larch, and spruce, a spread of non-forest communities was gradually taking place. Not only the diversity of herbaceous plant taxa increased but also their proportion in the vegetation of the contemporary landscape of the region around Horoszki, as evidenced by the increasing proportion of herbaceous plant pollen. Thus after a fairly short period of more compact boreal pine–birch forests, climatic changes led to the increasing thinning of forest communities and the formation of forest tundra of a continental type.

At present, the tree species of the forest tundra belt in oceanic regions are birches; in extreme continental regions, larch and spruce (Walter 1970).

The increasing continentality of the climate is indicated by a strong expansion of some herbaceous plants, e.g. *Artemisia* and Chenopodiaceae, which may be associated with steppe habitats and Poaceae undiff. and Cyperaceae which also may come in part from tundra and steppe communities. *Helianthemum nummularium* type, *Pimpinella major* type, *Campanula*, *Cerastium* type, *Arenaria* type, *Rumex acetosella* (fruit, Pl. 6, fig. 20), *Aster* type, Rubiaceae, and Rosaceae undiff. were probably associated with steppe habitats or the drier forms of tundra.

The presence of *Betula nana* and *Salix polaris* type documents the occurrence of dwarf shrub tundra communities, while the relatively high diversity of herbaceous taxa implies tussock-tundra communities.

A cover of meadow-tundra vegetation, in wet habitats is represented by pollen of *Thalictrum*, *Rumex acetosa* type, *Oxyria digyna* type, *Ranunculus acris* type, *Lysimachia* sp., *Sanguisorba officinalis*, *Valeriana officinalis*, *Polygonum aviculare* type, *Polygonum bistorta/viviparum* as well as *Plantago major*, *P. media*, and *P. lanceolata* and abundant fruits of *Ranunculus sceleratus* as well as *Urtica dioica* seed (Pl. 6, fig. 25). On mires and other wetland habitats, the mosses *Calliergon trifarium*, *Drepanocladus revolvens*, and *D. sendtneri* occurred. The presence of mires is documented by macroremains of *Chamaedaphne calyculata* and an increasing proportion of *Sphagnum* spores, which is contemporary with the increase in herbaceous plant pollen, mainly Cyperaceae, Poaceae undiff., Chenopodiaceae, as well as *Betula nana*, and *Salix polaris* type.

The research of Jorgenson (1984, after Walker 1995) in Alaska has demonstrated that the development of tussock tundra communities is dependent on the process of soil paludification and the formation of a moss layer with *Sphagnum*. This process takes place in cold soils, when the layer of soil that thaws becomes thinner, which in turn causes a decrease in available nutrients and an increase in soil moisture. This promotes the spread of mires, followed by the succession of vascular plants. At the reconstruction of the succession of vegetation on the basis of the pollen diagram from Horoszki the process described by Jorgensen (op. cit.) may have taken place in periods of climate deterioration, with a decrease in temperature and the amount of heat reaching the soil. Kolstrup (1990) also points to the development of peat in modern Arctic regions with permafrost, where drainage is impeded.

The palaeobotanical data from the profile at Horoszki indicate that the vegetation of southern Podlasie was a highly complex one during the youngest part of the Brörup interstadial. The flora was a mosaic of forest, tundra, and probably also steppe communities.

Aquatic and littoral vegetation

The most characteristic change in the development of the local flora at the beginning of the Brörup interstadial (zone HD-14) is a sharp decline of pollen of *Phragmites* type, Cyperaceae, and other reedswamp taxa present in the Herning stadial. On this basis of this a partial regression is inferred of reedswamp and tall sedge communities around the basin. However, the presence of *Carex elata* fruits, remains of *Drepanocladus revolvens*, and *D. aduncus* shows that communities of this type were still present. Very high AP values (mainly *Betula alba* type) and the abundance of macroscopic remains of tree birches suggest the nearby presence of birch forest at the edges of the basin. The disappearance of *Pediastrum* colonies in the sediment may be evidence of an increased shading of the water in littoral areas. Macrophyte communities are represented by sporadic fruits of *Najas flexilis*, *N. marina*, and *Ceratophyllum demersum*, as well as pollen of *Myriophyllum verticillatum*.

During the climatic oscillation represented by pollen zone HD-15 NAP–*Betula* a change is observed in the composition of the sediment from strongly organic (*substantia humosa*) to sandy gyttja silt. *Pediastrum* colonies reappeared in the sediment with high percentages. At the same time there is a slight increase in the proportion of *Phragmites* type and Cyperaceae pollen, which may suggest an increase in the importance of reedswamp habitats. Raising values of *Pediastrum* colonies probably indicate an improvement in light conditions in the lake.

Following the intra-Brörup cold oscillation through local zones HD-16 – HD-18, the proportion of organic matter increased almost fourfold. Initially this was *substantia humosa*, reflecting little of the nature of the changes, but peat was formed which together with another decrease in the proportion of *Pediastrum* are evidence of a fall in the water level in the lake and overgrown marginal parts, leaving only little open water for *Pediastrum* to bloom. These changes, however, did not have a significant effect on the composition of the aquatic flora in relation to zone HD-15. The profusion of *Najas flexilis* fruits indicates its dominance in the macrophyte communities. Beside, *Najas flexilis, Potamogeton praelongus, Nuphar pumila*, and *Ceratophyllum* (*?demersum*) were components of these communities, as evidenced by the high proportion of *Ceratophyllum* hairs. In shallow marginal water, *Chara contraria* and *Nitella syncarpa* were found, *Eleocharis palustris* (Pl. 6, fig. 17) and *Elatine hydropiper* occurring in the marginal zone.

During the later part of the Brörup interstadial (pollen zones HD-19 and HD-20) a return took place in reedswamp communities in the local vegetation, as expressed by an increase in pollen of *Phragmites* type (also seeds cf. *Phragmites*) and Cyperaceae. In reedswamp communities, there also occurred: *Sparganium* (pollen of *Sparganium* type), *Typha*, *Lysimachia thyrsiflora*, *Menyanthes trifoliata*, *Cicuta virosa* (pollen of *C. virosa* type) as well as *Equisetum* and *Osmunda*. It is likely that some of the spores of Filicales monoletae (=Polypodiaceae s.l.) may also be associated with taxa growing in these habitats. *Bidens tripartitus* and *Ranunculus sceleratus* (abundant fruit) formed terrophyte communities in the marginal parts of the basin, which dried out in summer.

The presence of mossy-sedge reedswamp communities is confirmed by nuts of *Carex rostrata/vesicaria*, *C. elata*, *C.* cf. *elongata*, abundant remains of *Drepanocladus revolvens*, and *Calliergon trifarium*. Increasing values of *Sphagnum* spores and the presence of *Scheuchzeria palustris* seeds (Pl. 6, fig. 12) are evidence of the development of peat bogs. An abundant macroscopic remains of *Eleocharis ovata* is evidence of phytocoenoses with *Eleocharis ovata* and *Elatine hydropiper* on the shore, which would be exposed for short periods.

Macrophyte communities were formed by *Nuphar pumila*, *Nymphaea alba* type, *Ceratophyllum demersum*, *Potamogeton sukaczevii*, *P. pusillus*, *P. praelongus*, *P. obtusifolius* (Pl. 5, fig. 25), *P. perfoliatus* (Pl. 5, figs 23, 24), *P.* cf. *lucens* (Pl. 6, fig. 3), *Myriophyllum alterniflorum*, *M. verticillatum*, *M. spicatum*, *Najas flexilis*, and *Batrachium* (fruit). In shallower parts of the basin *Callitriche* occurred (fruit). Marginal shallow parts held communities with *Chara contraria* (oogonia). Of other stoneworts, *Nitella syncarpa* was present in this zone.

Besides phytocoenoses associated with meso- and eutrophic habitats, oligotrophic communities also appeared, indicated by the presence of *Isoetës* spores (Pl. 1, fig. 6), pollen of *Litorella*, and *Hydrocotyle vulgaris*.

Rederstall stadial

EV3, Gramineae–*Artemisia*–*Betula nana* R PAZ

HD-21, NAP–*Pinus*–*P. cembra* type L PAZ and HD-22 NAP–*Betula nana*–*Salix polaris* type (*Pinus cembra* type) L PAZ, HDM-8 and the oldest part of HDM-9 L MAZ

Increasing continental climate during the Rederstall stadial transformed the flora in the direction of the further spread of open steppe and tundra communities and in the end to their domination in the landscape. Forest communities, decreased which is noticed by the high variety of taxa and the continuing increase in the frequency of NAP. Together with high proportions of Poaceae undiff., Cyperaceae, *Artemisia*, and Chenopodiaceae, the frequency of *Betula nana*, *Salix polaris* type pollen, and Bryales spores increase, with a simultaneous drastic decline in the AP curve. It may be inferred that in the Rederstall stadial the transitional belt of forest tundra (and forest steppe?) shifted further south. Nevertheless, in the region of Horoszki, single trees and small groups of trees persisted (the vicinity of the basin, river valleys), which is suggested by the macroscopic remains of tree birches, larch, and spruce. In the shrub layer *Juniperus*, *Alnus viridis*, *Ribes alpina*, *Myricaria germanica*, and *Myrica gale* occurred. The presence of these two last taxa may indicate the continuing presence of an oceanic climate or their relict character at this time.

The rich taxonomic composition indicates a considerable variety of communities within the broad category of tundra vegetation. *Betula nana* (also macroremains), and shrub willows (*Salix polaris* type) formed a dwarf shrub tundra, with a rich carpet of the mosses *Drepanocladus revolvens*, *Calliergon trifarium*, and *Sphagnum* as well as herbaceous plants, represented by the pollen of *Armeria maritima* (see Pl. 3, figs 12, 13), *Cerastium* cf. *alpinum*, *Dryas*, *Geum* type, *Saxifraga cernua* type, *S. hirculus* type, *S. stellaris* type, *Campanula*, *Dianthus* type, *Trollius*, *Thalictrum*, and cf. *Oxyria digyna*. In these communities ericaceous dwarf shrubs existed e.g. *Vaccinium*, *Calluna vulgaris*, *Bruckenthalia spiculifolia*, and *Empetrum*. Representatives of the Cyperaceae family played an important role in the vegetation in the area. This conclusion can be drawn on the basis of the present role played by swamps with moss-sedge vegetation in the landscape of the East European forest tundra (Kac 1975). Unfortunately, pollen analysis does not permit detailed identification within the Cyperaceae family, and only a few macroscopic remains of sedges were found in this material (*Eleocharis ovata*, *Carex vesicaria/rostrata*, *Carex* sp. div.).

In the Rederstall stadial, another expansion of moist meadow communities took place, with the presence of such taxa as *Plantago major*, *P. lanceolata*, *Gentiana pneumonanthe* type, *Polygonum aviculare*, *P. bistorta/viviparum*, *P. persicaria*, *Mentha* type, *Potentilla* type, *Bidens* type, *Caltha* type, *Urtica*, *Rumex longifolius* type, *Ranunculus acris* type, *R. flammula* type, *Rhinanthus* type, and *Dianthus* type (including the genus *Saponaria*).

Dry habitats also occurred, indicated by the very high proportion of *Artemisia*, Poaceae undiff., and Chenopodiaceae. These taxa may have formed meadow steppe communities, which were the source of such taxa as *Anemone* type, *Helianthemum alpestre* type, *H. nummularium* type, *Gypsophila fastigiata* type, cf. *Jurinea*, *Linum austriacum* type (Pl. 2, figs 1–2), *Centaurea scabiosa* type, *Rumex acetosella*, *Phyteuma*, *Sagina* type, *Sedum*, *Serratula* type, Rubiaceae, and Cichoriaceae. Pollen of *Plantago maritima* sensu stricto is an evidence in favour of the presence of the abovementioned steppe-like communities or steppes with halophile communities.

Aquatic and littoral vegetation

The change of peaty deposit to silt is evidence of an increase in the water level in the lake. At the same time, the proportion of organic matter in the sediment falls drastically. The considerable increase in the proportion of *Pediastrum* may suggest an improvement in light conditions in the water. The increase of *Phragmites* type pollen is evidence of further spread of reedswamp communities, while the high values of Cyperaceae may indicate of the increase in the area of tall sedge reeds. It is most probably from these moss-sedge communities that the seeds of *Menyanthes trifoliata* and *Comarum palustre* originate (Pl. 6, fig. 22). *Rumex maritimus* occurred in the most eutrophic habitats.

In macrophyte communities, a dominant role was played by species of the genus *Batrachium*, which is expressed in the abundant occurrence of the seeds of this genus and an increase in *Ranunculus flammula* type pollen. *Callitriche* must have been a fairly frequent component of aquatic communities, its fruit being quite abundantly represented in the sediment of the time. Among macrophytes, *Potamogeton filiformis* (Pl. 5, fig. 26) is a new element. The pollen of *Utricularia* is also present.

Another piece of evidence indicating an increase in the water level in the lake is the particularly abundant occurrence of the stonworts *Nitella syncarpa* and *Chara contraria*. The communities now formed by these species are represented in alkaline meso– and eutrophic waters (Tomaszewicz 1979), where they usually form their own facial communities with a small proportion of representatives of the macrophytes and reedswamp plants (Podbielkowski & Tomaszewicz, 1996).

Odderade interstadial

EV4, *Pinus–Betula* R PAZ

HD-23 – HD-26 L PAZ, the middle and lower part of HDM-9 and HDM-10 L MAZ

HD-23, *Betula* L PAZ

The very rapid rise in the *Betula alba* type curve is a reflection of the expansion of tree birches, with the simultaneous restriction of open communities. These changes mark the beginning of the next phase in the development of forest vegetation in the vicinity of Horoszki, which is characteristic of the beginning of the Early Vistulian Odderade interstadial.

The spread of birch forests in central Europe is confirmed in many pollen diagrams covering this period (Averdieck 1967, Erd 1973, Menke & Tynni 1984, Jastrzębska-Mamełka 1985, Behre & Lade 1986, Mamakowa 1989, Hahne et al. 1994, Caspers 1997). At sites where plant macrofossil analysis was carried out, macroremains of various tree birches were found. In the material from Horoszki, enormous amounts of nuts and catkin scales of *Betula* sect. *Albae* were noted. Judging by the results of pollen analysis, birch was the most important forest-forming species in this phase of the Odderade interstadial. Very low values of *Pinus sylvestris* type and *P. cembra* pollen and the absence of *Larix* pollen and macroremains would point to the genuine absence of these trees in the area investigated. As for spruce, the continuous, (below 1%) curve of its pollen may point in favour of its occurrence *in situ* (cf. Robertsson 1988). Such a suggestion is made possible by the presence of a *Picea abies* seed with the comparable percentage share of its pollen in the material from Horoszki at the end of the Brörup interstadial. Late Glacial and Holocene sites are also known from the Carpathians, in which the macroremains of spruce are present together with very low (below 1%) pollen curves (Środoń 1990b, Harmata 1995). Of other trees, *Populus* wood was recorded in the birch phase of the Odderade interstadial. Thus in the initial phase of this interstadial, birch forests dominated in the area under study, with an admixture of *Populus* and *Salix,* and perhaps also a small proportion of spruce. As in the case of the Brörup interstadial, these must have been reasonably spaced and sunlit forests. The landscape as a whole was probably one of a birch forest tundra type.

