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Palaeoecological evidence of changes in vegetation and climate during the Holocene in the pre-Polar Urals, northeast European Russia

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ABSTRACT: This study investigated Holocene tree-line history and climatic change in the pre-Polar Urals, northeast European Russia. A sediment core from Mezhgornoe Lake situated at the present-day alpine tree-line was studied for pollen, plant macrofossils, Cladocera and diatoms. A peat section from Vangyr Mire in the nearby mixed mountain taiga zone was analysed for pollen. The results suggest that the study area experienced a climatic optimum in the early Holocene and that summer temperatures were at least 2°C warmer than today. Tree birch immigrated to the Mezhgornoe Lake area at the onset of the Holocene. Mixed spruce forests followed at ca. 9500–9000 ^{14}C yr BP. Climate was moist and the water level of Mezhgornoe Lake rose rapidly. The hypsithermal phase lasted until ca. 5500–4500 ^{14}C yr BP, after which the mixed forest withdrew from the Mezhgornoe catchment as a result of the climate cooling. The gradual altitudinal downward shift of vegetation zones resulted in the present situation, with larch forming the tree-line. Copyright © 2003 John Wiley & Sons, Ltd.

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KEYWORDS: Holocene; northern Russia; tree-line; lake-level changes; palaeoclimate.

Introduction

It is commonly believed that the anthropogenically increased concentrations of atmospheric greenhouse gases will increase temperatures, especially in continental high-latitude regions (IPCC, 2001). As a result, it is likely that forest vegetation will advance northwards (arctic tree-line) and upwards (alpine tree-line). These shifts in the forest line can have significant feedbacks to climate, i.e. changes in the albedo and carbon storage (Betts, 2000). The Holocene records of environmental changes in vegetation and lacustrine systems can be used to validate biome models and to provide possible analogues for future changes in the environment.

Holocene environmental changes in the northeast of European Russia have been studied mainly using tree megafossils (e.g. Kremenetski *et al.*, 1998; MacDonald *et al.*, 2000) and palaeobotanical analyses of peat deposits (e.g. Kaakinen and Eronen, 2000; Oksanen *et al.*, 2001), and have been concentrated on lowland environments. Climatic conditions have varied throughout the Holocene, and changing temperatures and humidity have strongly affected the arctic tree-line, vegetation cover and distribution of permafrost around the forest–tundra ecotone. Forest establishment in northern Russia took place at the beginning of the Holocene; between 9000 and 7000 ^{14}C yr BP the forest line had advanced to the Barents Sea coastline (Kremenetski *et al.*, 1998; MacDonald *et al.*, 2000). Based on tree megafossils the withdrawal of the forest line to its present position took place between 4000 and 3000 ^{14}C yr BP (Kremenetski *et al.*, 1998; MacDonald *et al.*, 2000). Permafrost aggradation in peatlands commenced ca. 3000 ^{14}C yr BP (Oksanen *et al.*, 2001).

No detailed palaeoenvironmental studies from the alpine tree-line zone in the northern Ural Mountains have been published in English. An advantage of studying climate change in alpine ecosystems is the short migration lags of trees owing to the steep ecozonal gradient (e.g. Kullman and Kjällgren, 2000). This paper focuses on the tree-line dynamics and changes in climate and aquatic ecosystems during the Holocene in the pre-Polar Urals region, northeast European Russia. Pollen, plant macrofossil, cladoceran and diatom analyses have been applied to extract palaeoecological and palaeoclimatic information from lake sediments from a site located at the

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present-day alpine tree-line (Lake Mezhgornoe). To provide vegetation history on the regional scale, these studies were supplemented by the pollen record from a peat section from a nearby site in the mixed mountain taiga (Vangyr Mire).

Study area

The study area is situated on the western slopes of the Ural Mountains, Komi Republic, in the northeast of European Russia (Fig. 1A and B). The Pechora region west of the mountain area is characterised by extensive lowlands (< 200 m a.s.l.). Typically, the mountain tops in the area vary from 1000 to 1600 m a.s.l. with the highest at 1894 m a.s.l. Bedrock in the area consists of Early and Middle Ordovician sedimentary rocks. Thick Quaternary sediments cover the bedrock in lowland areas. The Kara and Barents ice-sheets did not reach the study area during the Weichselian (Mangerud *et al.*, 1999; Svendsen *et al.*, 1999; Gataullin *et al.* 2001). However, traces of small alpine glaciers have been found in the Urals south of the ice-sheet limit (Valery Astakhov, personal communication, 2001). Many U-shaped valleys characterise the area, and scattered till deposits have been observed during fieldwork. The study area is practically free of permafrost at lower elevations, but discontinuous and then continuous permafrost occur towards higher altitudes (Oberman and Borozinetsh, 1988).

In the Pechora lowlands the arctic tree-line runs in a largely east–west direction along 67–68°N latitude, corresponding to the zone of discontinuous permafrost. Spruce (*Picea abies* sl.) is the dominant tree species at tree-line in the lowland areas. The alpine tree-line is formed by larch (*Larix sibirica*) (Fig. 1C) at ca. 550–600 m a.s.l. Mixed mountain taiga with spruce and white birch (*Betula pubescens*) prevails in the lower valleys of the study area and Siberian fir (*Abies sibirica*) is often dominant at higher altitudes. Some peatland areas are present in flat valley bottoms and also on slopes at the tree-line. The modern climate in the area is characterized by cold winters and cool summers (Table 1).

The central Mezhgornoe Lake (65°15′28″N; 59°39′59″E; 550 m a.s. l.) lies on the western slope of the Ural Mountains (Fig. 1B), in a mountain saddle between two other lakes (Figs 1C and 2). The alpine tree-line occured only 20 m higher (ca. 570 m a.s.l.) than the lake (Figs 2 and 4A, and Table 2). At

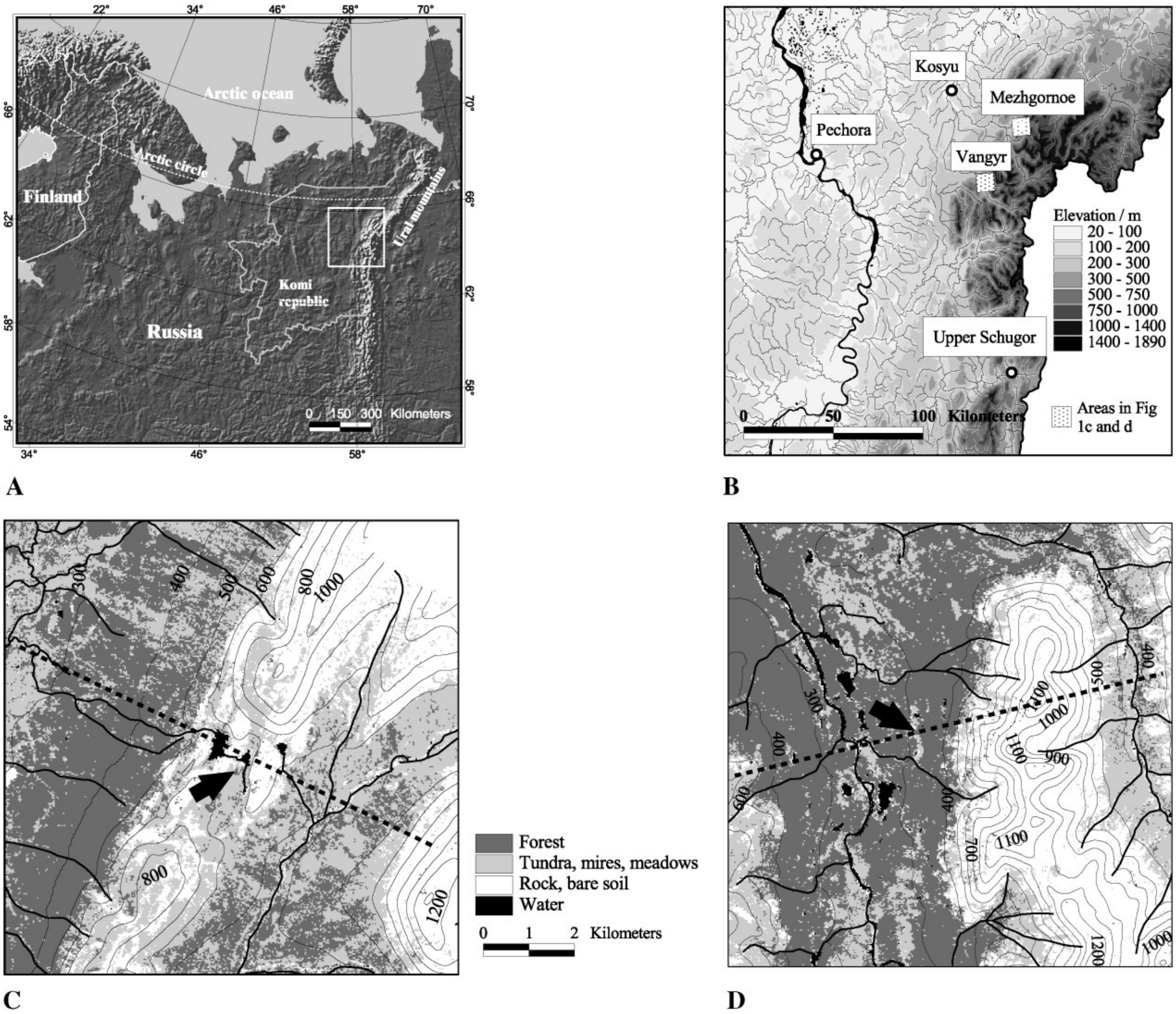


Figure 1 (A) Location of the study area in the pre-Polar Urals, north European Russia. The area indicated by the white rectangle in Fig. 1A, is shown enlarged in Fig. 1B. (B) Location of the study sites and meteorological stations. (C) Detailed view of the surroundings of Lake Mezhgornoe. The location of the lake is marked by an arrow. The broken line indicates the transect in Fig. 4A. (D) Detailed view of the surroundings of Vangyr Mire. The location of the mire is marked by an arrow. The broken line indicates the transect in Fig. 4B