It is noticed in pollen diagram that the percentage decline in individual herbaceous plant taxa is not accompanied by any marked impoverishment in the variety of NAP taxa. The taxa which disappeared are almost exclusively those which in the Rederstall stadial represented steppe habitats, namely Chenopodiaceae, *Linum austriacum* type, *Helianthemum*, *Anemone* type, *Arenaria* type, Caryophyllaceae, and others. Despite a considerable decline (e.g. of Cyperaceae) the taxa of wet habitats persisted, represented by *Filipendula*, *Dianthus* type (including *Saponaria*), and others. In this group even some new taxa appeared, e.g. *Cirsium*/*Carduus*, *Lysimachia* undiff., *Cicuta virosa* type, *Sparganium* type, and *Typha latifolia*. A similar tendency is observable in plant macrofossil remains, since in this phase of the Odderade such species appear as *Rumex maritimus*, *Elatine hydropiper*, *Mentha aquatica*, *Menyanthes trifoliata*, *Lycopus europaeus*, *Alisma plantago–aquatica*, and *Stachys palustris* (Pl. 6, fig. 27). At the same time the proportion of *Sphagnum* spores decreases, which only appears to be at odds with the above facts. A marked spread of trees took place in this area, where previously communities of open herbaceous vegetation had dominated. This evidence of a considerable improvement in climatic conditions, temperature being the most important in determining the distribution of vegetation (Aleksandrova 1980, Walker 1995). For this reason, the increase in the proportion of trees should be interpreted as a warming of the climate. The warming may have caused the level of the permafrost to become much lower or to disappear altogether so water could reach into deeper layers, thus altering the water relations in the soil. This is perhaps the explanation for the almost complete absence of *Sphagnum* spores in this part of the pollen diagram, associated with the disappearance of peat bogs and the spread of mesophilic communities of moist and marshy habitats, which had occurred from the previous stadial.

HD-24, *Pinus–Betula–Pinus cembra* type L PAZ

Following a pioneer birch phase, the Scots pine (*Pinus sylvestris*) spread rapidly. Much as in the Brörup interstadial, for a short time both of these trees were components of the tree flora. AP values in zone HD-24 are the highest, and this zone should be considered the climatic optimum of the Odderade interstadial. The boundary of forest tundra again shifted northward and boreal pine-birch forests developed, possibly including spruce. The clear decrease in the proportion of *Betula nana* pollen and the complete disappearance of *Salix polaris* type pollen suggests a temporary decrease in the area of tundra, though probably, as in the Brörup interstadial, forest communities were open park-like in character, at least in places. In the understorey of these forests *Pteridium* and other ferns occurred. The ground was formed by carpets of moss, especially *Drepanocladus aduncus* and *D. revolvens*. After a period of stabilization of these forests, the birch began to recede and to the end of the Odderade interstadial pine was the dominant tree in the area.

HD-25, *Pinus–Larix–Betula nana* (NAP) and HD-26, NAP–*Pinus–Larix* (*Salix polaris* type) L PAZ

The next stage of the vegetation succession brings with it the signs of the onset of another cooling. The climatic changes reflected as changes in vegetation composition point to a continental climate. Another tree to reappear in the vicinity of Horoszki was larch. Its spread, expressed both in high values of pollen and in the abundance of macroscopic remains, occurred at the same time as the expansion of open communities. At the same time, the development of peat bogs with *Sphagnum* took place, which, by analogy to the previous interstadial, can be considered a return of permafrost or of its decreased depth from the surface of the soil. A consequence of this was again the impeded downward penetration of water and the improved hydration of the top layers of the soil. This would be in accordance with the ecophysiological properties of the larch, whose transpiration coefficient is very high, higher than that of spruce and pine, for which reason it needs a lot of water in the substrate (Olaczek 1986). At the same time, the presence of spruce in situ (seeds) is confirmed.

Forest communities became increasingly accessible to sunlight and the area occupied by open communities increased. The boundary of the forest tundra again moved southward. The area of shrub tundra increased, as suggested by higher values of *Betula nana* pollen and the reappearance of *Salix polaris* type pollen. The formation of a layer of *Sphagnum* peat enabled the abundant development of various types of moss-sedge communities. Numerous representatives of the Ericaceae family grew on the peat bogs: *Bruckenthalia spiculifolia*, *Calluna vulgaris*, *Ledum*, *Vaccinium* type, *Arctostaphylos*, and *Empetrum*. Of other tundra communities, meadow communities in moist habitats flourished again, as is attested by such taxa as *Filipendula*, *Thalictrum*, *Geum* type, *Potentilla* type, *Ranunculus acris* type, *Plantago major*, *Polygonum aviculare* type, *P. bistorta/viviparum*, *Rumex acetosa* type, *Rhinanthus* type, *Sanguisorba officinalis*, *Solanum dulcamara*, *Trollius*, *Valeriana officinalis* type, *V. dioica* type, *Polemonium*, *Comarum palustre*, *Stellaria palustris* (seed), *Cicuta virosa* type, *Equisetum*, *Hydrocotyle vulgaris*, Apiaceae undiff., and *Botrychium lunaria*. The presence of *Saxifraga oppositifolia* type pollen is noteworthy. Beside *S. oppositifolia*, this taxon also contains arctic and arctic-alpine species growing on bare bedrock and its co-occurrence with such taxa as *Cerastium* cf. *alpinum*, *Polygonum bistorta/viviparum*, and cf. *Oxyria digyna* is evidence of the presence of arctic tundra communities. The abundant mossy layer was formed by mosses, whose vegetative remains are richly represented in the sediment and were certainly a significant component of these communities. Among these are *Drepanocladus revolvens*, *D. annuus*, *D. fluitans*, *D. vernicosus*, *D. exannulatus*, *Calliergon trifarium*, *C. fluitans*, *Messia triquetra*, and *Sphagnum subsecundum*. As towards the end of the Brörup interstadial also during the Odderade interstadial there were taxa on the basis of which we may infer the presence of communities of drier, more steppe-like habitats e.g. Poaceae undiff., *Artemisia*, Chenopodiaceae, Cyperaceae, *Anemone* type, *Arenaria* type, *Aster* type, *Astragalus danicus* type, *Campanula*, *Cytisus*, *Hypericum*, *Papaver rhoeas* type, *Plantago media*, *Pulsatilla*, *Rumex acetosella*, *Scleranthus perennis*, and *Silene vulgaris* type.

Aquatic and littoral vegetation

The improvement of the climate at the beginning of the Odderade interstadial made it possible for birch forest to expand again. The large amount of macroremains of *Betula* sect. *Albae*, the disappearance of *Phragmites* type pollen and the drastic decline in the proportion of Cyperaceae pollen suggest that birch also spread to reedswamp sites. At this time, a change also took place in the composition of the sediment, from silt to peat reflected as increase in organic matter (Fig. 3). This is evidence of a fall in the water level of the lake, which may be the result of a “drying” effect of the forest.

Nuts of C*arex elata* and *C. rostrata/vesicaria* in zone HDM-9 demonstrates that certain sedgeswamp communities still persisted in the area. Seeds of *Alisma plantago–aquatica, Typha*, pollen of *Sparganium* type, and *Typha latifolia* are evidence of various communities of reedswamp, including *Lycopus europaeus*, *Stachys palustris*, *Menyanthes trifoliata*, and *Mentha* cf. *aquatica*. In more oligotrophic habitats *Eleocharis ovata* and *Isoëtes* (spores) occurred.

In macrophyte communities *Potamogeton sukaczevii*, a species which is now extinct, was most frequent, *P. pusillus*, *Potamogeton natans*, *P. obtusifolius*, and *P.* cf *friesii* (Pl. 5, fig. 27) were also present. *Najas flexilis*, the *Najas* species which is least sensitive to temperatures (Mamakowa 1997) occurred, as well as *Myriophyllum spicatum* (pollen) and the fossil species *Myriophyllum* cf. *microcarpum*.

In the younger part of the Odderade interstadial, from the beginning of pollen zone HD-25, the spread of reedswamp communities took place, reflected in the reappearance and increasing proportion of the pollen of *Phragmites* type and Cyperaceae. Pollen of *Menyanthes trifoliata* and *Lysimachia thyrsiflora* reappears. The expansion of peat bogs in the vicinity of the lake is evidenced by increasing values of *Sphagnum* and Bryales spores, and the presence of *Scheuchzeria* pollen. The change from peat to lake deposits (organic silts), which continue to be present to the top of the profile suggests an increase in the water level in the basin.

In macrophyte communities, the genera *Batrachium* and *Callitriche* played a significant role towards the end of the interstadial, which is indicated by the abundant occurrence of macroremains in zone HDM-10. Communities of the stoneworts *Nitella syncarpa* and *N. gracilis* were very widespread in the lake at Horoszki during the second part of the Odderade interstadial. Both these species now form submerged communities in which they are totally dominant (Podbielkowski & Tomaszewicz 1996). The *Nitella gracilis* community develops on a peaty substrate (op. cit.). Since, in the material from Horoszki, significant quantities of oospores appeared in only one sample, it cannot be ruled out that they came from runoff from the marginal, peaty part of the lake.

PLENIVISTULIAN

In the stratotype section from Oerel in NW Germany (Behre & Lade 1986), two (Oerel and Glinde) Middle Vistulian interstadials were first distinguished. These interstadials are separated by layers of sand, correlated with cold periods. Palaeobotanical data indicate that both in the Oerel and in the Glinde interstadial the landscape of Lower Saxony was woodless and that a dwarf shrub tundra vegetation dominated (Behre 1989). The profile from Oerel, however, does not document the character of the vegetation in stadial periods.

Since biogenic sediments representing the Plenivistulian (Middle Weichselian) occur in the profile from Horoszki, an attempt to distinguish stadials and interstadials must be fully based on biostratigraphy since this time interval is beyond the reach of radiocarbon dating. On one hand this is difficult but on the other hand it provides the opportunity to trace changes in vegetation not only during interstadials but also during stadials.

In distinguishing chronostratigraphic units in the Plenivistulian, the author interpreted those parts of the pollen diagram in which the shape of the curves may suggest changes in vegetation (increase in AP) caused by climatic oscillation as interstadials and a decrease in AP and increase in NAP as stadials. Bearing in mind the general tendency for climatic changes in the direction of maximum cooling, the magnitude of these oscillations must have been small, hence the reaction of the vegetation to these changes may be expected to have been minor in Poland.

The boundary between the Early and Middle (=pleni =full) Vistulian (Weichselian) is placed above the Odderade interstadial (Behre 1989, Kozarski 1991, Hahne et al. 1994). From this period a constant decline in temperature is suggested. The development of a virtually treeless flora in the area of central Europe was a consequence of this. Palaeobotanical data obtained from lake sediments at Horoszki also indicate a very small proportion of trees in the vegetation. Relatively small fluctuations in the main diagnostic taxa are another feature of the pleniglacial plant succession at Horoszki; this may reflect relatively small changes in the local vegetation during this period.

The clear decrease in pollen of *Pinus sylvestris* type marks the end of the period with milder climatic conditions and the renewed dominance of open communities in the region of Horoszki. The proportion of tree birches did not, however, change much and the sporadic presence of macroscopic remains is presumably evidence of their permanent occurrence in the neighbourhood. Despite the fact that the *Larix* curve has a low percentage and is not continuous in parts, the larch must have been present in situ at least as individual trees, as indicated by needles found in the top part of the profile. A similar situation may have applied to spruce, though its macroscopic remains were not recorded. Low values of *Populus* pollen and occasional pollen grains of *Sorbus* cf. *aucuparia* show the presence of these trees in the vicinity. Pollen of thermophilous broadleaved trees represents long-distance transport in conditions of the openness of the plant cover over large areas. The presence of *Pinus cembra* type pollen can probably be explained in a similar way, however, it is a matter of debate. Mamakowa (1998) found *Pinus cembra* needles in the Eemian profile of the Wąwał locality together with only promille quantities of *P. cembra* type pollen. Some doubts, however, my be raised by the presence of *Alnus* wood fragments, accompanied by a relatively low pollen curve of *Alnus* undiff. pollen. Since the fragments of wood were too small to identify which species of *Alnus* they represent, *Alnus viridis* cannot be ruled out, the pollen which occurs in discontinuous form throughout the Vistulian part. It cannot be ruled out either that the abovementioned fragments of *Alnus* wood represent roots of a much younger age.

Undoubtedly, by the end of the Odderade interstadial the forest was thinning and steppe tundra communities expanded, while during the Plenivistulian the lake at Horoszki was located far north of the forest margin, this time for a longer period.

Throughout the Plenivistulian, open communities of various habitats dominated the landscape. Trees occurred as small scattered stands. The floristic composition obtained both by pollen analysis and macroscopic remains shows a high diversity of habitats occupied by different plant communities. On one hand the occurrence of dwarf birch, shrub willows (*Salix polaris* type pollen) are evidence of the spread of shrub tundra with many forms of undergrowth layer. On the other hand the presence of very high percentage values of the pollen of Poaceae undiff., *Artemisia*, and Chenopodiaceae would indicate the occurrence of dry steppe habitats. This suggests steppe-tundra formation. Interpretation of palaeobotanical data and reconstruction of the vegetation poses considerable difficulties since tundra and steppe do not occur together, or hardly at all.

A similar floristic relationship was already present in the Early Vistulian stadials and towards the end of interstadials.

All that has been said above constitutes the reason for which the composition and changes in the vegetation of the vicinity of Horoszki during the Plenivistulian have been described divided into a number of parts. A common description has been made of local pollen zones HD-27 to HD-31 as well as HD-32 to HD-37; there are separate ones for zones HD-38 and HD-39. This description has been preceded by a general presentation of the concept of Pleistocene steppe tundra.

The concept of Pleistocene steppe-tundra

The vegetation changes in the Plenivistulian were minor. The basic type of vegetation was, in the author's opinion, of an open steppe tundra character.