Table 1 Climate averages (1961–1990) of the study area. The precipitation record from Verhni Sugor is very incomplete, consisting only of 11 out of the 30 yr. The locations of the weather stations are shown in Fig. 1B

	Mean July temperature (°C)	Mean January temperature (°C)	Annual precipitation (mm)
Pechora station (65° 07′ N; 57° 06′E; 56 m a.s.l.)	16.1	−20.3	555
Verhni Sugor (64° 02′ N; 59° 30′E; 290 m a.s.l.)	14.9	−20.6	830
Mezhgornoe Lakes (65° 15′ N; 59°40′E; 550 m a.s.l.)	12.4[a]		
Vangyr Mire (65° 00′ N; 59° 15′E; 300 m a.s.l.)	14.4[a]		

[a] Estimated on the basis of altitudinal and latitudinal gradients.

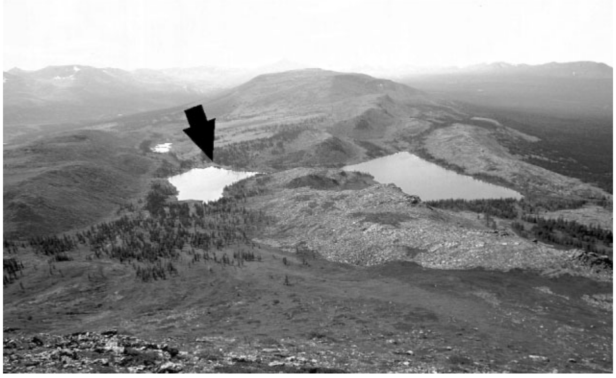


Figure 2 View from 900 m elevation of the central (left) and western (right) Mezhgornoe lakes. Sparse larch stands can be seen around the lakes. Fir and mixed mountain taiga forests are present in the lower valleys (top right-hand corner). The arrow indicates the central Mezhgornoe lake, from which the core was sampled

Figure 3 View of the Vangyr river valley. The arrow indicates the location of the sampled mire, which is surrounded by mixed mountain forests

Table 2 Description of the main vegetation types in different elevation zones. Lowland taiga measurements are from the area near Kosyu river (see Fig. 1B). The others are from Mezhgornoe and Vangyr. All were measured during summer 1998. Elevation zones are approximate. *n* is the number of measured sites. From every site, three 10-m radius circles were measured. Tree species percentages are crown cover percentages of total vegetation cover. Birch cover also includes some other less common deciduous leaved trees (species in genera *Sorbus, Alnus* and *Prunus*). The 'other' category consists of the field-layer vegetation, stones, etc.

Vegetation, zone	Elevation (m a.s.l)	Tree, volume ($m^3 ha^{-1}$)	n	Spruce (%)	Fir (%)	Birch (%)	Larch (%)	Other (%)
Lowland mixed and spruce dominated taiga	< 220	132.5	7	34.0	0.0	19.8	0.0	47.2
Alpine mixed and spruce dominated forest	220–320	96.8	5	16.3	7.7	23.3	3.0	49.7
Fir dominated forest	320–470	92.8	10	8.0	18.7	16.0	2.7	54.6
Larch forest	470–600	63.7	6	0.1	0.1	7.5	27.8	65.5
Lower alpine meadow and heath	500–800	—	8	0.0	0.1	0.8	1.1	98.0

present, larch is the dominant tree species in the catchment area of the lake, with two specimens of Siberian fir also observed during fieldwork. Fir in particular, as well as spruce, mountain birch (*Betula pubescens* ssp. *czerepanovii*) and white birch are common at lower elevations. This mixed mountain taiga appears ca. 100 m lower than the study site. Scots pine (*Pinus sylvestris*) is absent in the study area. The nearest pines can be found 10–20 km away from the study area in lowland bogs, and the nearest upland pine forests grow on sandy areas near the Usa and Pechora rivers, approximately 100 km from the Mezhgornoe site. Areas above the tree-line are characterised by patchy alpine meadows and shrub–lichen-dominated tundra vegetation. The steep and rocky slopes and the highest altitudes are almost bare. Peatlands cover ca. 15% of the study area.

Vangyr Mire (unofficial name) (65°00′N; 59°15′E; 300 m a.s.l.) is situated in the Vangyr River valley, west of the Ural Mountains (Figs 1B, 1D and 3). The present vegetation in the area is mainly mixed mountain taiga with spruce, birch, larch and Siberian fir (Fig. 4B, Table 2). Pine occurs farther away to the west in lowland bogs. At higher altitudes the proportion of Siberian fir increases, and at the tree-line larch and in some locations mountain birch form a narrow belt below the alpine meadow and shrub–lichen-dominated tundra vegetation. Steep slopes and areas at high elevations are bare. Peatlands also cover ca. 15% of the area.

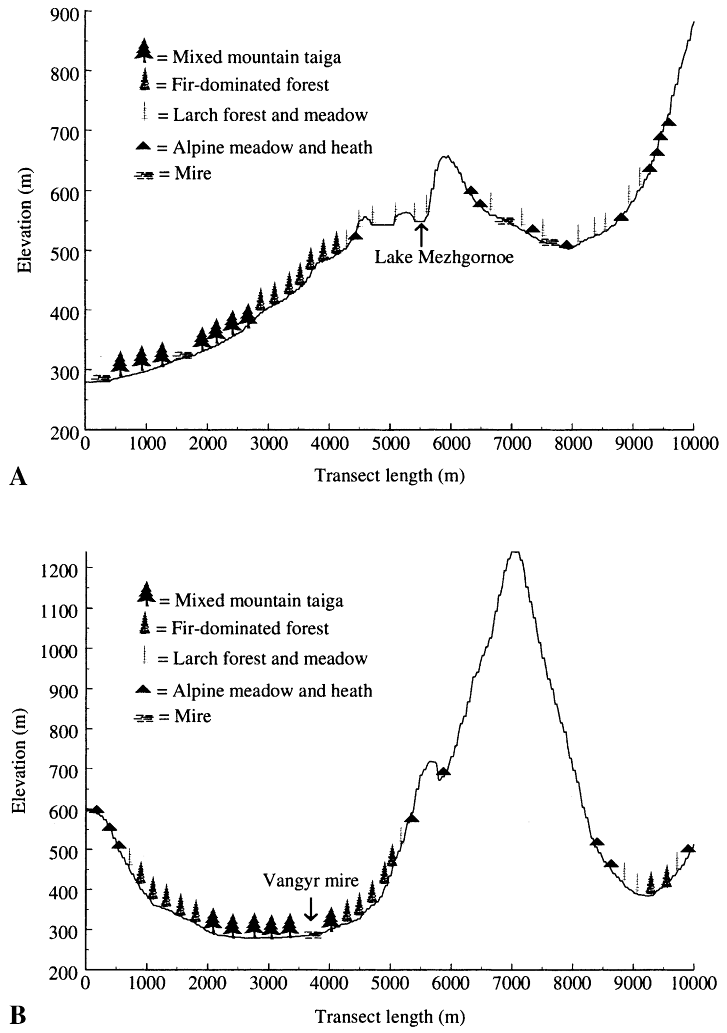


Figure 4 Schematic representation of the vegetation zones in relation to elevation in (A) Mezhgornoe (position of transect shown in Fig. 1C) and (B) Vangyr (position of transect shown in Fig. 1D)

Material and methods

Sampling and dating

Fieldwork was carried out in spring and summer 1998. The 50-cm cores from Mezhgornoe Lake were collected with a Russian corer of 5 cm diameter, and the uppermost sediment was obtained using a Glew corer. The peat deposits from Vangyr Mire were collected with a Russian corer. The middle part of Mezhgornoe Lake was too deep (17 m) for successful coring so material was retrieved ca. 20 m from the western shore in a water depth of 2.0 m. The sediment was packed in plastic and stored in a cold room. Sediments were described according to the visual characteristics (Table 3) and loss-on-ignition analysis was carried out at 10-cm intervals.

Chronological control was provided by a series of conventional (Hel-xx) and AMS (Hela-xx) ^{14}C datings (Stuiver and Polach, 1977) from bulk sediment and terrestrial macrofossils in the Dating Laboratory of the University of Helsinki (Table 4). The dates were calibrated using the CALIB *4.1* program (Stuiver and Reimer, 1993).