The concept of Pleistocene steppe tundra first appeared in association with studies of the fossil remains of mammals by Russian palaeontologists. Nehring (1890, after Hibbert 1982) described a vertebrate fauna of a steppe character found in late Pleistocene loesses of central Europe. On the basis of this he characterized the climate of the time as steppe, with features of arctic climate. Later Tugarinov (1929, after Hibbert 1982), on the basis of vertebrate faunas of northern Eurasia, stated that fossil vertebrate assemblages, representing both the modern arctic and steppe elements, may have occurred together because climatic and ecological conditions were suitable for both. On the basis of the taxonomic composition of these faunas it was suggested that the environment of the time was an open landscape, definitely dry, rather cold, with little precipitation in winter. Büdel (1949, after Hibbert 1982) demonstrated that the late Pleistocene loess sediments in Europe are strictly associated with steppe vegetation. A characteristic feature of pollen spectra representing this vegetation was the combination of a low proportion of tree pollen and high grass pollen frequency and motherworts (*Artemisia*) in areas in which steppe vegetation does not occur today. Büdel (op. cit.) postulated the occurrence in Europe of a zone of dry climate in the range of the maximum of the last glaciation, in which the accumulation of loess took place. He associated two broad vegetational zones, namely loessotundra (“Lösstundra”) in north-western Europe, and, to the south, (“Löss-steppe”), which stretched east as far as central Asia. In his opinion, the forest belt which today separates the Arctic from the steppe belt did not exist at this time. The loess-tundra was as much steppe as it was tundra, and, with the exception of some small residual areas, does not occur in the modern Arctic.

A general characterization of the pollen spectra of tundra, steppe and steppe-tundra was given by Lavrenko (1981). According to this author the tundra in Eurasia is characterized by pollen spectra in which tree pollen is present with very low values. However, the pollen of birches of the *Nanae* and *Fruticosae* sect. does occur there, as do the spores of the subarctic species of the genus *Lycopodium*, and subarctic and boreal species of *Selaginella* (among others, *S. selaginoides*). Moreover, pollen mainly of Poaceae, Cyperaceae, Ericaceae, and some other dicotyledonous families is present. In turn, spectra reflecting steppe landscapes are also characterized by a small proportion of tree pollen (pine, tree birches, and larch) while pollen of Chenopodiaceae, *Artemisia*, and Poaceae is present in abundance. Of other families, pollen of Polygonaceae, Rosaceae, Papilionaceae, and Compositae is frequently found. Steppe-tundra spectra have, in his opinion, both tundra and steppe elements. Their characteristic feature, especially found in sediments from the last ice age is the co-occurrence of *Betula nana* pollen with high values of Chenopodiaceae and *Artemisia* pollen (cf. Lagerbäck & Robertsson 1988). It seems that pollen of Chenopodiaceae is of particular diagnostic value in the interpretation of the pollen spectra of steppe tundra. Representatives of this family do not occur in the tundra zone, while the northernmost stands of this family are those of the xerothermic dwarf shrubs *Ceratoides papposa* and *Kochia prostrata*, occurring in steppes and deserts, especially in salty soils. Both these species have been recorded in Pleistocene glacial sediments (Lavrenko 1981).

There is a fairly rich floristic and phytosociological literature concerned with modern extrazonal steppe vegetation. Interesting data are presented by Yurtsev (1974, 1978, 1982), who described, from an area of the taiga zone in northeast Asia (Yakutia), extrazonal steppe communities in the basins of the great Siberian rivers, such as Yana, Indigirka, Kolyma, Omolon. He also found steppe communities on the Chukotka Peninsula and Wrangle Island. The steppe character of these communities is indicated by Poaceae (with the genera *Helicotrichon*, *Kobresia*, *Stipa*, *Koeleria*, *Festuca*, *Poa*, and others), Cyperaceae (genus *Carex*), *Artemisia*, and *Potentilla*, *Thalictrum*, *Polygonum*, *Stellaria*, *Saxifraga*, *Arenaria*, *Oxytropis*, *Papaver*, and *Pulsatilla*. The ecophysiological features of these plants indicate their adaptation to strongly continental (steppe) conditions. Their steppe nature is also indicated by a discontinuous layer of aboveground vegetation, an extremely dense root system, and steppe seasonal dynamics (Yurtsev 1974, 1982). They occur together with zonal vegetation, i.e. tundra and various species of trees and shrubs e.g. *Larix*, *Pinus*, *Betula*, and *Salix*. Steppe meadows in northern Yakutia are often accompanied by halophyte communities with *Puccinella*, *Hordeum*, and *Chenopodium*. These occupy habitats at the bottom of gorges and ravines which dry out in summer, and at the shores of drying lakes where the accumulation of sulphate and soda efflorescences takes place (Yurtsev 1982).

Generally, steppe communities in north-western Yakutia are attached to dry, southerly slopes, which contrast markedly with the tundra background. Yurtsev (1974) calls such a co-occurrence of steppe species and arctic-alpine ones by the name of steppe-tundra. A mosaic of these two types of community occurs quite frequently on Chukotka today. This author considers steppe plant communities in northeast Asia to be Pleistocene relicts of a geographical nature, from a period of cold and dry climate. Similar relationships in the vegetation have been described by Boucher (1954, after Aleksandrova 1980) from the central, continental part of Greenland.

As has already been said, the concept of Pleistocene steppe-tundra was created by researchers of fossil vertebrate faunas, who tried to link the coexistence of arctic and steppe mammals during the last glaciation, on one hand, with attempts, on the other, to reconstruct the environment in which the giant mammals e.g. mammoth, woolly rhinoceros, bison, and saiga lived. These giant herbivores needed an environment with a very high production of plant biomass, which the tundra could not provide; nor were they adapted to a thick snow cover. Both conditions, however, seem to be met by steppe and its vegetation. These and many other arguments in favour of steppe communities during the last glaciation at the northern latitudes in Eurasia and America are quoted by Guthrie (1982, 1990), together with a broad discussion. This author even postulates the existence during the last glacial of a special plant formation, so-called “mammoth steppe”, thus emphasizing the uniqueness of this formation and its close relationship with the extinct megafauna.

Frenzel (1968) called the belt of woodless vegetation arctic steppe (“Kältesteppe”), which stretched from the British Isles to the Bering Strait at the maximum of the last glaciation.

On the basis of palaeobotanical data and finds of Pleistocene megafauna occurring in the arctic steppe belt and dated from 80 000 BP and onwards, we may assume that steppe-tundra occupied most of northern Eurasia not only during the maximum of the Vistulian but also earlier. The long-standing relationships of the flora of eastern and central Europe (and perhaps also western Europe) with east-Asian floras throughout the Pleistocene are confirmed, for instance, by the presence of the extinct species *Potamogeton sukaczevii* in the Late Pleistocene floras of Russia, Belarus, Lithuania and Poland, this being the last of the extinct species closely related to the modern far-eastern species *Potamogeton maackianus* (Velichkevich & Granoszewski 1996, Field et al. 2000).

HD-27 – HD-31 L PAZ, HDM-11 and the older part of HDM-12 L MAZ

HD-27, Poaceae–*Pinus cembra* type, HD-28, NAP–*Pinus* (*Pinus cembra* type), HD-29, Poaceae–Cyperaceae–*Artemisia* (*Pinus*), HD-30, *Pinus*–NAP–*P. cembra* type, and HD-31, Poaceae–*Juniperus*–*Ranunculus flammula* type

The section of the Plenivistulian spanning zones HD-27 – HD-31 is characterized by high pine pollen values (*Pinus sylvestris* type). Together with birch, larch, and possibly spruce it formed single stands of trees in a generally open landscape. In drier habitats, juniper occurred in clumps of pine. The undergrowth layer was formed by *Calluna vulgaris*, *Chimaphilla umbellata*, *Pyrola* as well as Polypodiaceae and *Pteridium*. Along watercourses there also grew tree willows (*Salix* undiff. pollen). On wet sites, *Myrica* (pollen *M. gale* type) and *Myricaria germanica* occurred. *Juniperus*, *Alnus viridis*, *Hippophaë rhamnoides* as well as *Ephedra distachya* (pollen *E. distachya* type) occurred occasionally. The presence of these shrubs confirms the openness of the landscape.

Betula nana, *Salix polaris*, as well as *Calluna*, *Ledum*, *Empetrum*, *Chamaedaphne* (seed), *Vaccinium*, and *Bruckenthalia spiculifolia* constituted the dwarf shrub tundra.

The almost constant presence of the spores of *Sphagnum* and Bryales as well as macroremains of the mosses *Drepanocladus exannulatus*, *D. aduncus*, *D. revolvens*, *Calliergon trifarium*, *C. turgescens*, *Meesia triquetra*, and *Amblystegium varium* points to a high moisture contents of the substrate as well as the development of moss-sedge and moss-meadow communities. Wet meadows communities were source of pollen: *Caltha* type, *Cirsium/Carduus*, *Filipendula*, *Geranium*, *Viscaria vulgaris* type (seed of *Lychnis. flos-cuculi/Viscaria vulgaris* also present, Pl. 6, fig. 29), *Mentha* type (also fruit of *M.* cf. *aquatica*), *Plantago major*, *P. lanceolata*, *Polygonum aviculare* type, *P. persicaria* type, *Potentilla* type, *Comarum palustre*, *Lotus*, *Ranunculus acris* type, *Rumex acetosa* type, *Rhinanthus* type, *Sagina*, *Sanguisorba officinalis*, *Solanum dulcamara*, *S. nigrum*, *Stachys* type, *Stellaria holostea*, *Succisa pratensis*, *Thalictrum*, *Trifolium* type, *Trollius*, *Parnassia palustris* (Pl. 3, figs 4,5) Apiaceae undiff., *Valeriana officinalis* type, *Veratrum* (Pl. 1, fig. 8), *Veronica*, and *Vicia* type.

The arctic-alpine character of these communities is demonstrated by the presence of *Oxyria digyna* type, *Oxytropis*, *Armeria maritima* type, *Gentiana campestris* type, *Astragalus alpinus*, *A. danicus* type, *Pleurospermum austriacum*, *Polygonum bistorta/viviparum*, *Rubus chamaemorus* (Pl. 2, figs 5,6) *Saxifraga hirculus* type, and *S. oppositifolia* type. The presence of *Selaginella selaginoides* and *S. helvetica* as well as *Botrychium lunaria* type is noteworthy. Doubtless they must have grown in very different associations, or peat bogs of different kinds (*Drosera*), or else in communities closer to wet meadows or moist grasslands. In modern tundra this variability in a unit of area is enormous and dependent on the microrelief of the landscape, exposition, as well as microclimatic conditions.

Besides the described moss-meadow communities associated with peat habitats, there are taxa in the material from Horoszki whose presence support the occurrence at this time of rich communities of herbs on drier, peat-free soils. Presumably they occupied higher-lying sites, where good drainage enabled the runoff of excess water from the soil. The great variety of pollen taxa may suggest flowering steppe meadows. In the light of palynological data it would seem reasonable to accept the presence in the vicinity of Horoszki at this time, beside the above-described tundra vegetation, of Poaceae – *Artemisia* steppe communities with a high proportion of Chenopodiaceae. The representatives of Asteraceae and Cichoriaceae had a large share in these. Also such pollen types as *Aster* and *Achillea* most probably had their source in these communities, of which the following taxa are also representatives: *Anemone* type, *Bupleurum* type, *Campanula*, *Centaurea nigra* type, *C. scabiosa* (Pl. 4, figs 1, 2), *Helianthemum nummularium* type, *Herniaria* type, *Hypericum*, *Linum catharticum* type, *Onobrychis* type *Pimpinella major* type, *Plantago media*, Rubiaceae, *Rumex acetosella*, *Scleranthus perennis*, *S. annuus*, *Sempervivum*, *Spergularia* type, and Caryophyllaceae. Among shrubs, there grew *Genista*, and *Cytisus*. The presence of *Plantago maritima* pollen might indicate the occurrence of salty habitats, perhaps on the margins of periodically drying water bodies.

Despite the fact that, in the vegetation history recorded from zones HD-27 do HD-31, in general no major changes took place, it is possible to distinguish pollen zones in whose spectra slight increases in the values of tree pollen may be noted, which are presumably the result of climatic change.

In L PAZ HD-28 and HD-30 an increase takes place in percentage value of *Pinus sylvestris* type pollen. This need not necessarily be a reflection of an increased proportion of pine in the vegetation of the vicinity of Horoszki, but was most probably still the result of long distance transport. It cannot be ruled out that a slight improvement in climatic conditions made possible a slightly greater spread of pine and thus a reduction in the distance of transport for its pollen from elsewhere to the lake at Horoszki. An improvement in the climate may also have brought about more abundant flowering and pollen production.

In the author's opinion, these zones may correspond to the two first interstadials of the Plenivistulian, i.e. the Oerel interstadial – HD-28 NAP–*Pinus* and the Glinde interstadial – HD-30 *Pinups*–NAP–*P. cembra* type The character of the vegetation in the region around Horoszki is close to that of vegetation at the stratotype site, where the Oerel and Glinde interstadials were distinguished by Behre (1989).

In chronostratigraphic alternative "B" this would be the older part of the Schalkholz stadial.

Aquatic and littoral vegetation

Throughout zones HD-27 – HD-31 reedswamp communities were probably dominant in the marginal zone of the basin as reflected by high values of *Phragmites* type and Cyperaceae pollen. As earlier, *Menyanthes trifoliata*, *Cicuta virosa* type, *Lysimachia thyrsiflora*, *Sparganium* type as well as *Equisetum* were components of these communities. Pollen of *Comarum palustre* shows the occurrence of communities of the moss-sedge type.

Macrophytes are represented by particularly high proportions of *Ranunculus flammula* type pollen. It is most likely that in material from Horoszki this type represents the genus *Batrachium*, fruits of which are also abundant. The fairly numerous fruits of *Callitriche* indicate its role in the composition of littoral macrophyte communities. Communities of other macrophytes were most probably fairly poor and are represented only by pollen of *Potamogeton*. Pollen of *Utricularia* (Pl. 1, fig. 13) is also noted.

The presence of *Isoetës* spores as well as *Lobelia* pollen is interesting. Their occurrence is evidence of mesophilic and oligotrophic conditions in at least part of the lake. At present, *Lobelia dortmanna*, *Isoetës lacustris*, *Litorella uniflora*, and *Myriophyllum alternifolium* are components of the macrophyte flora of so-called Lobelian lakes, which are distinguished by specific physical and chemical characteristics of the water (Kraska & Piotrowicz 1994). The first three species prefer conditions with a low pH and a low content of calcium ions, while *M. alterniflorum* requires a higher pH and higher calcium concentration (Kraska et al. 1994). The occurrence of *Lobelia* and *Isoetës* and the disappearance of stonewort communities, and the strong limitation of communities of macrophytes such as *Najas*, *Nuphar*, and *Potamogeton* may be evidence of lowered trophy of the water of the lake and thus a colder climate. Abundant appearances of algae of the genera *Pediastrum* and *Botryococcus* may be indicative of favourable light relations in the lake.

HD-32 – HD-37 L PAZ, the younger part of HDM-12 and the older and middle part of HDM-13 L MAZ

HD-32, NAP–*Betula*–*B. nana* (*Pinus*), HD-33, Poaceae–*Artemisia*–*Betula nana*, HD-34, NAP–*Pinus cembra* type, HD-35, Poaceae–Cyperaceae–*Pinus*, HD-36, Cyperaceae–Poaceae–*Artemisia*, and HD-37, Poaceae–*Pinus*

Local pollen zones HD-32 to HD-37 seem to reflect a more stable period in the history of the vegetation. They are characterized primarily by a higher proportion of tundra and steppe communities, i.e. an even greater openness of the landscape than in previous zones. At the beginning of the zone described, the proportion of *Juniperus* and dwarf shrubs of the Ericaceae family, mainly *Calluna* and *Bruckenthalia*, increased. The increase in the openness of the landscape and history of the vegetation may also be reflected by the slightly increased proportions of wind-pollinated thermophilous trees such as *Quercus*, *Ulmus*, *Alnus glutinosa* type, and *Corylus*. Undoubtedly their pollen in the spectra of these zones comes from long-distance transport. *Pinus cembra* type pollen most likely has the same source.

Despite the strong expansion of open communities as well as the shift southwards of the boundary of continuous forest, in the region of Horoszki there most probably occurred small stands of tree birches with some poplars and larches, and possibly also spruce and Scots pine. The presence of alder trees is also a possibility, as evidenced by the higher proportion of their pollen in spectra and above all the presence of *Alnus* wood (HD-33).

Palynological data at the beginning of the section described suggest a greater spread of shrubs and dwarf shrubs associated with tundra communities, such as *Betula nana*, *Salix polaris* type, and various Ericaceae. In park woods, *Juniperus* as well as *Pteridium* formed the understorey. In more elevated spots, probably on the hummocks of peat bogs, *Calluna vulgaris* occurred fairly abundantly. A continuous curve of *Sphagnum* and Bryales spores, as well as an abundance of vegetative remains of mosses is evidence of the fact that part of the area was swampy and that various oligotrophic phytocoenoses occurred. On their hummocks, tundra communities could develop, with *Betula nana*, *Salix polaris* type, and *Alnus viridis*. The dwarf shrub layer consisted of *Empetrum*, *Ledum*, *Calluna vulgaris*, *Chimaphilla umbellata*, *Vaccinium* type as well as *Bruckenthalia spiculifolia*. Wetter soils were occupied by moss-sedge vegetation with a high proportion of *Drepanocladus aduncus*, as well as various representatives of Cyperaceae, Poaceae, *Menyanthes trifoliata*, and species of the genus *Equisetum*. On peaty sites there occurred, among others, *Rubus chamaemorus*, and *Saxifraga hirculus* type.

The flora of this section of the Vistulian indicates that in the vicinity of Horoszki at this time there also occurred drier varieties of tundra. The occurrence of arctic-alpine turf or meadows may be suggested by the presence of *Armeria maritima* type (types A and B), *Astragalus alpinus*, *A. danicus* type, *Cerastium* cf. *alpinum*, *Silene* cf. *vulgaris* (seed, Pl. 6, fig. 31), *Gentiana campestris* type, *Hedysarum*, *Oxyria digyna*, *Polygonum bistorta/viviparum*, *Sweertia perennis* (Pl. 3, fig. 10) *Saxifraga granulata* type, *S. oppositifolia* type, *S. stellaris* type, *Selaginella helvetica*, *S. selaginoides*, *Lycopodium alpinum* as well as the boreal species *L. annotinum* and *Huperzia selago*. Tall herb communities are represented by pollen of *Filipendula*, *Sanguisorba officinalis*, *Rumex acetosa* type, *R. longifolius* type, *Vale-*

riana officinalis type, *Solanum dulcamara*, *Potentilla* type, *Thalictrum*, *Plantago major*, *P. lanceolata*, *Ranunculus acris* type, *Lychnis viscaria* type, *Epilobium*, *Pleurospermum austriacum*, Apiaceae undiff., and spores of *Botrychium lunaria* type. Spores of *Osmunda cinnamomea* type (Pl. 4, fig. 19) as well as Filicales (=Polypodiaceae s.l.) were probably associated with these habitats.

Besides tundra, or forest tundra communities, plant communities whose floristic composition supports their steppe character existed at this time. Their floristic base consisted primarily of various representatives of the Poaceae, Chenopodiaceae and partly Cyperaceae as well as the genus *Artemisia*. These communities occupied well-drained sites, perhaps some southward-facing slopes, or terraces above the flood-plain. Most likely these steppe or steppe-like communities were the source of the following pollen types: *Bupleurum*, *Centaurea scabiosa* type, *Cerastium* type, Cichoriaceae, *Achillea* type, *Aster* type, Asteraceae undiff., *Genista* type, *Gypsophila fascigiata* type, *Helianthemum nummularium* type, *Herniaria* type, *Knautia*, *Ononis* type, *Pimpinella major* type, *Pulsatilla*, *Scleranthus perennis*, *Sempervivum*, and Rubiaceae. *Rumex acetosella*, *Polygonum aviculare* type, and *Illecebrum verticillatum* grew in sandy habitats.

In the middle part of zones HD-33 and HD-34 new taxa appear, which are evidence of a rich composition of steppe communities. Pollen of *Ephedra distachya* type and *E. fragilis* type comes from these communities. *Sambucus racemosa* and *S. nigra* should be associated with these habitats, as well as *Viburnum*. Among herbaceous plants pollen of the following species reappears *Centaurea jacea* type, *Ambrosia* type, *Campanula*, *Chamaenerion*, *Euphrasia*, *Ficaria*, *Helianthemum alpestre* type, *Jasione*, cf. *Phyteuma*, *Polemonium*, *Prunella* type, *Sagina* type, and *Scleranthus perennis*.

The richness of the steppe and steppe-like communities does not mean that the communities of various forms of tundra underwent a drastic restriction. Both dwarf shrub and moss-herb tundra continued to be present around the lake at Horoszki. Most likely there was also parkland with tree birches, Scots pine, larch, poplar, and possibly spruce and alder.

In the upper zones of the section of the Plenivistulian described (HD-35 – HD-37) an increase took place in the values of *Pinus sylvestris* type while the curves of other trees stayed unchanged. Macroremains of tree birches and larch appeared in the sediment. At the same time, the proportion of the tundra species *Betula nana*, *Salix polaris* type, as well as representatives of the Ericaceae declined. A less peaty character of the region of Horoszki may be suggested by the declining trend of the *Sphagnum* curve, though the presence of the vegetative remains of *Sphagnum palustre*, *Drepanocladus aduncus*, *D. revolvens*, *Bryum neodamense*, *Calliergon trifarium* as well as fruits of *Carex rostrata/vesicaria*, and *Carex* sp. div. provides evidence of a continuous presence of moss-sedge and moss-herb communities. The decline in the values of Chenopodiaceae and *Artemisia* may signal a slight recession of steppe communities at the same time as tundra communities. However, the recession of open communities was not accompanied by any significant decrease in the variety of taxa in these two groups of habitat.

The gradual rise in the *Pinus sylvestris* type curve with constant curves of other trees and the simultaneous though only slight increase in the absolute concentration of pine pollen in the sediment (Fig. 7) could suggest a slight increase in its presence. This expansion of pine seems to take place in two stages. After an initial increase in its values in zone HD-35, the rate of its spread fell in zone HD-36, maintaining its values at a roughly constant level with an accompanying increase in the proportion of Poaceae undiff., after which, in the next pollen zone, HD-37, pine continued its expansion. Since this trend was long-lived, it seems appropriate to consider this phenomenon a reaction to improving climate.

To sum up, the author thinks that in the part of the Plenivistulian represented by zones HD-32 – HD-37, the slight increases in values of the pollen of trees and shrubs in zones HD-32 NAP–*Betula*–*B. nana* (*Pinus*) and HD-35 Poaceae-Cyperaceae–*Pinus* may represent the Moershoofd and Hengelo interstadials. The increase in AP in zone HD-37 Poaceae–*Pinus* signals changing climatic conditions in the younger part of stadial PV9, preceding the next interstadial.

In the alternative interpretation “B”, this would be the younger part of the Schalkholz stadial.

Aquatic and littoral vegetation

In the section of the Plenivistulian represented by zones HD-32 – HD-7 no major changes may be observed in littoral vegetation. Reedswamp communities were enriched by new elements, namely *Iris pseudoacorus* (*Iris pseudoacorus* type pollen) and *Sagittaria* (pollen). The presence of the first of these taxa may suggest a rise in calcium ions in the water (Podbielkowski & Tomaszewicz 1996). A similar conclusion may be drawn from the reappearance of *Myriophyllum alternifolium* and the presence of communities of *Nitella syncarpa* and *N. gracilis*. These algae occur in calcium-rich waters and frequently appear and reappear rather suddenly (op. cit.). In macrophyte communities, an increase in the diversity may be observed. Pollen of *Nuphar* and *Nymphaea alba* type appears again. Endocarp of *Potamogeton vaginatus* (Pl. 6, fig. 1) is present. Despite the presence of taxa which are undoubtedly evidence of eutrophic habitat conditions, communities of more meso– or even oligotrophic waters developed, as demonstrated by the presence of *Lobelia* pollen and *Isoëtes* spores.

HD-38 *Pinups*–NAP; the younger part of HDM-13 L MAZ

The Scots pine reached its maximum range in the vicinity of Horoszki in this part of the Plenivistulian. The presence of fragments of wood is evidence of its occurrence in situ. Since the pine is a species with a very broad spectrum of ecology and habitat, its expansion probably took place in both moist and dry habitats. Its very low pollen concentration is evidence of a restricted expansion (Fig. 7). An improvement in climatic conditions is supported by the fact that the increase in the proportion of pine is accompanied by a slight increase in the concentration of *Betula alba* type pollen. Any improvement in the climate may have only been slight and these changes in pollen spectra may not only be the result of local deposition but also of long distance transport from areas lying further south. In surface spectra in open tundra landscapes pine pollen may constitute up to 34% of the total sum, or even more (Aario 1940, Środoń 1960, Lichti-Fedorovich & Ritchie 1968). Doubtless there may have been different reasons for an increase in pine pollen in the zones described. For instance we cannot rule out the presence of dwarf mountain pine (*Pinus mugho*), for which both pollen and wood can not be separated from *P. sylvestris* in palaeobotanical analysis. The cones of *P. mugho* reported from sediments in Gołków, central Poland (Janczyk-Kopikowa 1966, Mamakowa 1989) were assigned to Early Vistulian sediments (Brörup).

Thus at this time in the region of Horoszki, the vegetation of open habitats was still dominant. The only trees present were Scots pine, tree birches, in mires *Betula humilis* (macroremains), larch, poplar, and willow as well as single spruces. The pollen of *Pinus cembra* most probably comes entirely from distant transport.

The vegetation history represented by zone HD-38 have been correlated by the author with the Denekamp interstadial in the chronostratigraphic “A” variant, or alternatively with the Oerel interstadial in variant “B”.

HD-39, Poaceae–*Betula nana*; the younger part of HDM-13 L MAZ

Changes in the vegetation of this zone are characterized primarily by the recession of Scots pine to its complete disappearance as well as the re-expansion of communities of open areas. The vegetation of shrub tundra spread still further, as demonstrated by increasing values of *Betula nana* as well as *Salix polaris* type pollen. At the same time steppe communities developed strongly, as expressed primarily in the robust expansion of grasses, in increasing *Artemisia* trend as well as an increase in the proportion of such taxa as Chenopodiaceae, Cichoriaceae, Asteraceae, and *Cerastium* type. Taxa pointing to the development of steppe communities reappeared again: *Linum austriacum* type, *Bupleurum*, *Helianthemum nummularium* type, *Herniaria*, *Jasione* and many others present in the flora of the vicinity of Horoszki before the increase in *Pinus sylvestris* type values. All these changes point to a deterioration in climatic conditions. This time these changes were sufficiently significant to cause, most probably, the complete dominance of treeless communities, while the composition of pollen spectra in this region suggests a continental arctic climate.

The changes in chronostratigraphic variant

“A” are thought to be the beginning of the main stadial, as would also be indicated by the radiocarbon dating of 22 500 ± 1000 BP. Should this date be too young, zone HD-38 could be considered to be the second stadial of the Plenivistulian with a correlation with the Ebersdorf stadial.

Aquatic and littoral vegetation

(HD-38 together with HD-39 L PAZ as well as the younger part of HDM-13 L MAZ)

In the two top pollen zones the macroscopic remains representing local vegetation are not numerous. Together with pollen data it may, however, be assumed that reedswamp communities still occurred in the littoral zone, with *Typha latifolia*, *Alisma plantago-aquatica*, and *Sparganium* as well those of mossy-sedge rushes. This is supported by both the proportions of *Phragmites* type and *Cyperaceae* pollen which remain at a constant level, as well as relatively abundant moss remains, mainly *Drepanocladus aduncus*, *D. revolvens*, and *Calliergon trifarium*.

Macrophyte communities are represented by pollen of *Potamogeton*, *Nuphar* (?*pumila*), all three species of *Myriophyllum*, as well as *Callitriche* and *Batrachium* fruits. *Zannichellia palustris* subsp. *pedicellata* is a new element in these communities. Fruits were found in several samples at depths of 4.04 m to 3.73 m. The occurrence of this subspecies is evidence of a strongly eutrophic environment (Podbielkowski & Tomaszewicz 1996). It also grows in salty waters. At present it forms a community with *Najas marina* and *N. minor* (Tomaszewicz 1979). It occurs at various depths in the marginal shallows of lakes, in which it frequently appears ephemerally (Podbielkowski & Tomaszewicz 1996). Perhaps its sudden appearance and disappearance in the sediment at Horoszki may be explained in this way, and its presence suggests the occurrence, in the marginal belt of the lake, of habitats with variable water levels and thus a high mineral content.