In the text calibrated dates are denoted as 'cal. yr BP' and uncalibrated ages as 'yr BP'. Most dates from Mezhgornoe Lake were obtained from bulk sediment because of the lack of suitable macrofossils. Only one date (Hela-495) is based on terrestrial macrofossil material. To estimate the accuracy of the bulk sediment dates a surface sample (0–0.5 cm, Hela-485) was also dated. This sample was collected with the Glew corer. Dates from Vangyr Mire are from bulk peat. Roots were removed as completely as possible.

Table 3 Sediment lithology of Lake Mezhgornoe, northeast European Russia

Depth (cm)	Sediment description	Loss-on-ignition (%)
0–260	Grey-brown silt-gyttja	7–15
260–290	Greyish gyttja-silt	4–5
290–300	Grey-brown silt-gyttja	8
300–310	Greyish gyttja-silt	5
310–325	Silt with coarse detritus (*Equisetum*—wood trunk or branch)	7

Pollen analysis

From the cores, 0.5 cm^3 of fresh sediment was sampled at 5–10 cm intervals. The laboratory treatment followed standard KOH, HF and acetolysis methods (Fægri and Iversen, 1989). Two *Lycopodium* tablets (Stockmarr, 1971) were added for

Table 4 Radiocarbon dates from Lake Mezhgornoe and Vangyr Mire. For the uncertainty range of the reassessed age estimates, see Fig. 5

Laboratory code	Dated material	Sample	δ^{13}C	Age BP	Reassessed age BP	Calibrated age BP	Notes
Hela-485	Bulk	Mezhgornoe 0–0.5		980 ± 65	−50		Difference ca. 1800 ^{14}C yr
Hela-375	Bulk	Mezhgornoe 65–67	−25.9	4740 ± 65	2940	3130	−1800 ^{14}C yr
Hela-374	Bulk	Mezhgornoe 152–154	−27.9	8795 ± 115	7000	7810	−1800 ^{14}C yr
Hela-373	Bulk	Mezhgornoe 233–235	−29.3	11050 ± 100	9250	10450	−1800 ^{14}C yr
Hel-4163	Bulk	Mezhgornoe 310–325	−27.8	11250 ± 140			Difference ca.1220 ^{14}C yr
Hela-495	Plant macrofossil	Mezhgornoe 315–320		10035 ± 115		11440	
Hel-4351	Peat	Vangyr mire 65–75	−28.5	1530 ± 80		1410	
Hel-4352	Peat	Vangyr mire 225–235	−28.1	4930 ± 80		5650	
Hel-4353	Peat	Vangyr mire 340–350	−26.2	7250 ± 90		8090	
Hel-4244	Peat	Vangyr mire 380–400	−27.1	7870 ± 160		8620	

estimation of pollen concentrations and accumulation rates. The samples were mounted in glycerol and stained with safranine. A minimum of 300 terrestrial pollen grains was counted. The total pollen sum of terrestrial plants is the basic sum for the percentage calculations. The percentages for taxa within spores and aquatics are estimated from the basic sum added with the total sum of spores or the total sum of aquatic pollen. The sample age between dated intervals was calculated by linear interpolation. Pollen accumulation rates were calculated using calibrated ^{14}C ages. Conifer stomata found in the pollen slides were differentiated to genus level with the help of reference slides. Pollen nomenclature follows Moore *et al.* (1991), except in *Compositae tubuliflorae* and *Compositae liguliflorae.*

Macrofossil analysis

For plant macrofossil analysis, volumetric samples (20–30 cm^3) at 5-cm intervals were taken. In a few cases very little sediment was available and the subsamples were small, less than 10 cm^3. The sediment was soaked overnight, or longer if needed, in sodium pyrophosphate ($Na_4P_2O_7.xH_2O$) solution in order to break up the sediment. The sediment was then sieved through a 125 μm mesh and analysed for plant macrofossils. The remains of trees, particularly of conifers, were studied in order to obtain a more precise picture of past shifts of the tree-line. Birch seeds were divided into three groups: tree birch, dwarf birch and birch when reliable identification was not possible. The identification of small pieces of conifer needles was based on the stomata. Mosses were identified only from the lowermost 40 cm where they dominated. Nomenclature follows Eurola *et al.* (1992) for mosses and Hämet-Ahti *et al.* (1998) for vascular plants.

Cladocera analysis

As the cladoceran concentration was low, large subsamples (ca. 2 cm^3) were used. Subsamples were heated in 10% KOH for 30 min using a magnetic stirrer. The sediment samples contained organic matter, which did not penetrate the ca. 40 μm mesh recommended by Frey (1986). Therefore the samples had to be sieved through a 100 μm mesh with a very strong pressure of tap water and unfortunately many smaller remains, such as postabdomens, must have been lost because they were rare in the samples analysed. The samples were mounted with glycerol jelly stained with safranine. About 250–300 cladoceran remains were counted from each sample where possible.

As there were large variations between the quantities of planktonic and littoral Cladocera, representing different habitats, the percentages for littoral forms were calculated based on the basic sum of total littoral Cladocera. Thus a more reliable general picture of their succession within the littoral zone was obtained. The proportions for planktonic forms were calculated based on the basic sum of total Cladocera remains. The cladoceran nomenclature follows Flössner (1972). *Eurycercus* head pores were circular, unlike those of *E. lamellatus*, and the taxon is called *Eurycercus sp.* At least two types of *Chydorus* carapaces and headshields could be distinguished (not calculated separately) and are called here *Chydorus sphaericus* s.l. (cf. Frey, 1982). Numerous unidentified medium-size *Alona* type carapaces and headshields were found (*Alona* sp.).

Diatom analysis

Diatom slide preparation followed standard procedure (Battarbee, 1986) using the water-bath method (Renberg, 1990). Diatom concentration was determined using microsphere markers (Battarbee and Kneen, 1982). Between 300 and 400 valves were counted for most levels. The diatom abundance was low at the three lowermost levels, and only 100–150 valves were counted between 320 and 300 cm. Diatom nomenclature follows Krammer and Lange-Bertalot (1986–1991) and AL:PE guidelines (Cameron *et al.*, 1999). pH was reconstructed using the AL:PE transfer function (Cameron *et al.*, 1999). The reconstruction of epilimnetic total phosphorus concentration (TP) was performed using the CALIBRATE 0.85 software of Juggins and ter Braak (1997, unpublished) and a training set collected from 61 lakes in southern Finland (Kauppila *et al.*, 2002). Because the calibration set has not been collected in the study area, the phosphorus reconstructions are not used to infer exact past TP concentrations but rather are used to summarise trends in the relative abundances of diatom taxa with different nutrient requirements.

Results and interpretation

Lithology and dating

The organic content of the 3.25 m thick sediment sequence of Mezhgornoe Lake (Table 3) is low through the entire core. The

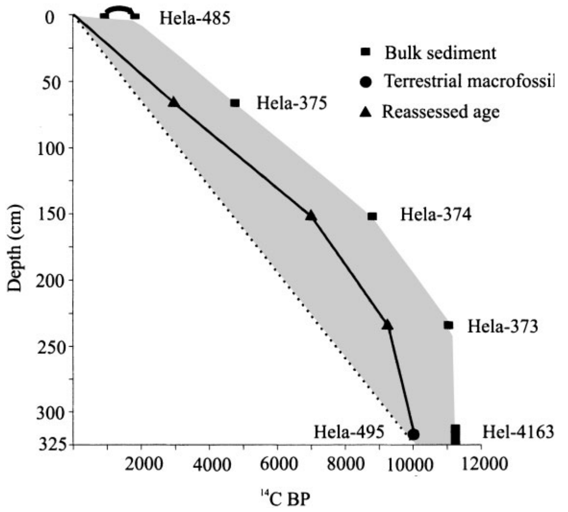


Figure 5 Age–depth model for the Lake Mezhgornoe core, northeast European Russia. The grey area indicates the range of uncertainty of the dates (see text). The broken line was drawn from the only macrofossil date to the present-day. The right-hand edge of the grey area shows the dates from bulk sediments. The solid line shows the age–depth model that was calibrated for calculation of pollen accumulation and sedimentation rates

grain size is slightly coarser in the lowermost part (310–325 cm). The lowermost sediment also contains coarse plant remains.

The dating results of Mezhgornoe Lake are problematic (Table 4 and Fig. 5). Because of the lack of suitable macrofossils, dates were determined from bulk sediment with all the sources of error involved.

The bulk sediment date Hel-4163 from the lowermost part of the core is ca. 1200 ^{14}C yr older than the parallel date from terrestrial macrofossils (Hela-495). The surface bulk sediment sample (0–0.5 cm) gives a ^{14}C age of 980 ± 65 yr BP. During the atmospheric nuclear weapon testings in the 1950s and early 1960s large amounts of radiocarbon were generated in the atmosphere. Dwing to this, the recent ^{14}C values are ca. 10% higher compared with a 'normal' stage (Levin *et al.*, 1985; Manning *et al.*, 1990). As a result, dates from recent material are ca. 800 ^{14}C yr too young. Adding the bomb effect to the ^{14}C date, the surface sediment is ca. 1800 yr old.