CHANGES IN CLIMATE ON THE BASIS OF PALAEOBOTANICAL DATA

Besides gaining a knowledge of the history of vegetation and stratigraphy, one of the more important aims of palaeobotanical research is to reconstruct the changes in climatic conditions (temperature, light, moisture) prevailing in the past. This analysis is based firstly on the knowledge of modern climatic requirements of plants, and shifts in the northern and upper forest limit (Iversen 1944, Wasylikowa 1964, Kolstrup 1980, Paus 1992, Litt et al. 1996, Birks et al. 1996) and secondly on the assumption that the ecological requirements of species have not undergone any fundamental changes during the Quaternary. These assumptions indicate that only remains determined down to species can serve as indicators of climate. In this respect, analysis of plant macrofossils provides better possibilities than pollen analysis.

Since there are more palynological than macrofossil data from various periods of the Quaternary, methods of palaeoclimate reconstruction based exclusively on palynological data have been developed in the past 10–20 years (Guiot et al. 1989, Guiot 1990, Field et al. 1994, Cheddadi et al. 1998)

To analyse the climate of the section of the Pleistocene covered by the lake deposits from Horoszki Duże, the author used the method of climatic plant indicators.

LATE WARTANIAN GLACIATION

HD-1 L PAZ

The pollen spectra of the late glacial deposits have a high proportion of Tertiary sporomorphs, and, moreover, some pollen of Tertiary and Quaternary types are probably redeposited. The dominance of plants indicating open vegetation with *Betula nana*, *Salix polaris* type and a large proportion of heliophytes (*Helianthemum*, Chenopodiaceae, and Poaceae) would points to moderately cold climatic conditions. The presence of *Calliergon trifarium* and a high proportion of Bryales spores have the same implications. On the other hand, the presence of a nut (fragment) of *Betula* sect. *Albae* and the assumption that at least some of the *Pinus sylvestris* type pollen comes from the vicinity of Horoszki permit the conclusion that the average temperature of the warmest month was about +12°C. The high values of *Juniperus* show the lowest temperature of the warmest month was greater than +10°C.

HD-2 L PAZ

The spread of birch-pine forest communities, the marked increase in sporomorph concentration (Fig. 7) and the increase in organic matter content in the sediment indicate an improvement in climatic conditions after the late Wartanian Glaciation. The find of fruits and fruit scales of tree birches points to a mean July temperature of +12°C – +13°C. Herbaceous plants also suggest July temperatures of at least this order. This is indicated by *Solanum dulcamara*, which today occurs in areas where mean July temperatures do not fall below +13°C (Kolstrup 1980), while *Typha* seeds may even indicate a mean July temperature that is +1°C higher (op. cit.). The increased diversity of the aquatic flora also reflects an improved climate, e.g. *Najas marina*, *Ceratophyllum*, *Nuphar*, and *Potamogeton* are present. *Najas marina* may even indicate a minimum July temperature of +17°C (Mamakowa 1997). The presence of aquatic taxa is particularly significant in the protocratic phase of the interglacial, because they rapidly migrate than trees. Many authors (Iversen 1964, Wasylikowa 1964) consider temperature to be the main climatic factor determining plant distribution.

On the other hand, the presence of heliophyte communities associated with a colder climate (*Betula nana*, *Salix polaris* type, and *Saxifraga oppositifolia* type) in the vegetation of the protocratic part of the interglacial would point to continental features of the climate.

HD-3 and HD-4 L PAZ

The retreat of pioneer birch-pine forest and the appearance of the thermophilous trees *Ulmus*, *Quercus*, and *Fraxinus* show further improvement in the climate. Today *Ulmus scabra* does not grow in areas with a mean July temperature below +16°C, while the two other species of elm even have higher thermal requirements (Kanerwa 1956). The appearance of pollen of broadleaved trees may also indicate an increase in annual rainfall, though their modern distribution is within the same range of annual rainfall as those of pine and birch, i.e. 100 to 3000 mm (Mamakowa 1997). Changes of the climate from a continental to a more oceanic one are indicated by the first appearance of *Hedera helix* pollen towards the end of zone HD-4. The climatic indicator value of *H. helix* lies in its highly specific thermal requirements in winter, since it flowers if the temperature of the coldest month does not fall below –1,7°C to –2°C (Iversen 1944, Zagwijn 1994). The presence of *Peplis* pollen also indicates temperate climatic conditions.

The strong expansion of elm-ash riverine communities with a high proportion of oak (HD-4) is a clear evidence of an increasing oceanic character of the climate. Riverine elm-ash forest is a thermophilous community and is today primarily found in the southern and south-eastern part of central Europe, the north-eastern boundary of its range running through Poland (Matuszkiewicz & Borowik 1957).

HD-5 and HD-6 L PAZ

According to Frenzel (1991) the beginning of the lime period is also the beginning of the climatic optimum of the Eemian interglacial. During this phase, taxa with the greatest thermal requirements are most abundant in the material from Horoszki, e.g. *Hedera helix*, and *Vitis sylvestris* type. At present, the submediterranean taxon *Vitis vinifera* L. subsp. *sylvestris* (C.C. Gmelin) Hegi grows in southern Europe on isolated sites in the valleys of large rivers in the lowland part of Austria, southern Germany and south-western Switzerland (Hegi 1965). To the south-eastern it occurs in the basin of the rivers Dnieper, Dniester and Prut (Rozhaniets 1950). The appearance of *Viscum* suggests a mean temperature of the warmest month above +16°C (Iversen 1944) and the presence of *Trapa natans* indicates at least +18^{o} C (Litt et al. 1996).

Tilia platyphyllos and *T. tomentosa* are present together with the abovementioned indicator species. In the Eemian, the northern limits of these species lay much further to the north-east (Frenzel 1991). At present, the limiting factor close to the northern limit of their range seems to be a mean temperature in July, which is +17,5°C for *T. platyphyllos* and not below +21°C for *T. tomentosa* (op. cit.). All the above taxa indicate a very mild, warm climate with moderate rainfall though higher than at present in the same area. This is in accordance with earlier data from the literature (Mamakowa 1989, Frenzel 1991, Litt et al. 1996, Zagwijn 1996, Aalbersberg & Litt 1998).

HD-7 and HD-8 L PAZ

The second part of the climatic optimum of the Eemian interglacial is characterized by the dominance of hornbeam forest (Mamakowa 1989, Frenzel 1991, Litt et al. 1996). In the profile from Horoszki Duże there is still a high proportion of lime species in these L PAZs, and *Tilia cordata* type has its maximum. The two remaining species reached their maxima in the previous zone, but macroscopic remains of both *T. platyphyllos* and *T. tomentosa* proves their presence in the vegetation around Horoszki, despite fairly low pollen frequency. This allows the assumption that the minimum temperature of the warmest month is the same in this part of the optimum as in the previous zone. Towards the end of zone HD-7 the next indicator species appear, namely, *Buxus sempervirens* and *Ilex aquifolium* type. Their climatic significance is similar with respect to the requirement of the minimum temperature of the coldest month, which is about 0°C (Iversen 1944, Zagwijn 1996). These taxa indicate an increase in precipitation and thereby an increase in the oceanic character of the climate. For *Buxus sempervirens* the lower limit of annual rainfall is today 650 mm, but the best conditions are with annual rainfall over 1000 mm (Mai 1988, Zagwijn 1996). For *Ilex aquifolium* the minimum value of annual rainfall is 500 mm (Mamakowa 1997). An increase in annual rainfall is also confirmed by the continuous presence of *Picea abies* pollen and macroremains in both zones and, from the beginning of zone HD-8, also *Abies alba*. In zone HD-8, *Larix* (seed) is noted for the first time. For all three of these taxa, the minimum annual rainfall is 500 mm (op. cit.). Pollen of *Tilia tomentosa* type, and *T. platyphyllos* type disappears, while *Hedera helix*, *Buxus sempervirens*, and *Ilex aquifolium* type are still present. From this it may be inferred that the increase in annual precipitation was accompanied by a small decline in the mean temperature of the warmest month to about +18°C (*Buxus sempervirens*). The mean temperature of the coldest was approximately 0°C, which is indicated by the simultaneous occurrence of *Picea*, *Abies*, and *Larix*. The mean January temperatures for *Abies alba* and *Larix decidua* range from -5^o to +7°C while those for *Picea abies* from <-12°C to +7°C (Mamakowa 1997). If we add an almost continuous presence of *Calluna vulgaris* and occasional grains of *Fagus sylvatica* to the above species, we obtain a picture of a climate with a strongly oceanic character, not only in comparison with the modern climate in this area, but even with the older part of the climatic optimum of the Eemian.

HD-9 L PAZ

The most important change of vegetation composition in this zone is the recession or disappearance of thermophilous elements (*Carpinus*, *Corylus avellana*, *Tilia cordata*, *Buxus sempervirens*, and *Viscum*) in the older part of the zone. At the same time, the expansion of *Picea abies*, *Abies alba*, *Pinus sylvestris*, tree birches (*Betula alba* type), *Populus*, and *Quercus* takes place. These changes in the vegetation lead to the conclusion that thermal conditions decreased in relation to those of the previous zone, accompanied by an increase in the precipitation; the minimum annual rainfall for *Picea abies* and *Abies alba*, is evidence of this, being 500 mm, 200 mm higher than the minimum requirement for *Carpinus*. From the disappearance of *Buxus sempervirens* and *Viscum*, in the younger part of the zone, we may infer a slight decrease in the mean temperature of both the warmest and the coldest months.

The above conclusions are consistent with data from the literature (Mamakowa 1989, Abby & Tauber 1995, Zagwijn 1996, Litt et al. 1996, Cheddadi et al. 1998, Rioual et al. 2001). However, there are no data in the material from Horoszki Duże that might point to the large decrease in winter temperatures in the hornbeam period that Field et al. (1994) suggested.

HD-10 – HD-12 L PAZ

The expansion of forest communities with a dominance of *Pinus sylvestris*, tree birches and a considerable proportion of spruce and larch and, from zone HD-11, also *Betula nana* and *Juniperus*, indicates a boreal type of climate. This assumption is supported also by the presence of the micro– and macrospores of *Selaginella selaginoides* (Pl. 5, fig. 1) and the remains of *Calliergon trifarium*. The presence of *Selaginella selaginoides* suggests that the temperature of the warmest month did not exceed +17^{o}C (Tobolski 1991) or +20°C (Mamakowa 1997).

While floristic composition can be used to infer a fall of summer temperatures, this is less certain with respect to winter temperature. The presence of *Betula nana* is point to the highest temperature of the coldest month definitely did not exceed 0°C, because today the maximum mean January temperature for the dwarf birch is 0°C (Mamakowa 1997). From this we may assume that, in the analysed period of the Eemian, favourable thermal conditions for *Betula nana* may have already come into existence but no drastic decrease in winter temperatures had yet taken place.

EARLY VISTULIAN

HD-13 L PAZ – Herning stadial

The dominance of open communities in the first stadial of the Early Vistulian suggests that the northern forest line was situtaed south from Horoszki, although the presence of *Betula* sect. Albae, *B.* cf. *pubescens*, and *Larix* proves at least the presence of these trees *in situ*. Assuming thus that the water basin at Horoszki lay at the northern forest limit at this time, this may suggest a temperature of the warmest month of around +12° – +13°C (Wasylikowa 1964, Szczepanek 1971b). This value may have even been higher, if we consider the presence of *Larix*, since the minimum July temperature for *Larix decidua* is +17°C (Mamakowa 1997). Unfortunately, the material from Horoszki only allow us to determine the find as *Larix* sp.

This level abounds in a variety of macroscopic remains of aquatic and reedswamp plants. *Potamogeton pussilus* suggests mean July temperatures of at least +13°C (Mamakowa 1997), while *Typha* indicates +14°C, and *Rumex maritimus* would even suggest +15°C (Tobolski 1991). The theory that aquatics after spread into an area are slower to react than terrestrial plants and may persist in water bodies for a longer time despite a deterioration in general thermal conditions seems to be applicable here (Iversen 1954, 1964, Szafer 1954, Wasylikowa 1964). This phenomenon takes place at the beginning of cold periods in which the presence of aquatic species can be considered climatic relicts. Their value as indicators of temperature during the beginning of cold intervals are thus restricted. Due to rapid spread, however, they are highly sensitive indicators of climatic improvements following cold oscillations (Iversen 1954, 1964, Szafer 1954, Wasylikowa 1964).

The climate in central and western Europe during the Vistulian stadials is suggested to have been strongly continental (Kolstrup 1990). A high proportion of Poaceae, *Artemisia*, Cyperaceae, Chenopodiaceae, and the presence of *Ephedra fragilis* type would indicate a continental character. Overall, we cannot rule out that the requirements of species have changed with respect to specific climatic parameters over time and their modern distribution is determined by slightly altered climatic requirements.

HD-14 – HD-20 L PAZ – Brörup interstadial

The improvement in climate which took place in the Brörup interstadial is reflected in the existence of dense forests, birch at the beginning of the interstadial, then birch-pine and birch-spruce-larch wood with the participation of stone pine. This indicates a northward shift of the forest limit. The minimum July temperature must therefore have been at least +12° – +13°C. The presence of *Carex elata* nuts and the perianth of *Rumex maritimus* would even indicate +15°C.

Following the birch period, a return is observed in zone HD-15 to open communities with a very high proportion of *Artemisia*, Poaceae, and Chenopodiaceae, and an increase in *Betula nana*. This doubtless reflects the deterioration and increasingly continental character of the climate. Macroremains of tree birches indicate, however, that the mean July temperature did not fall below +10°C (Mamakowa 1997).

In the subsequent zones of the Brörup a return took place of birch-pine communities with larch (needles, seed). Together with *Ceratophyllum demersum* (fruits), this may indicate a mean July temperature of about +15°C, although the northernmost fruiting specimens of this species lie within the +12° C July isotherm (Wasylikowa 1964). The presence of *Najas marina* fruits would thus even suggest a July mean of about +17°C; it must, however, be borne in mind that a lake-type body of water may have had a specific microclimate (Iversen 1954, 1964, Szafer 1954, Wasylikowa 1964) different from the general climate, which was of a boreal type. The presence of *Pinus cembra*, however, indicates a temperature probably a little lower.

From the middle of the interstadial the proportion of the vegetation of open spaces increased. A particularly high proportion of Poaceae, *Artemisia*, and Chenopodiaceae points to a strong continentality of the climate.

HD-21 and HD-22 L PAZ – Rederstall stadial

Herbaceous communities dominated in the landscape of the second stadial of the Early Vistulian. The northern forest limit was located south of the lake at Horoszki. The occurrence of macroscopic remains of tree birches and larch most probably indicates mean July temperature of ca. +10°C and only spars stands of these trees. Beside herbaceous plants, the increased values of *Betula nana* and *Salix polaris* type also favour deterioration in climatic conditions and an increase in continentality. The presence of *Dryas* pollen points to a subarctic climate.