Several studies have shown that because of hardwater or reservoir effects bulk sediment dates from arctic lakes are in many cases older than terrestrial macrofossil dates from the same level (Deevey *et al.*, 1954; Donner *et al.*, 1971; Olsson and Vasari, 1995; Abbott and Stafford, 1996; Barnekow *et al.*, 1998; Paus, 2000). The carbonate ion content of the water in Lake Mezhgornoe was 16.3 ± 2.5 mg l^{-1} during spring 1998 and 7.1 ± 0.71 mg l^{-1} during summer 1998. Because of the ice cover during spring, lake water is more influenced by ground-water. Bedrock in the area consists mainly of Early and Middle Ordovician sediment are rocks that result in a hardwater effect.

Owing to the relatively steep slopes of the lake, redeposition of older material also could have affected the ^{14}C dates. However, there is no indication of redeposition or even a hiatus in the relative pollen evidence. Roots of aquatic plants penetrating downwards may also affect the dates so that they appear younger than the actual age of the sediment. On the contrary, the parallel date from bulk sediment from the lowermost part of the core appears older compared with the date determined from macrofossils. Therefore, the root effect appears to be minimal. It is probable that the hardwater effect caused by the local bedrock is the most likely reason for the problematic ^{14}C dates.

The hardwater effect in Mezhgornoe Lake apparently has not been constant through its sedimentation history (cf. Barnekow *et al.*, 1998; Paus, 2000). The hardwater effect appears less pronounced at the beginning of the Holocene (ca. 1200 yr) than it is at present (ca. 1800 yr). This is probably due to a larger proportion of terrestrial macrofossils in the lowermost part of the core, as well as the fact that the coring point was shallow during the early Holocene (see text below) and therefore the exchange with atmospheric CO_2 was probably more effective.

No terrestrial macrofossils were available for supplementary dating. In the age–depth model (Fig. 5) it is assumed that after the early Holocene, the hardwater effect has been the same as in the surface sample, even if this is unlikely. Dates Hela-375, Hela-374 and Hela-373 from bulk sediment were corrected by 1800 ^{14}C yr and the dates were then calibrated (Table 4). The uncertainty of the dates has to be taken into account when estimating the reliability of the results or the interpretation.

According to the age–depth model used the sedimentation rate of Mezhgornoe was highest (0.8 mm yr^{-1}) in the lowermost part of the record. The reason for a decreased sedimentation rate afterwards could be afforestation of the catchment area, hence decreased erosion and input of allochthonous material, and also increasing distance to the shoreline because of the rising lake-level.

The main components of the 4 m thick Vangyr peat section are *Carex, Sphagnum* and nanolignine. *Carex* dominates the lowermost 3.5 m, whereas the uppermost 50 cm is dominated by *Sphagnum*.

Dates from Vangyr Mire were determined from bulk peat samples. These also probably contain many sources of error, e.g. deep penetration of roots, decomposition of old peat and vertically redistributed dissolved organic carbon (Nilsson *et al.*, 2001). The dates from Vangyr Mire, however, appear logical and we have no reason to doubt the reliability of the dating results. In Vangyr Mire the peat accumulation rates were 0.9 mm yr^{-1} between 350 and 400 cm and subsequently 0.4–0.5 mm yr^{-1}.

Pollen and macrofossils from Mezhgornoe Lake

The pollen stratigraphy (Fig. 6A and B) of Mezhgornoe Lake has been divided into four local pollen assemblage zones (PoM I to PoM IV). Pollen accumulation rates of selected taxa and total pollen accumulation rate and concentration are shown in Fig. 7. The same zonation was used for both pollen and macrofossil (MaM I to MaM IV, Fig. 8) stratigraphy. The dates in parentheses (in the zone descriptions) are derived from the age–depth model. For the uncertainty range of the model see Fig. 5.

PoM I (325–275 cm; 10 000–9600 yr BP; 11 500–10 900 cal. yr BP). Cyperaceae and other herb pollen are dominant. The proportion of *Betula* pollen gradually increases from 20% to 40%. Conifer pollen, i.e. *Picea, Pinus* and *Abies* is present only in small quantities. Rosaceae and *Epilobium* peaks follow the peak of *Artemisia* in the lowermost part of the zone. The upper boundary of the zone is defined by the onset of the Cyperaceae decrease. Pollen concentrations are relatively low. The accumulation rates of Cyperaceae are highest (1500–2900 grains cm^{-2} yr^{-1}) in the lowermost part of the zone. Conifer pollen is present but the accumulation rates are still low, e.g. the pollen accumulation rate of *Picea* is less than 150 grains cm^{-2} yr^{-1}. Pollen accumulation rate for *Betula* varies between 500 and 2000 grains cm^{-2} yr^{-1}. *Juniperus* and *Salix* have maximum pollen accumulation rates in this zone.

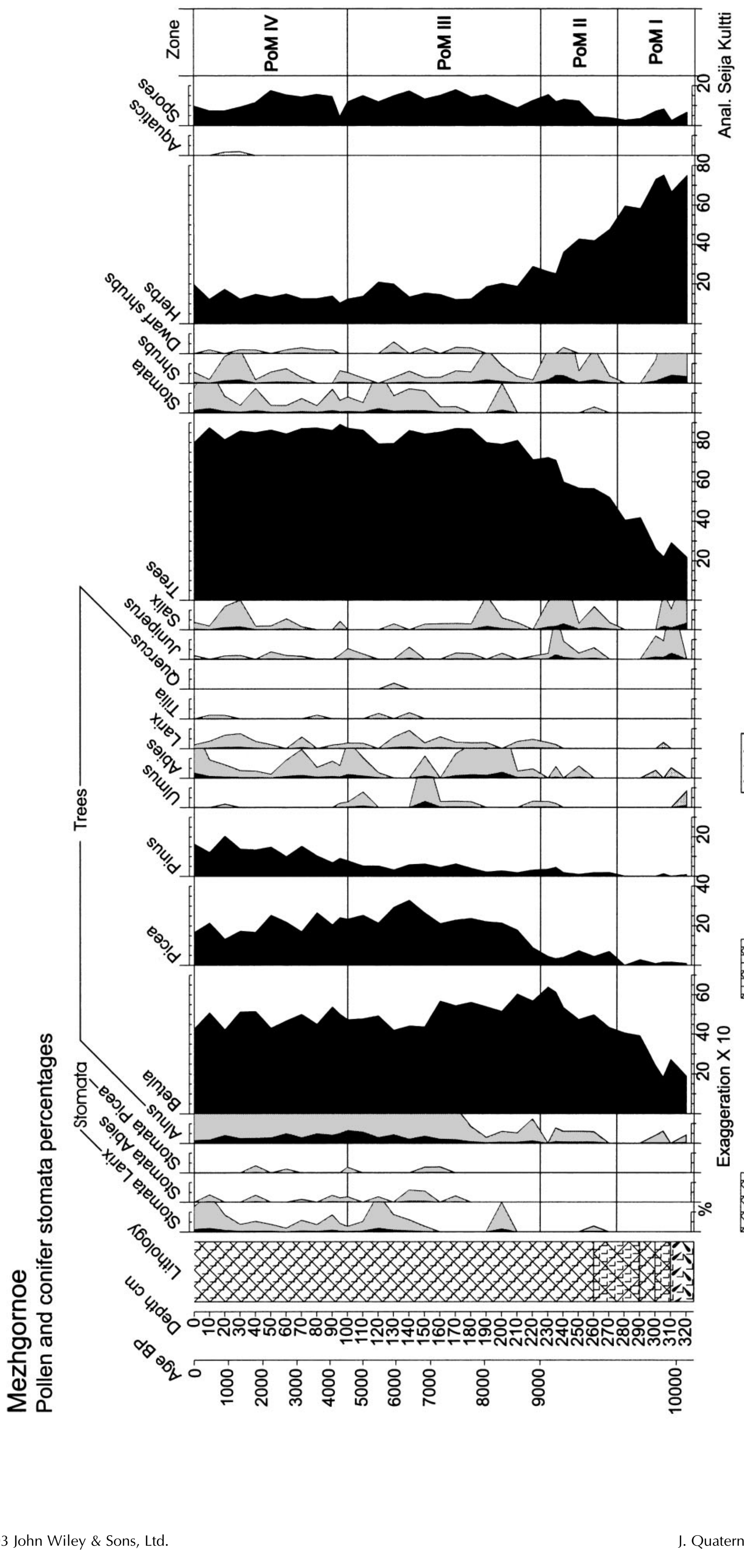
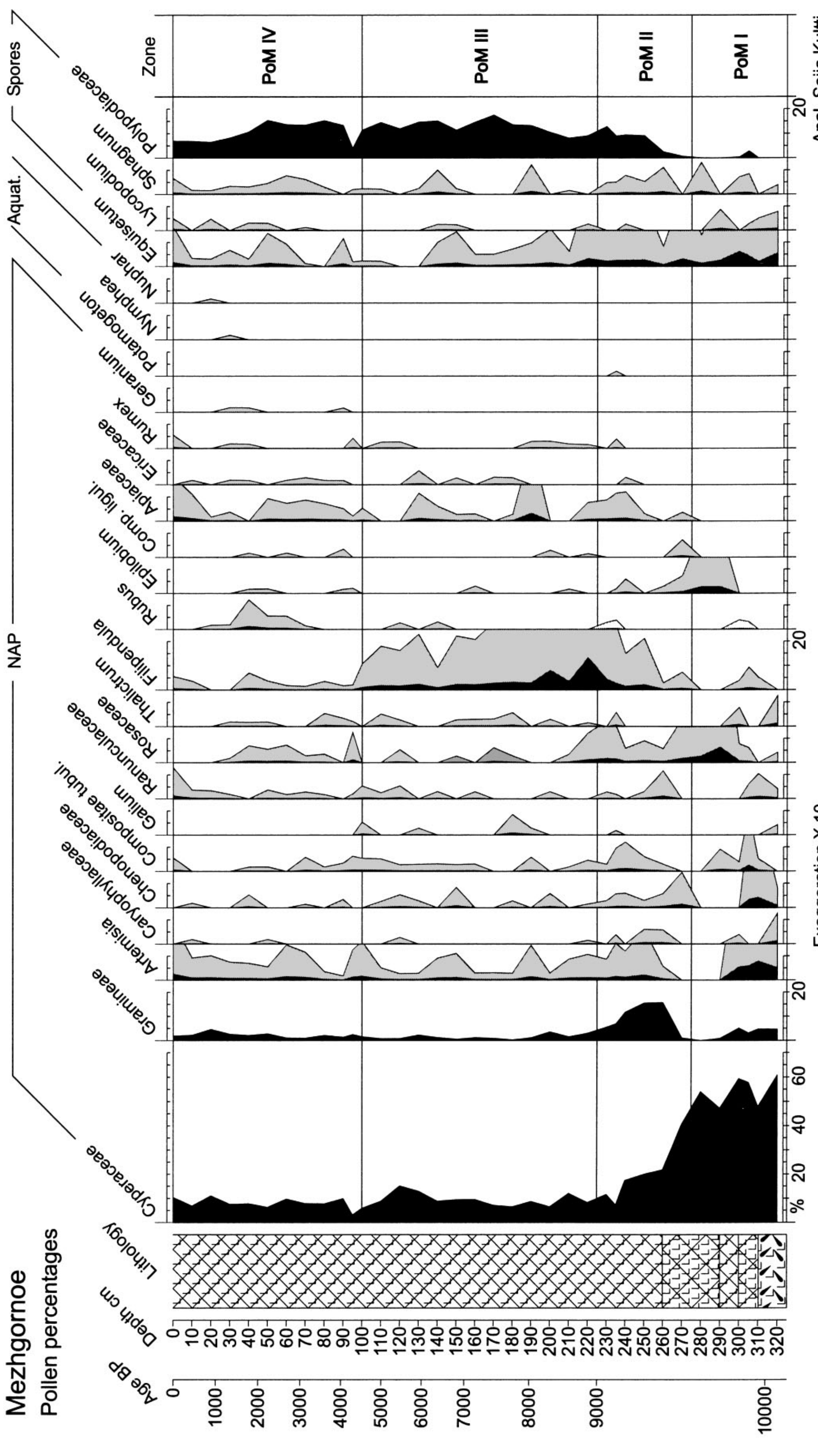


Figure 6 Relative pollen and conifer stomata diagrams from Lake Mezhgornoe, northeast European Russia. (A) Stomata and pollen curves for trees and shrubs. (B) Non-arboreal pollen (NAP), aquatic pollen and spores



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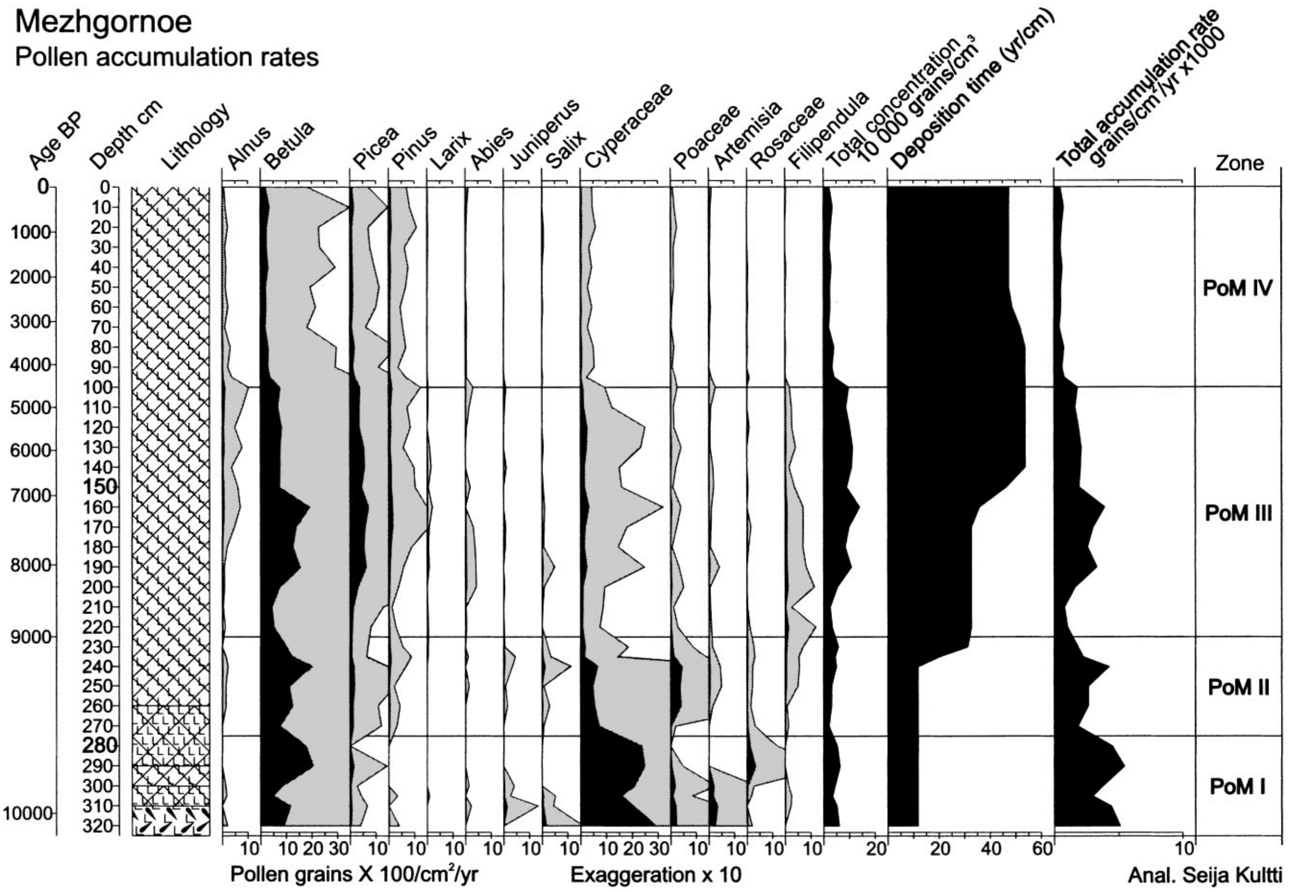

Figure 7 Pollen accumulation rates of selected taxa and total pollen concentrations from Lake Mezhgornoe, northeast European Russia. Sediment symbols as in Fig. 6A

MaM I. Fragments of mosses, leaves and stems dominate the lowermost 40 cm. Frequent *Betula* seeds were found, and they represent both tree and dwarf birch types. Seeds of *Carex* are quite abundant in this zone. Tissues of Cyperaceae, *Equisetum* and *Eriophorum* were found. In addition some seeds of herbs, such as *Potentilla palustris, Primula stricta* type, *Rorippa cf. palustris* and *Ranunculus acris* type were found.

The pollen and macrofossil flora indicates light-demanding vegetation containing birch (including tree birch), juniper, willow and herbs such as *Artemisia, Primula*, Rosaceae and grasses. Conifers were probably absent from the area, as pollen accumulation rates of conifers are low and conifer stomata and needles are absent (Clayden *et al.*, 1996, 1997; Hansen *et al.*, 1996). The high abundance of *Carex* and *Betula* seeds suggests a proximal source for the seeds. Probably the coring point was near to the shoreline at the beginning of the Holocene. The moss and herb species indicate nutrient rich (meso/eutrophic) and moist growing conditions (Eurola *et al.*, 1992).

PoM II (275–225 cm; 9600–9000 yr BP; 10 900–10 000 cal. yr BP). *Betula* and Gramineae reach percentage maxima. The first *Larix* stomata appear at the lower boundary of the zone. Conifer pollen occurs at relatively low proportions. The upper boundary of the zone is defined by an increase in *Picea*. The continuous record of *Abies* pollen begins. The relative proportion of tree pollen increases from 50% to 70%. Accumulation rates of *Picea* pollen are around 150 grains $\mathrm{cm^{-2}\,yr^{-1}}$. *Betula* pollen accumulation rates rise up to 2000 grains $\mathrm{cm^{-2}\,yr^{-1}}$ and Gramineae up to 450 grains $\mathrm{cm^{-2}\,yr^{-1}}$. However, these values may be affected by the change in the age–depth model at 233–235 cm. Parallel changes in the pollen accumulation and sedimentation rates are not necessarily signs of changing vegetation if pollen percentages and concentrations do not change at the same time (Birks, 1981; Davis *et al.*, 1984). Total pollen concentration rises from 22 000 grains $\mathrm{cm^{-3}}$ to 60 000 grains $\mathrm{cm^{-3}}$.