The mean temperature of the coldest month was approximately 0°C (*Betula nana* – macroremains) but probably lower, while the mean temperature of the warmest month was about +10°C. The presence of *Najas flexilis* suggests a minimum July temperature of at least +13°C (Mamakowa 1997), and *Rumex maritimus* even to +15°C. The minimum July temperatures for these two species need not necessarily reflect the conditions of the regional climate.

Towards the second stadial of the Early Vistulian the reappearance of plants with greater thermal requirements is observed, e.g. *Carex elata*, *Typha* sp., and *Lycopus europaeus*, the lowest mean July temperature of which is +15°C (Kolstrup 1980, Mamakowa 1997).

HD-23 – HD-26 L PAZ – Odderade interstadial

The return of birch forest at the beginning of the Odderade interstadial is evidence of an increase in the minimum July temperature to +12° – +13°C. If we take into account the presence of *Rumex maritimus, Typha, Carex elata, Ceratophyllum demersum* we may assume that the minimum value of July temperature was ca. +15°C.

The birch phase of this interstadial was much shorter than the birch phase of the Brörup, which may suggest a generally greater continentality of the climate of the Odderade interstadial as compared with that of the Brörup (cf. Lagerbäck & Robertsson 1988). The recession of birch was accompanied by the spread of *Pinus sylvestris*, *Larix*, and *Picea* (?*abies*). The presence of these taxa in the region around Horoszki Duże is confirmed by macroscopic remains. The development of these forests *in situ* shows that the lowest July temperatures in this region of Poland most probably exceeded +13°C. Assuming that *Larix* is represented by *L. decidua*, the minimum of the warmest month may even have been +17°C (Mamakowa 1997).

For most of the taxa in the flora of Horoszki, the range of temperature tolerance in winter lies in the region of about +7° to +10° C to even +12°C. The occurrence of macroremains of *Betula nana*, *B. humilis*, and *Ledum* pollen implies that the highest temperature of the coldest month was not higher than 0°C (op. cit.).

PLENIVISTULIAN

HD-27 – HD-39 L PAZ

The boundary Early/Pleni– Vistulian is put above the Odderade interstadial (Behre 1989). The attempt to trace climatic changes during stadials of the Pleistocene is a much more complicated task than analysis of interglacial periods, especially the last interglacial, or interstadials of the Early Vistulian. The Plenivistulian, was characterized by very unstable conditions, both in terms of climate and environment (Kolstrup 1990).

AP frequency shows that the lake at Horoszki was situated outside the northern line of closed forest for a considerable time. From this we may assume that the temperature of the warmest month to have fallen to about +10°C. However, the aquatic vegetation suggests higher temperatures. The presence of *Myriophyllum spicatum* and *M. verticillatum* indicates a temperature of about +13° – +15°C (Kolstrup 1980, Mamakowa 1997). The abundant appearance of *Ranunculus flammula* type pollen in the zones HD-31 and HD-32 and the abundant presence of *Batrachium* fruits would also imply at least +13°C for July. The many fruits of *Callitriche* are also evidence of July temperatures above +10°C (Mamakowa 1997). All aquatic taxa continue to occur at least from the Odderade interstadial, which, in line with the opinion expressed above, may be the effect of the delay of changes in the microclimate of the aquatic environment. Among terrestrial plants, the occurrence of *Pteridium aquilinum* indicates a July temperature of approximately +14°C (Tobolski 1991). The uninterrupted presence of *Betula nana* in the flora indicates that the maximum temperature of the coldest month did not exceed 0°C.

From an almost continuous presence of *Armeria maritima* it may also be deduced that snowfall was not high, since this species tolerates only a thin snow cover (Kolstrup 1980). This feature of *Armeria maritima* speaks in favour of the occurrence of climatic conditions like those which may now be found in steppe regions, where snow cover is very thin.

The *Larix* needles and perianth of *Rumex maritimus*, present towards the end of zone HD-37, constitute evidence in favour of an increase in the temperature of the warmest month, to as much as +15° – +17°C. In zone HD-38, further signs of an improving climate may be observed e.g. an increase in *Pinus sylvestris* type and the reappearance of *Betula* cf. *humilis* macroremains and fragments of *Alnus* wood. The climatic conditions most probably made it possible for the forest limit to move slightly northward.

A drastic fall in AP values in the top zone (HD-39), caused mainly by a decrease in the values of *Pinus sylvestris* type and an increase in the proportion of *Betula nana* pollen, signals a fairly rapid deterioration of the climate. These data permit the assumption that Scots pine receded from the region of Horoszki, from which it may be deduced that the mean temperature of the warmest month fell below +10°C.

SUMMARY OF RESULTS

The subject of the paper is analysis of the development of the flora and climatic changes of the late Wartanian (Saalian) Glaciation, the Eemian interglacial and the Vistulian (Weichselian) Glaciation, based on palaeobotanical investigations of the fossil lake sediments at Horoszki Duże, eastern Poland (Figs 1, 2).

Pollen analysis and plant macrofossil analysis were used as methods of investigation.

The lake sediments were described using the method of Troels-Smith (1955). Analyses of organic matter and carbonates content were also carried out, as well as grain size distribution.

The results of the pollen analysis are presented in a percentage pollen diagram (Fig. 3) and a diagram of sporomorph concentration (Fig. 7), while the results of the analysis of macroscopic remains are in a quantitative diagram as the number of specimens in particular samples (Fig. 4).

The pollen succession from Horoszki has been divided into 39 local pollen assemblage zones (L PAZ). See Fig. 3.

On the basis of the results of pollen analysis it was determined that the fossil lake sediments from Horoszki Duże represent the late Wartanian Glaciation (HD-1 L PAZ), the complete succession of the vegetation of the Eemian interglacial (HD-2 – HD-12 L PAZ which correspond to 7 regional pollen zones (R PAZs) distinguished for Poland by Mamakowa (1989), and the complete succession of the Early Vistulian (HD-13 – HD-26 L PAZ).

Within the Plenivistulian part of the profile, which contains 13 local pollen assemblage zones (HD-27 – HD-39) two alternatives of chronostratigraphic division have been given. At a depth of 1.74 m in L PAZ HD-38 there is a radiocarbon dating of 22 500 ± 1000 BP carried out on peaty silt. In the “A” variant it has been assumed that increases in AP values correspond to climatic variation of interstadial rank while falls in AP and increases in NAP correspond to periods of poorer climatic conditions, i.e. stadials. Should this alternative be correct, the profile would in fact contain all the interstadials distinguished in the Plenivistulian in western Europe, i.e. Oerel, Glinde, Moershoofd, Hengelo and Denekamp (Tab. 5). In alternative “B”, it was assumed that perhaps the entire section represents the first Plenivistulian stadial, Schalkholz. Pollen zone HD-38, in which the increase in AP was greater, to a maximum of 68% (mainly *Pinus sylvestris* type pollen) would only correspond to the first interstadial of the Plenivistulian, Oerel, while the topmost zone HD-39 should in this situation correspond to the second Plenivistulian stadial, Ebersdorf (Tab. 5).

Late Wartanian HD-1 L PAZ

The vegetation history recorded in the lake sediments at Horoszki Duże begins during a period in which the landscape shows considerable openness with only a small proportion of trees (*Pinus*, *Betula*, and *Larix*) in the vicinity of the lake. The presence of *Betula nana*, *Salix polaris* type, high values of *Artemisia*, Chenopodiaceae, and Poaceae undiff. point to moderately cold climatic conditions.

Eemian interglacial (HD-2 – HD-12 L PAZ)

E1, *Pinus–Betula* R PAZ

(HD-2 L PAZ)

The development of pioneer birch-pine forests marks the lower boundary of the Eemian succession. In the older part of this period, open communities associated with a cooler climate played a role but the presence of certain plants indicates a considerable improvement in the climate. The fruits of *Najas marina* may even suggest the mean July temperature to have been +17°C. Poplar-willow floodplain forests resembling the modern association *Salici–Populetum* also appeared.

E2, *Pinus–Betula–Ulmus* R PAZ

(HD-3 L PAZ)

Pine-birch forests still played a considerable role in the vegetation of the vicinity of the lake, but their significance gradually decreased. Poplar-willow floodplain forests gained some new species, namely *Ulmus* and *Quercus*, *Fraxinus* joining in the younger part of the zone.

A new type of forest developed, of the elm-ash floodplain type. This is evidence of a constantly improving climate. The presence of *Ulmus* suggests July temperature of at least +16°C.

E3, *Quercus–Fraxinus–Ulmus* R PAZ

(HD-4 L PAZ)

The most important changes of forest communities to be recorded at this level are the successional changes of elm-ash floodplain forest into elm – oak – ash floodplain forest of the *Ficario–Ulmetum* type or the western European *Ulmo–Quercetum*. The change in climate from continental to more oceanic is supported not only by the strong expansion of riverine forests but also by the first appearance of *Hedera helix* pollen towards the end of the zone.

E4, *Corylus–Quercus–Tilia* R PAZ

(HD-5 and HD-6 L PAZ)

The most significant feature of vegetation changes during this period is the expansion of *Corylus avellana*. By then the following lime-hornbeam wood species are present: *Carpinus*, *Tilia cordata*, *T. platyphyllos*, and *T. tomentosa*. *Taxus baccata* reaches its maximum spread. In zone HD-6 deciduous multi-species forests of the lime-hornbeam type formed in this region. Alder (*Alnus glutinosa*) also expanded in this zone, as did ash-alder floodplain woods. The presence of *Trapa* and *Tilia tomentosa* indicates a very mild and warm climate with moderate annual rainfall, though higher than at present.

E5, *Carpinus–Corylus–Alnus* R PAZ

(HD-7 and HD-8 L PAZ)

In the older part of this zone, lime-hornbeam forests dominated and were rather like the present-day *Tilio–Carpinetum*. A fruit of *Tilia tomentosa*, for the first time was found here from the Eemian in Poland. In the younger zone (HD-8) the range of the hornbeam was at its greatest, and it was the dominant tree in Podlasie in this zone. The presence of fir and spruce is evidence of the climate being moister, while the presence of *Buxus*, *Viscum*, *Ilex aquifolium*, and *Hedera helix* is proof of relatively high winter temperatures. Thus it seems the climate of this period had pronounced oceanic features.

E6, *Picea–Abies–Alnus* R PAZ

(HD-9)

This is the period of the maximum spread of spruce and fir. In the older part of the zone the proportion of hornbeam was still relatively high, firs occurring in the mesotrophic lime-hornbeam habitats. In the younger part of the profile, lime-hornbeam communities became poorer, boreal pine-spruce forests with birch being the dominant forest type. All the thermophilous trees, including *Abies*, ceased to occur in this zone. An increase in moisture was accompanied by a deterioration in the climatic conditions with respect to temperature.

E7, *Pinus* R PAZ

(HD-10, HD-11 and HD-12 L PAZ)

In most habitats, the dominant forest community was pine boreal forest. Spruce, tree birches, larch, poplars, and tree willows were present. The importance of various communities of open habitats increased. The presence of *Betula nana* and *Sphagnum* points to the occurrence of acidophilic, oligotrophic peat bog communities. In zone HD-11, tree birches spread while pine decreased. Perhaps this was the result of a short-lived, sudden climatic change. The vegetation of the period is indicative of a distinctly boreal climate. Mean July temperature is unlikely to have exceeded +17° – +20°C and the highest January temperature did not exceed 0°C.

Early Vistulian (HD-13 – HD-26 L PAZ)

EV1, Gramineae–*Artemisia*–*Betula nana* R PAZ – Herning stadial

(HD-13)

The dominance of communities of open habitats and their considerable diversity were the most characteristic features of the vegetation of the first stadial of the Early Vistulian. Besides shrub tundra with dwarf birch and shrub willows, communities of the damp meadow and steppe type also occurred. Assuming that during this time the lake in Horoszki lay near the northern forest boundary, temperatures of the warmest month must have been ca. +12° – +13° C or a little higher.

EV2, *Betula*–*Pinus* R PAZ – Brörup interstadial

(HD-14 – HD-20)

The expansion of birch forest (HD-14) was interrupted by a brief cold oscillation (HD-15), after which birch woods returned and birch-pine forest developed, with *Picea abies*, *Larix*, and *Pinus cembra*/*sibirica*. Climatic conditions improved and the northern forest boundary moved north of Horoszki.

EV3, Gramineae–*Artemisia*–*Betula nana* R PAZ – Rederstall stadial

(HD-21 and HD-22 L PAZ)

The spread of both tundra and steppe communities took place again, as indicated by *Betula nana*, and *Salix polaris* type, in the former, and in the latter high values of *Artemisia*, Poaceae undiff., Chenopodiaceae, and Cyperaceae and a considerable diversity of herbaceous plant pollen. The presence of *Dryas* pollen indicates subarctic climatic conditions with an mean July temperature of +10°C.

EV4, *Pinus*–*Betula* R PAZ – Odderade interstadial

(HD-23 – HD-26)

The expansion of tree birches (HD-23) is evidence of a change in climatic conditions in the direction of a boreal one and is simultaneously the beginning of the second interstadial of the Early Vistulian, Odderade. After a brief birch phase the development of boreal pine forests took place, with larch, and perhaps also spruce.

Plenivistulian (HD-27 – HD-39 L PAZ)

HD-27 – HD-31 L PAZ

In these zones, plant communities of open habitats dominated. The presence of *Betula nana* and *Salix polaris* type together with a high diversity of taxa from habitats with different soil water conditions suggests the presence of a steppe tundra formation. Throughout this period the lake in Horoszki lay beyond the northern forest boundary, but it is highly likely that in certain periods small stands of tree birches, pine, and larch occurred. In this zone, in chronostratigraphic alternative “A” the Oerel and Glinde interstadials were distinguished, while in alternative “B” it was considered an older part of the Schalkholz stadial.

HD-32 – HD-37 L PAZ

These zones seem to reflect a more stable period in the vegetation succession. The significance of tundra and steppe communities increased further, although individual tree birches, pine and larch were probably consistent elements of the flora around Horoszki. In chronostratigraphic alternative “A” the Moershoofd and Hengelo interstadials were distinguished in this part of the profile, while in alternative “B” it was considered the younger part of the Schalkholz stadial.

HD-38 L PAZ

In this zone maximum spread of *Pinus sylvestris* in the region of Horoszki during the Plenivistulian took place. A slight improvement in climate made it possible for the forest boundary to move a little way north, although communities of open habitats continued to dominate. In chronostratigraphic alternative “A” this zone was considered to be the Denekamp interstadial, and in alternative “B” the Oerel interstadial.