MaM II. Aquatic plants, such as *Potamogeton, Callitriche* and *Nuphar*, dominate the zone. *Characeae* oospores appear in the sediment. *Carex* seeds are still present throughout the zone. At the end of the zone, conifer needles (first *Abies* and then *Picea*) appear.

The record indicates immigration of the conifer forest to the catchment area during this zone. The presence of *Larix* stomata indicates that larch was growing in the catchment area, probably as the first conifer species. The needles of Siberian fir and spruce indicate the presence of these species in the upper part of the zone. However, if the PoM II percentages and accumulation rates of *Picea* and *Abies* are compared with those of the uppermost pollen sample (reflecting the modern tree-line vegetation where Siberian fir is rare and spruce absent) where these values are rather high, it is possible that only sporadic spruce and Siberian fir trees grew in the catchment. The main components of the vegetation were birch and larch. The field and ground layers were most likely composed of willow, juniper, grasses and herbs, such as *Filipendula*. The substantial proportion of aquatic plants in the macrofossil record suggests that the lake-level had risen compared with the previous zone and suitable habitats were available for aquatic plants near the coring site.

PoM III (225–100 cm; 9000–4500 yr BP; 10 000–5000 cal. yr BP). The zone is characterised by high percentages of *Betula* and *Picea* and maximum total pollen concentrations and accumulation rates. Conifer stomata are present in most of the samples. At the lower boundary of the zone *Filipendula* reaches a maximum. The proportion of *Picea* rises to ca. 20% at 200 cm, and its pollen accumulation rate remains between 300 and 700

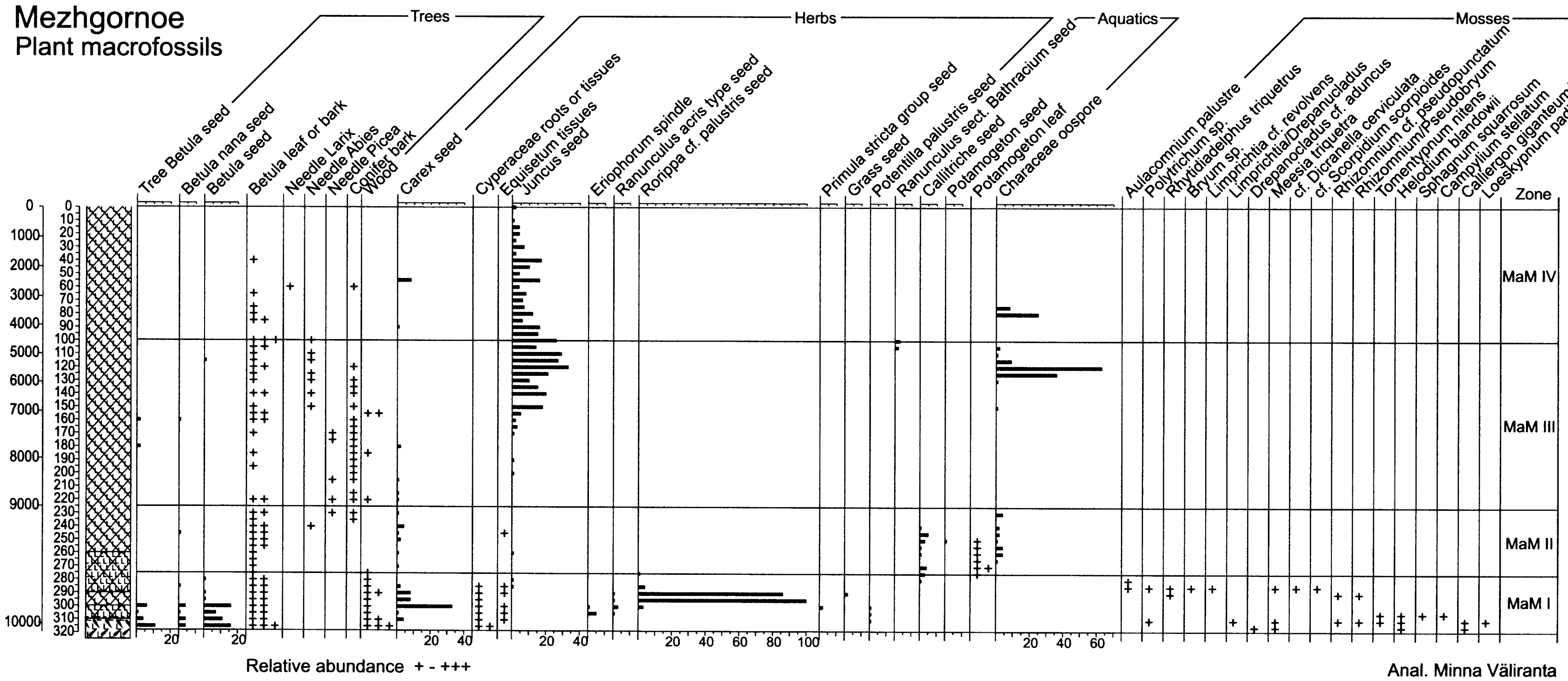

Figure 8 Plant macrofossils from Lake Mezhgornoe, northeast European Russia. The results are shown as concentrations per 20 cm^3 sediment. Bars indicate exact number of finds. Relative abundance is signified as + rare, + + occasional and + + + abundant. Sediment symbols as in Fig. 6A

grains cm^{-2} yr^{-1} until the end of this zone. *Abies* stomata start to appear in the upper part of the zone and they are subsequently present throughout the core.

MaM III. Most of the conifer remains were found within this zone. Remains consist of conifer bark, needles and stomata of *Picea* (lower part) and *Abies* (upper part). Some *Betula* seeds were also found. Remains of aquatic plants, except Characeae, were absent. *Juncus* and *Characeae* become more abundant towards the end of the zone.

The zone apparently represents the time of maximum forest density and tree species diversity. Pollen and macrofossil evidence indicate mixed spruce forest in the catchment area. Although macrofossil remains of *Picea* disappear from the record at 170 cm, some stomata were still observed in pollen slides until the end of the zone. Pollen percentages and accumulation rates, together with stomata evidence, indicate that the local mixed mountain taiga prevailed in the area until the end of the zone. Forest was composed of spruce, birch, Siberian fir, larch, and probably some alder in the last half of the zone, resembling most likely the modern mixed mountain taiga vegetation in the Vangyr Mire area. The ground vegetation consisted prominantly of *Filipendula*, Polypodiaceae, Cyperaceae and Gramineae. Light-demanding shrubs no longer played an important role. According to pollen accumulation rates the amount of spruce in the catchment area was at its maximum between 200 and 100 cm (ca. 8300–4500 yr BP). The accumulation rates are twice or even four times higher than in sections below and above, so uncertainty in the age–depth model does not have any significant effect on this interpretation. The occurrence of *Picea* needles suggests that spruce already grew abundantly in the vicinity of the lake between 9000 and 7000 yr BP. Based on finds of stomata and macrofossils, the proportion of Siberian fir and larch was probably higher between 7000 and 4500 yr BP than during the early Holocene. The total absence of aquatic plants in the lower part of the zone suggests higher lake-levels than in the previous zone, but *Juncus* in the upper part of the zone suggests a subsequent slight decrease in the lake-level.

PoM IV (100–0 cm; 4500 yr BP to present; 5000 cal. yr BP to present). *Betula, Picea* and *Pinus* pollen dominate. The relative proportion of *Pinus* rises at the lower boundary of the zone. Stomata of *Larix* are abundant throughout the zone. The last stomata of *Picea* are found at 40 cm. The total concentration decreases at the lower boundary of the zone. The pollen accumulation rates of *Picea* decrease gradually, reaching ca. 60 grains cm^{-2} yr^{-1} in the middle and upper part of the zone. *Betula* pollen accumulation rates also decrease at the lower boundary of the zone to between 200 and 300 grains cm^{-2} yr^{-1}.

MaM IV. Macrofossils are very scarce in this zone. Remains of conifers, *Larix* and unidentified conifer bark are found in only one sample. The most characteristic plant remains in this zone are *Juncus* and some Characeae.

The higher *Pinus* pollen percentages are probably a result of the decreased amount of birch and spruce pollen in this zone. The accumulation rates of *Pinus* remain relatively constant, suggesting long-distance transport of its pollen and the absence of Scots pine in the catchment area. The fact that spruce stomata were still present despite the decrease in pollen accumulation rates suggests that the withdrawal of the spruce forest was gradual rather than abrupt. The *Picea* pollen accumulation rates reach the present values at ca. 70 cm, ca. 3200–3100 yr BP, and the last stomata of spruce were found at 40 cm (ca. 1800 yr BP). Spruce was probably present only as individual trees. Today, spruce is found only at lower altitudes. The last stomata of *Abies* were found at 10 cm. Presently, only a few individuals of Siberian fir are growing in the catchment area. The abundant stomata of *Larix* indicate larch-dominated forest in the study site. The concentrations of *Juncus* seeds decrease towards the uppermost sediment, suggesting a slightly higher water-level.

Cladocera

The three lowermost samples (Fig. 9) (332.5–302.5 cm) contained so few cladoceran remains that it was not possible to produce reliable percentage calculations. Four faunal assemblage zones were determined for the rest of the sequence on the basis of analytical interpretation.

ClM I (292.5–242.5 cm; 9800–9300 yr BP; 11 100–10 500 cal. yr BP). At the beginning of the zone a littoral fauna (mainly *Chydorus sphaericus* s.l.) dominates. *Bosmina longirostris* rises to a prominent maximum and *Daphnia* increases. *Bosmina* (*Eubosmina*) appears.

The very low concentration of cladoceran remains in the lowermost samples (322.5–302.5 cm) indicates that the conditions at the coring site were not favourable for Cladocera. When conditions altered, *Chydorus sphaericus* s.l., a common pioneer species, became dominant. According to the dominance of littoral species the water-level was very low at first (cf. Alhonen, 1970; Sarmaja-Korjonen and Alhonen, 1999; Sarmaja-Korjonen and Hyvärinen, 1999; Sarmaja-Korjonen, 2001) and then slowly rose, indicated by the appearance of planktonic *Daphnia* and *Bosmina* (*Eubosmina*). *Bosmina longirostris* and *Chydorus sphaericus* are also indicators of eutrophy (Szeroczyńska, 1998), suggesting that the trophic state was relatively high.

ClM II (242.5–182.5 cm; 9300–7800 yr BP; 10 500–8700 cal. yr BP). *Bosmina* (*Eubosmina*) rises to a prominent maximum and replaces *B. longirostris*, which disappears. *Daphnia* decreases and subsequently occurs only sporadically. At the lower boundary of the zone *Leydigia leydigi* and *Alona affinis* increase. *Alona* sp. and *Chydorus sphaericus* s.l. are still the dominant chydorids.

The increase in *Eubosmina* suggests that the open water body increased and the lake-level rose. It is possible that the disappearance of *Bosmina longirostris* and the decrease in *Daphnia* reflect a change in the predation relationships in the new lake. The presence of *Leydigia leydigi*, according to Mäemets (1961), indicates meso- or eutrophic conditions. It is a profundal form (Mäemets, 1961), which is in agreement with the rising water-level.

ClM III (182.5–32.5 cm; 7800–1400 yr BP; 8700–1500 cal. yr BP). At the lower boundary *Alona affinis* suddenly becomes dominant. *Chydorus sphaericus* s.l. decreases and *Leydigia leydigi* disappears. *Alonella excisa* appears. *Bosmina* (*Eubosmina*) is the dominant planktonic taxon and has a minimum at 165–75 cm, increasing again towards the upper boundary.

The decrease in *Eubosmina* and its minimum possibly reflects a lower water level but, more likely, an increase in littoral forms, e.g. *Alona affinis*, in the basic sum of percentage calculations. There is no direct evidence of the cause of the considerable change in the littoral cladoceran assemblages. However, the almost contemporaneous shift in the diatom abundances (see below) suggests that there was a change in water chemistry. This change may have been caused by the lowering water-level, which also changed the feeding habitats of littoral Cladocera, i.e. the macrophytic composition, demonstrated by, for instance, the secceeding increase in *Juncus* seeds and the Characeae maximum (Fig. 8). It is also possible that the decrease in diatom-inferred pH (see below) was involved in the disappearance of *Leydigia leydigi* and the appearance of *Alonella excisa*.

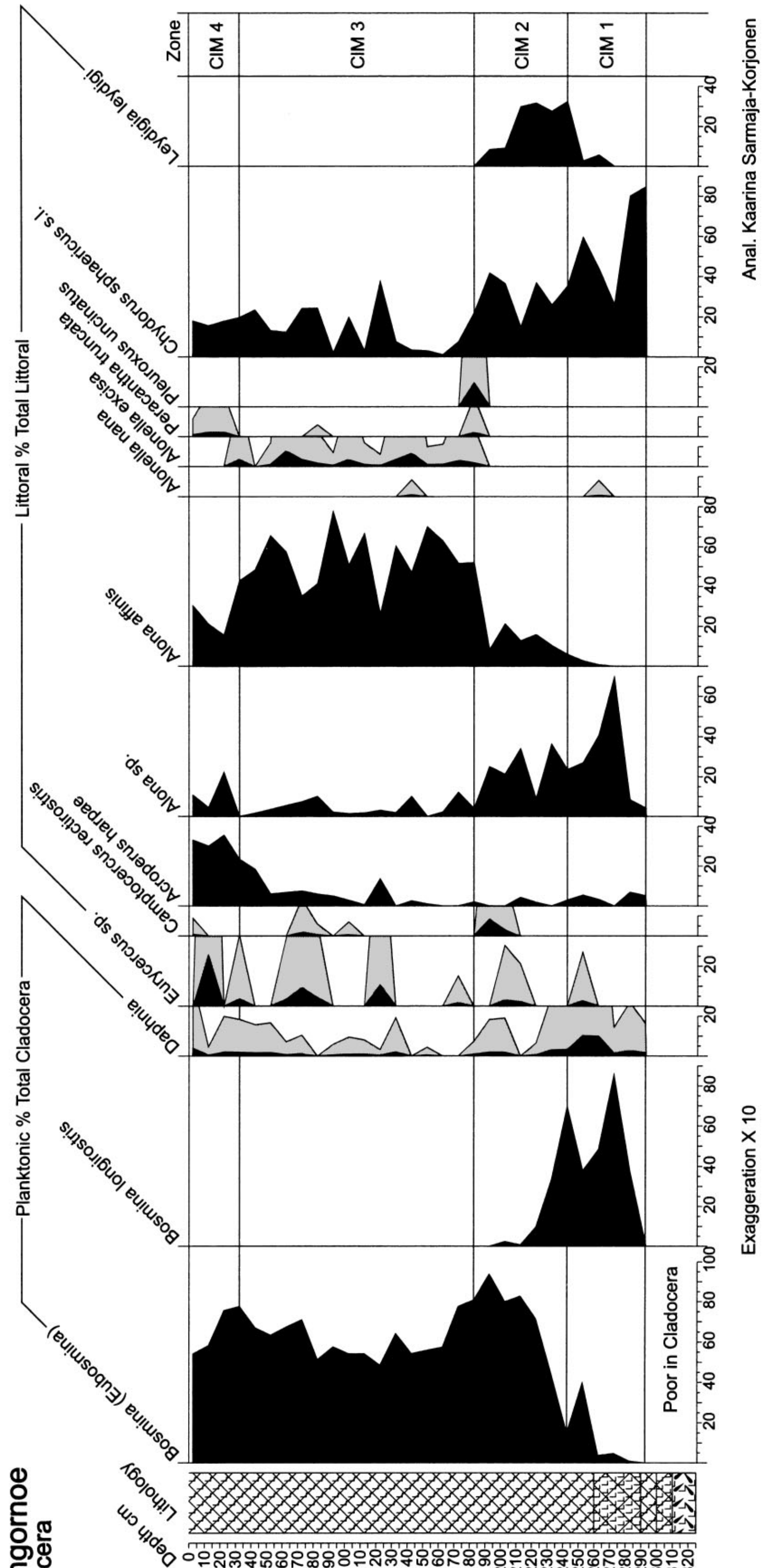

Figure 9 Relative Cladoceran diagram from Lake Mezhgornoe, northeast European Russia. As there were large variations between the quantities of planktonic and littoral Cladocera, representing these two different habitats, the percentages for littoral forms were calculated as the basic sum of total littoral Cladocera. Thus a more reliable general picture of their succession within the littoral zone was obtained. Sediment symbols as in Fig. 6A

ClM IV (32.5–2.5 cm; 1400 yr BP to present; 1500 yr BP to present). *Acroperus harpae* increases and *Alona affinis* decreases at the lower boundary of the zone. The chydorid assemblage (*Acroperus harpae, A. affinis, Chydorus sphaericus s.l.*) is typical for cold climates at high altitudes (Lotter *et al.*, 1997; Hofmann, 2000).

Diatoms

A total of 108 diatom species were identified. Three diatom assemblage zones (DiM) were distinguished based on the observed changes in species assemblages (Fig. 10). The diatom assemblages in the entire core are totally dominated by small benthic alkaliphilous *Fragilaria* and *Navicula* taxa. These species are common in alkaline tundra lakes from the Ural region (e.g. Stenin, 1972; Getsen *et al.*, 1994). *Fragilaria* taxa also; often occur in the cold-climate 'disturbed' conditions characteristic of Arctic and early post-glacial environments (e.g. Smol, 1988; Laing *et al.*, 1999).

DiM I (320–290 cm; 10 000–9800 yr BP; 11 400–11 100 cal. yr BP). This zone features the lowest diatom concentration (not plotted) and the presence of several taxa that may be of terrestrial origin (e.g. *Pinnularia ignobilis, Diatoma vulgare*). The sediment contains many broken diatom frustules. *Fragilaria* taxa (e.g. *F. pinnata, F. brevistriata, F. elliptica*) are the most abundant species. The relative abundance of diatom taxa that prefer higher nutrient concentrations increases by the end of the zone, resulting in an increase of the inferred total phosphorous (TP). Inferred pH also gradually increases to 7.8.