HD-39 L PAZ

Another change of climate in the direction of an arctic one with strongly continental features led to the complete recession of *Pinus sylvestris* from the region and absolute domination of communities of open areas. In chronostratigraphic alternative “A” this zone was considered the beginning of the main stadial, while in variant “B” the beginning of the Ebersdorf stadial.

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PLATES

Plate 1

1,2. *Selaginella helvetica*
3. *Betula nana*
4. *Alnus viridis*
5. *Pinus cembra* t.
6. *Isoetës*
7. *Myriophyllum alterniflorum*
8. *Veratrum*
9. *Nuphar*
10. *Larix*
11. *Nymphaea alba* t.
12. *Trapa*
13. *Utricularia*

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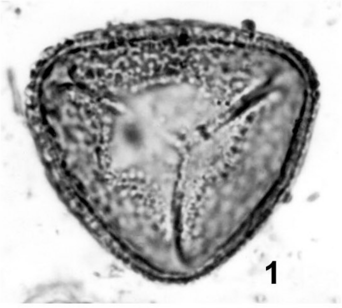
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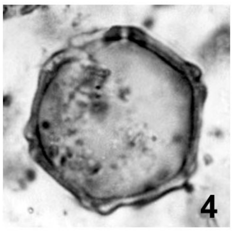
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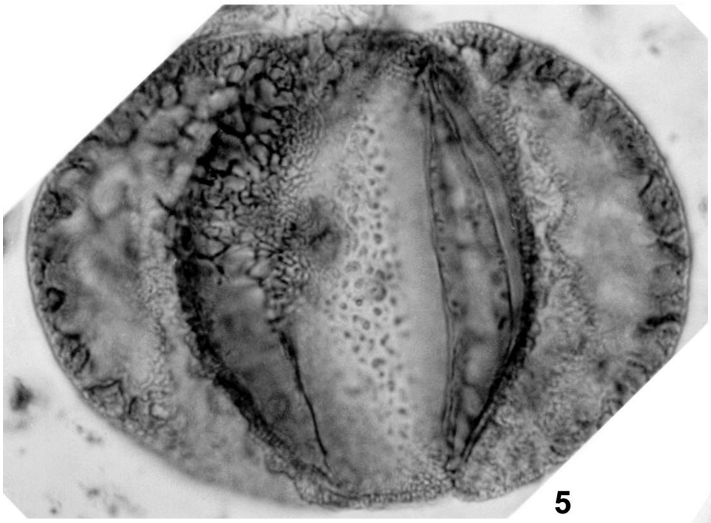
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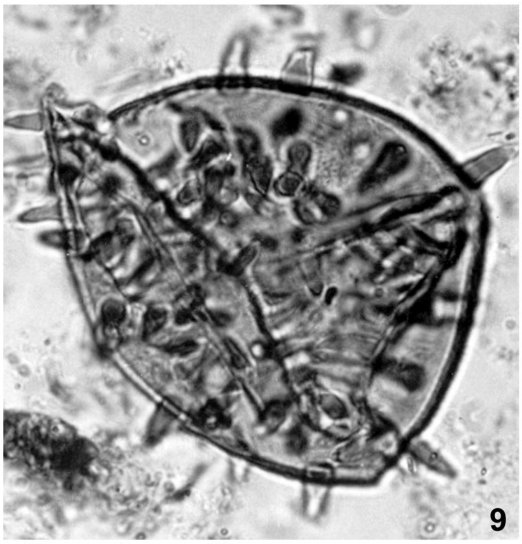
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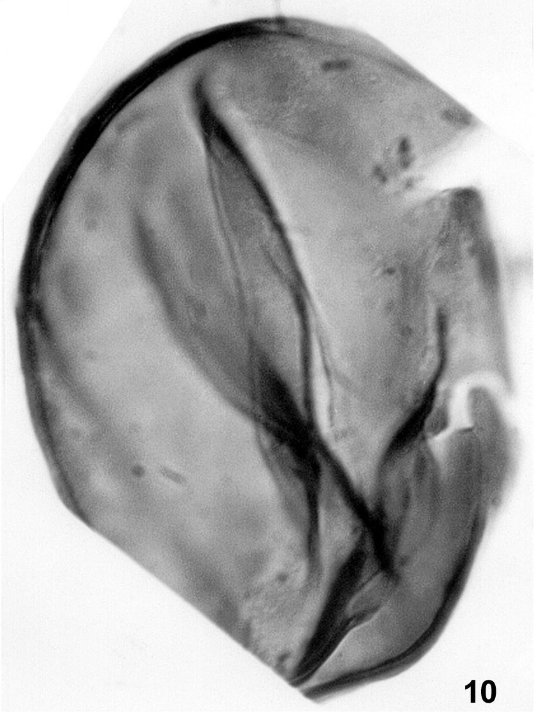
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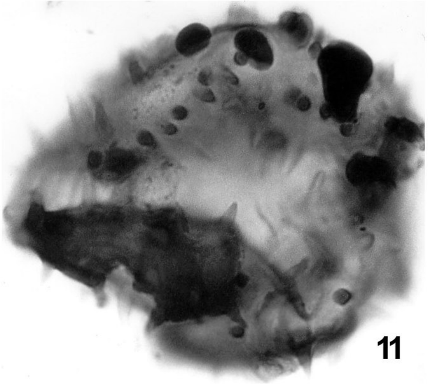
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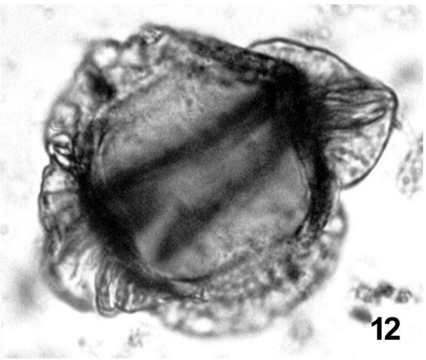
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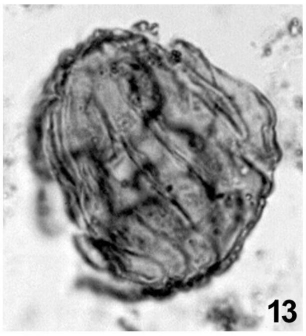
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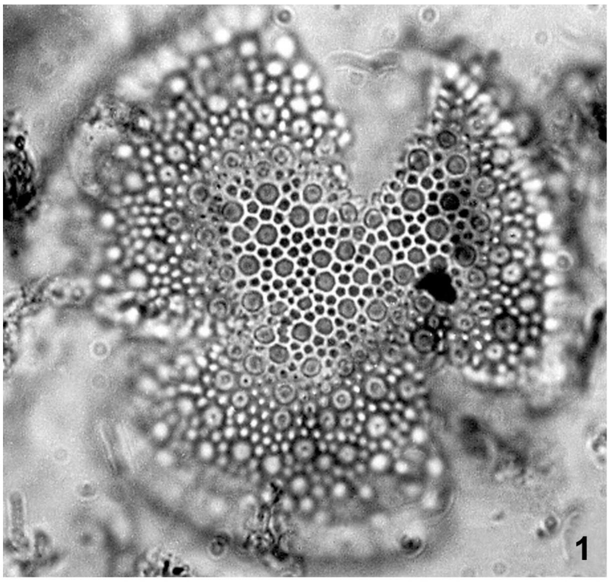
Plate 2

1,2. *Linum austriacum* t.
3,4. *Pulsatilla*
5,6. *Rubus chamaemorus*
7,8. *Lobelia*
9,10. *Valeriana dioica* t.
11,12. *Oxytropis* cf. *lapponica*
13,14. *Ononis* t.
15. *Hedysarum*
16,17. *Genista* t.

×1000, Photo. W. Granoszewski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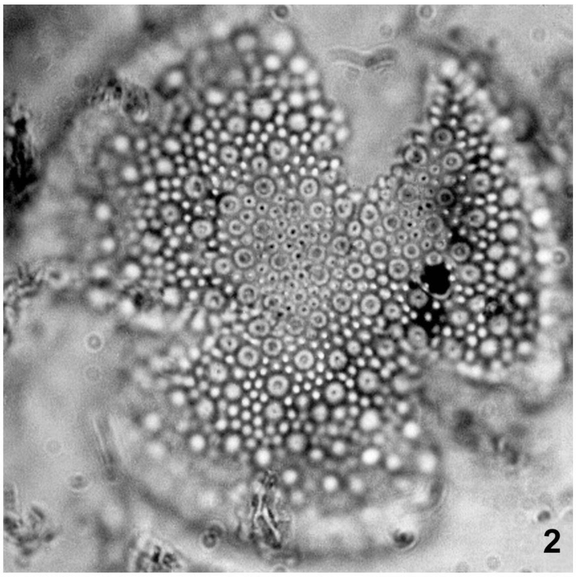
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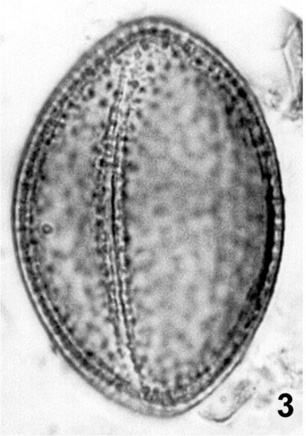
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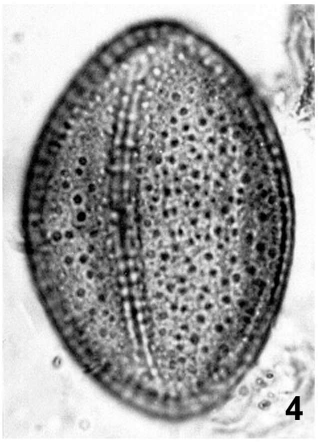
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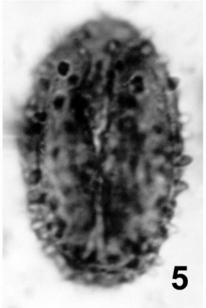
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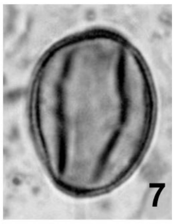
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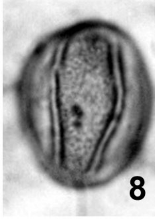
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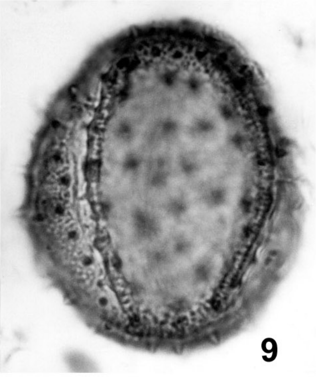
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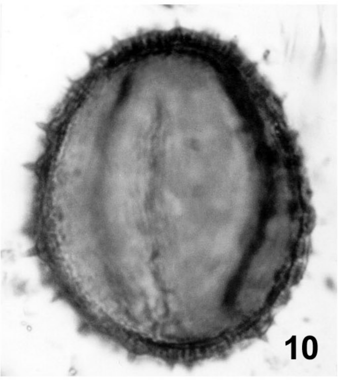
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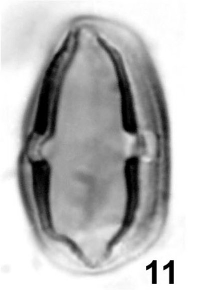
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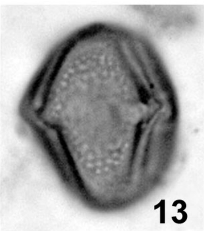
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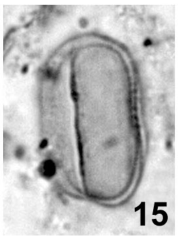
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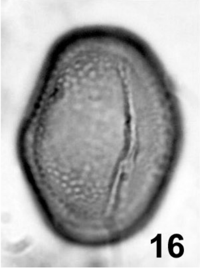
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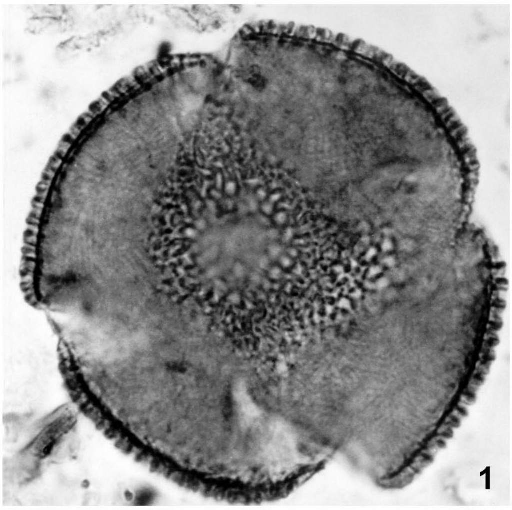
Plate 3

1–3. *Helleborus* cf. *purpurascens*
4,5. *Parnassia palustris*
6–9. *Bruckenthalia spiculifolia*
10. *Sweertia perennis*
11. *Bidens* t.
12,13. *Armeria maritima* t. B

×1000, Phot. W. Granoszewski

Plate 3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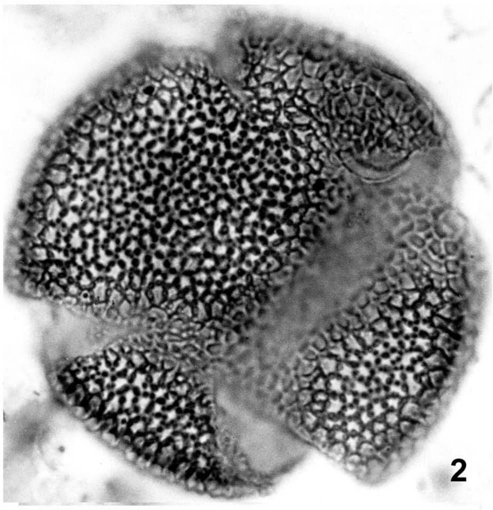
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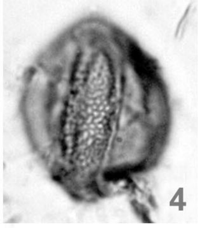
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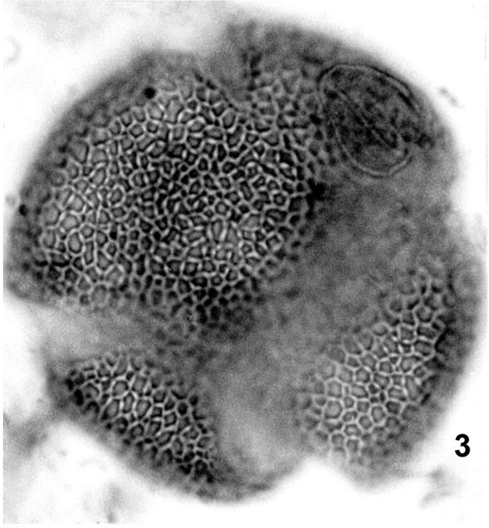
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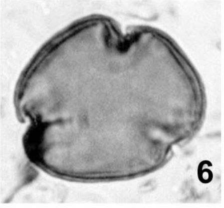
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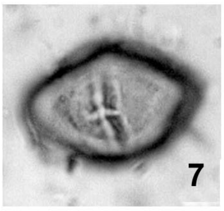
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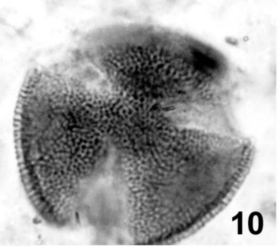
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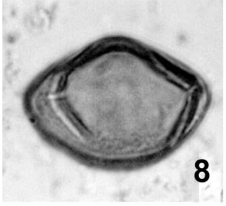
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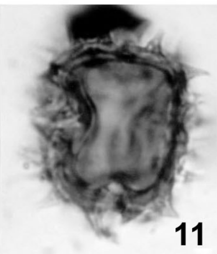
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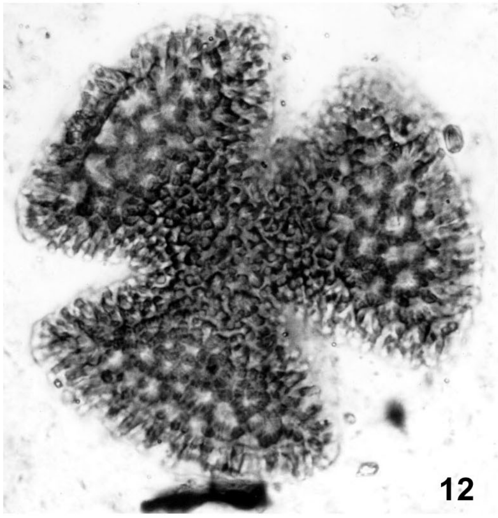
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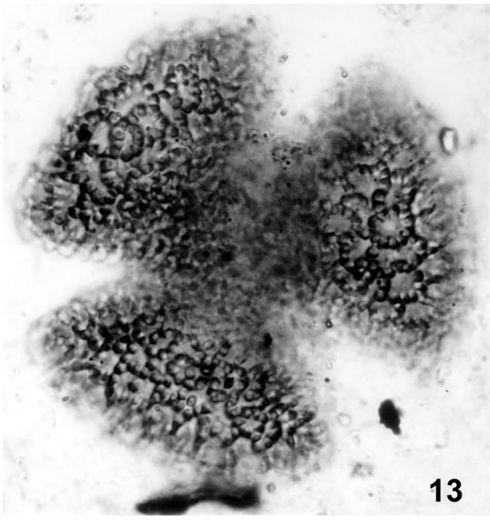
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Plate 4

- 1,2. *Centaurea scabiosa* t.
- 3. *Astrantia major* t.
- 4. *Gentiana campestris* t.
- 5,6. *Helianthemum alpestre* t.
- 7,8. *Cerastium* cf. *alpinum*
- 9,10. *Silene conica* t.
- 11,12. *Scleranthus annuus*
- 13,14. *S. perennis*
- 15,16. *Gypsophila fascigiata* t.
- 17. *Nyssa*
- 18. *Parthenocissus* t.
- 19. *Osmunda cinnamomea* t.

×1000, Photo. W. Granoszewski


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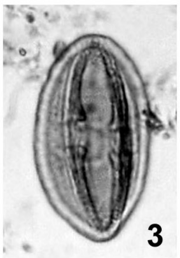
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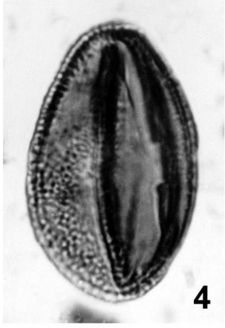
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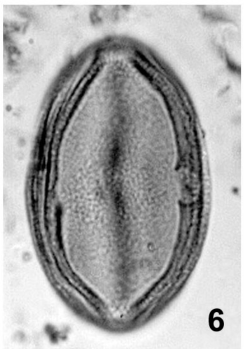
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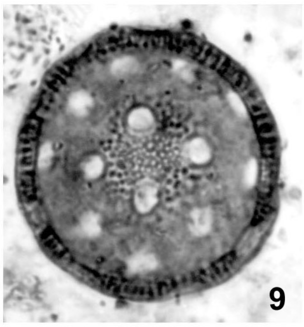
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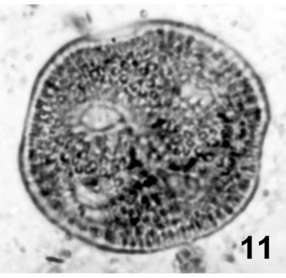
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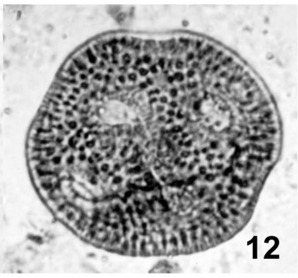
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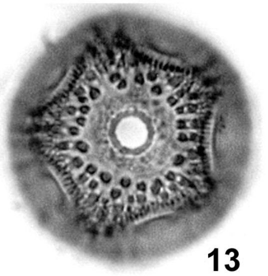
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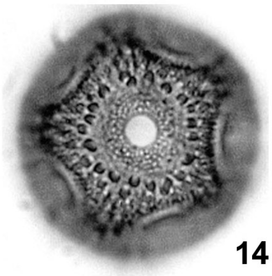
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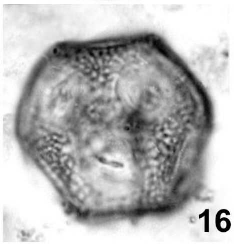
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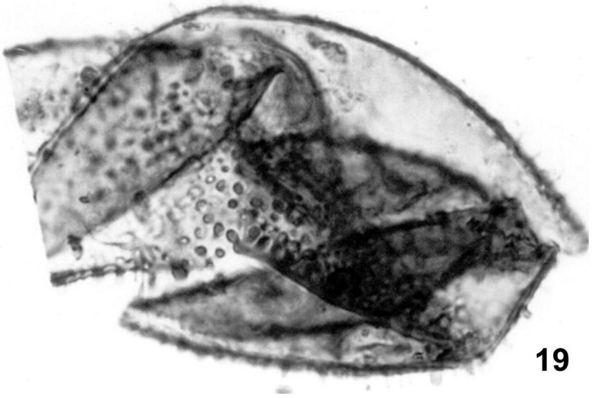
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Plate 5

1. *Selaginella selaginoides* (KRAM-P Q-132/223), macrospore, ×50
2. *Pinus sylvestris* (KRAM-P Q-132/172), seed, ×10
3. *P. sylvestris*, needle (KRAM-P Q-132/174), ×6
4. *Larix*, seed (KRAM-P Q-132/498), ×10
5. *Larix*, needle (KRAM-P Q-132/502), ×10
6. *Larix*, seed (KRAM-P Q-132/163), ×10

7,8. *P. abies*, fragments of needles (KRAM-P Q-132/161), ×10

9. *Betula* sectio *Albae* (KRAM-P Q-132/41), nut, ×12,5
10. *Betula* cf. *pubescens* (KRAM-P Q-132/39), fruit scale, ×10
11. *Betula pendula* (KRAM-P Q-132/), fruit scale, ×10
12. *Betula nana* (KRAM-P Q-132/36), fruit scale, ×21
13. *Betula* cf. *humilis* (KRAM-P Q-132/), ×??
14. *Betula nana* (KRAM-P Q-132/35), nut, ×25
15. *Betula nana* (KRAM-P Q-132/37), nut, ×21
16. *Carpinus betulus* (KRAM-P Q-132/66), nut, ×10
17. *Sambucus* cf. *nigra* (KRAM-P Q-132/218), stone, ×10

18–20. *Tilia tomentosa* (KRAM-P Q-132/235), fruit, ×6

21,22. *Potamogeton sukaczevii* (KRAM-P Q-132/563), endocarps, ×12

23. *P. perfoliatus* (KRAM-P Q-132/540), endocarp, ×12
24. *P. perfoliatus* (KRAM-P Q-132/534), endocarp, ×12
25. *P. obtusifolius* (KRAM-P Q-132/538), endocarp, ×12
26. *P. filiformis* (KRAM-P Q-132/529), endocarp, ×12
27. *P.* cf. *freesi* (KRAM-P Q-132/532), endocarp, ×12
28. *P. praelongus* (KRAM-P Q-132/544), endocarp, ×12

Photo. A. Pachoński

Plate 5


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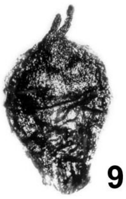
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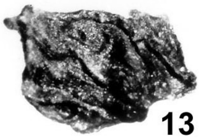
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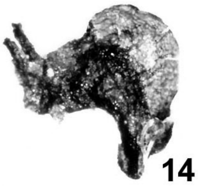
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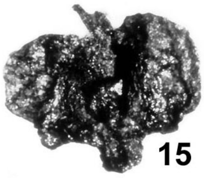
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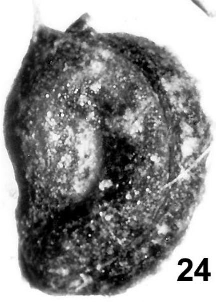
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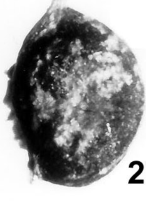
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Plate 6

1. *Potamogeton vaginatus* (KRAM-P Q-132/573), endocarp, ×12
2. *P. pussilus* (KRAM-P Q-132/557), endocarp, ×12
3. *P.* cf. *lucens* (KRAM-P Q-132/533), endocarp, ×12
4. *Myriophyllum* cf. *microcarpum* (KRAM-P Q-132/132), fruit, ×33
5. *Nuphar pumila* (KRAM-P Q-132/154), seed, ×10
6. *Najas marina* (KRAM-P Q-132/147), fruit, ×10
7. *N. flexilis* (KRAM-P Q-132/140), fruit, ×10
8. *N. minor* (KRAM-P Q-132/153), fruit, ×10
9. *Myriophyllum alterniflorum* (KRAM-P Q-132/130), fruit, ×21
10. *Ceratophyllum demersum* (KRAM-P Q-132/77), fruit, ×6
11. *C. submersum* (KRAM-P Q-132/80), fruit, ×6
12. *Scheuchzeria palustris* (KRAM-P Q-132/220), seed, ×10
13. *Zannichelia palustris* subsp. *pedicellata* (KRAM-P Q-132/240), fruit, ×10
14. *Ranunculus flammula* (KRAM-P Q-132/195), seed, ×23
15. *R. sceleratus* (KRAM-P Q-132/200), seed, ×28
16. *Eleocharis ovata* (KRAM-P Q-132/103), fruit, ×23
17. *E. palustris* (KRAM-P Q-132/105), fruit, ×18
18. *Bidens tripartita* (KRAM-P Q-132/60), fruit, ×10
19. *Rumex maritimus* (KRAM-P Q-132/212), fruit, ×10
20. *R. acetosella* (KRAM-P Q-132/208), fruit, ×30
21. *Batrachium* (KRAM-P Q-132/67), seed, ×20
22. *Comarum palustre* (KRAM-P Q-132/86), seed, ×21
23. *Fragaria* (KRAM-P Q-132/109), seed, ×21
24. *Potentilla supina* (KRAM-P Q-132/182), seed, ×28
25. *Urtica dioica* (KRAM-P Q-132/239), seed, ×25
26. *Chamaedaphne calyculata* (KRAM-P Q-132/82), seed, ×28
27. *Stachys palustris* (KRAM-P Q-132/226), fruit, ×20
28. *Scleranthus annus* (KRAM-P Q-132/222), calyx, ×20
29. *Lychnis flos-cuculi* vel *Viscaria vulgaris* (KRAM-P Q-132/123), seed, ×45
30. *Filipendula* cf. *vulgaris* (KRAM-P Q-132/108), seed, ×12
31. *Silene* cf. *vulgaris* (KRAM-P Q-132/224), seed, ×28
32. *Taraxacum* (KRAM-P Q-132/231), fruit, ×10

Photo. A. Pachoński

Plate 6


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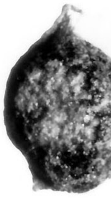
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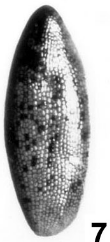
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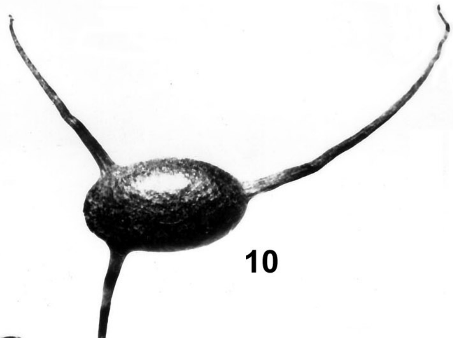
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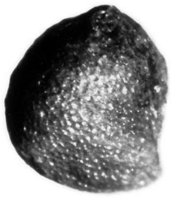
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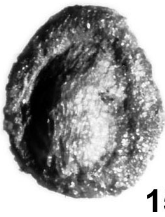
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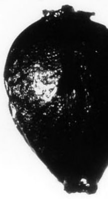
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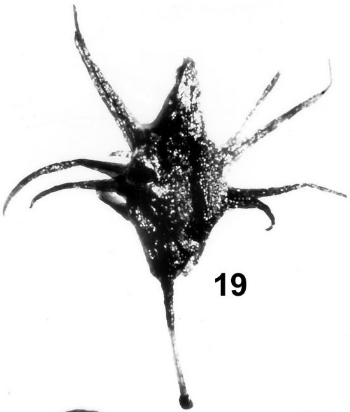
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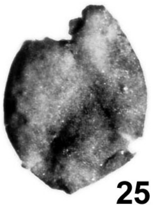
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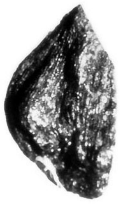
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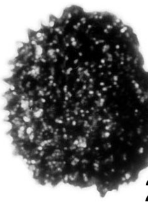
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