The occurrence of several terrestrial diatom taxa and the low diatom concentration (not plotted) implies that the lake was shallow. The section between 320 and 290 cm is minerogenic, suggesting high erosion and input from the catchment. It is, therefore, possible that *Eunotia* and *Pinnularia* taxa entered the lake sediment with the run-off from the shores. The increase in reconstructed TP is mainly signalled by the increased abundance of *F. pinnata*.

DiM II (290–170 cm; 9800–7400 yr BP; 11 100–8300 cal. yr BP). Within this zone, terrestrial taxa largely disappear. The diatom assemblage is dominated by several *Fragilaria* taxa. *Navicula submuralis* occurs at its highest abundance for the whole core. The species changes suggest that pH decreased but no trend is seen in diatom abundances regarding TP requirements. The disappearance of terrestrial diatoms and the increased organic sediment content suggest increased in-lake production and possible water-level rise. The gradual increase in diatoms with low pH optima between 290 and 170 cm can be related to the leaching of basic cations from the catchment soils and base cation depletion owing to the soil and vegetation development (e.g. Jones *et al.*, 1989). The decline in diatom-inferred TP also suggests progressive leaching of nutrients from the catchment.

DiM III (170–0 cm; 7400 yr BP to present; 8300 cal. yr BP to present). The sharp increase in the relative abundance of *F. elliptica* and *F. pseudoconstruens* and the decline in *F. pinnata* and *F. brevistriata* are the main features of the zone. *Navicula minima, N. seminulum* and *N. radiosa* increase. The diatom-inferred lake-water characteristics remain stable throughout the zone.

Supplementary pollen record from Vangyr Mire

The pollen stratigraphy (Fig. 11) of Vangyr Mire is divided into three local pollen assemblage zones. The pollen zonation is based on the changes in conifer pollen proportions. Only percentages of selected taxa are presented here.

VM I (400–262.5 cm; 8000–5600 yr BP; 8700–6300 cal. yr BP). The zone is characterised by high percentages of *Picea* pollen, typically ca. 30–50%. At the beginning of peat accumulation, Cyperaceae, *Menyanthes*, Rosaceae and *Potentilla* are also abundant. *Betula* pollen has an average percentage of 50% throughout the peat section.

At the bottom of the mire high proportions of Cyperaceae, *Menyanthes* and *Potentilla* probably reflect a local succession during the onset of mire development. Pollen evidence indicates mixed spruce–birch forest in the area.

VM II (262.5–117.5 cm; 5600–2600 yr BP; 6300–2700 cal. yr BP). Percentages of *Picea* (average ca. 25%) are slightly lower than in the previous zone. *Abies* is present in most of the samples in small quantities. Pollen of *Larix* is found in six samples.

The reduced proportion of spruce, increased percentages of Siberian fir and the first finds of larch suggest that the forest zones (Fig. 4) moved downwards on the nearby mountain slopes, with subalpine forest growing nearer to the Vangyr site than in the previous zone.

VM (III 0–117.5 cm; 2600 yr BP to present; 2700 cal yr BP to present). The lower boundary of this zone is defined by an increase in *Pinus* and *Abies*. The proportion of *Picea* within the zone is ca. 20%. *Larix* is present in most of the samples.

The raised proportion of Siberian fir and larch indicates further downward movement of the forest zones. Probably some individuals of both genera were mixed within spruce and birch forest in the valley bottom, as today.

It has to be pointed out that *Abies* and *Larix* pollen grains are rare (see also Clayden *et al.*, 1996) even when these species are abundant in the forest vegetation (Table 2), as the results from uppermost samples from both Mezhgornoe and Vangyr sites show.

General discussion and conclusions

Vegetation history at the alpine tree-line

At the very beginning of the Holocene, ca. 10 000 yr BP, climate was already warm enough for tree birch to grow in the vicinity of Mezhgornoe Lake, probably forming the upper forest belt. Today, in some locations in the study area, mountain birch also grows at the tree-line formed by larch forests, and birch even replaces larch on some steep slopes or on rocky ground. The oldest date for birch megafossils from Pechora lowland is 9440 yr BP (Kremenetski *et al.*, 1998). In the early Holocene, birch is also the earliest tree to reach Fennoscandia and north European Russian lowland areas (Hyvärinen, 1975; Seppä, 1996; Barnekow, 1999; Snyder *et al.*, 2000).

The expansion of spruce to the current tree-line took place ca. 9500 yr BP. The stomata and needle records suggest that larch was the first conifer to immigrate, followed by Siberian fir and spruce. At present, these species grow in the same order along the altitudinal gradient (Fig. 4). According to Surova *et al.* (1975) spruce was already growing in the polar Urals ca. 200 km northeast of Mezhgornoe Lake at the beginning of the Holocene and it reached the Barents Sea coastline at ca. 8500 yr BP, at the latest (Kremenetski *et al.*, 1998). This evidence suggests that expansion of spruce occurred very rapidly and contemporaneously in large areas of the Ural Mountains. In the Pechora lowland, at Ortino, spruce expanded north of its present position as early as 9000 yr BP (Kaakinen and Eronen,

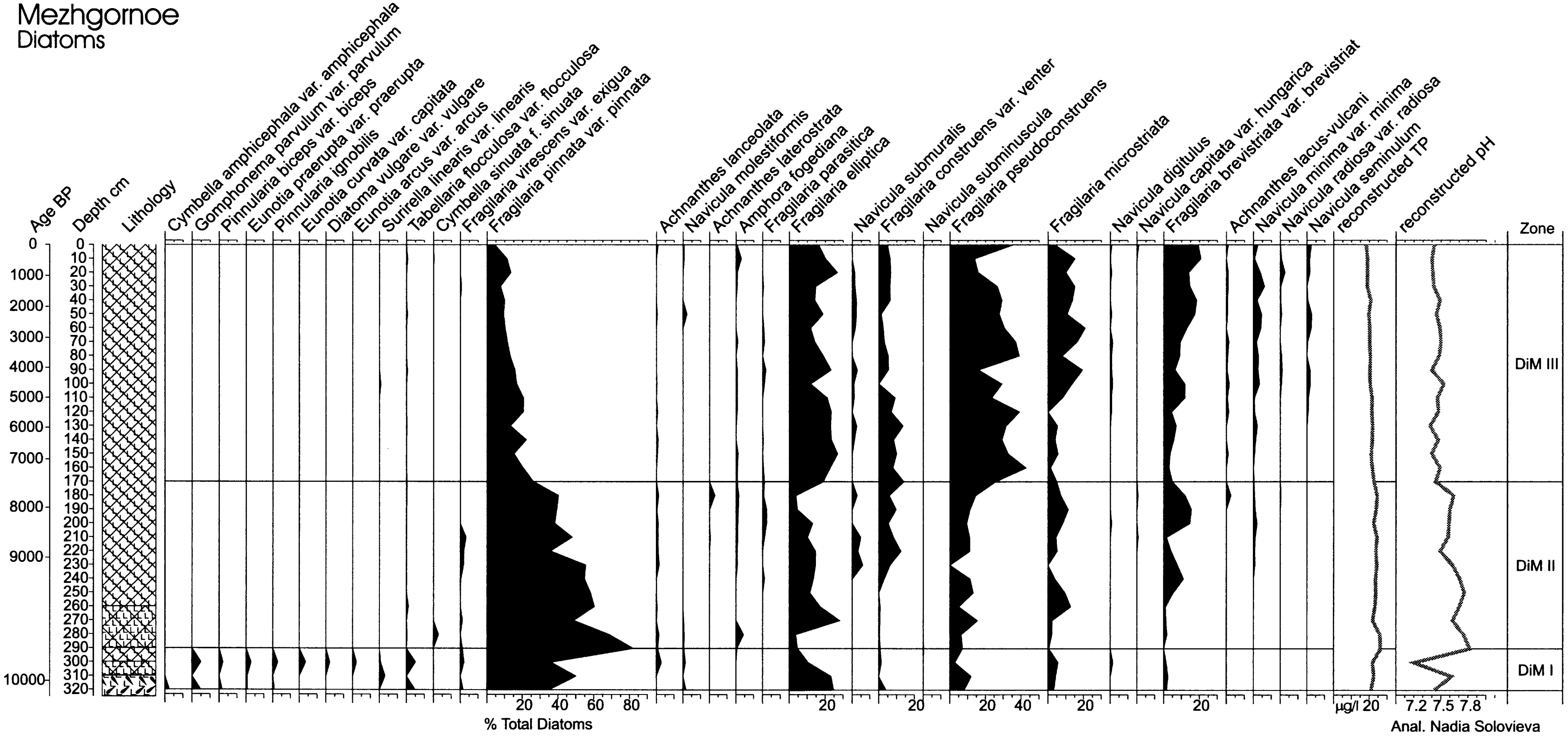

Figure 10 Relative diatom diagram from Lake Mezhgornoe, northeast European Russia, with taxa at abundance > 3%. Sediment symbols as in Fig. 6A

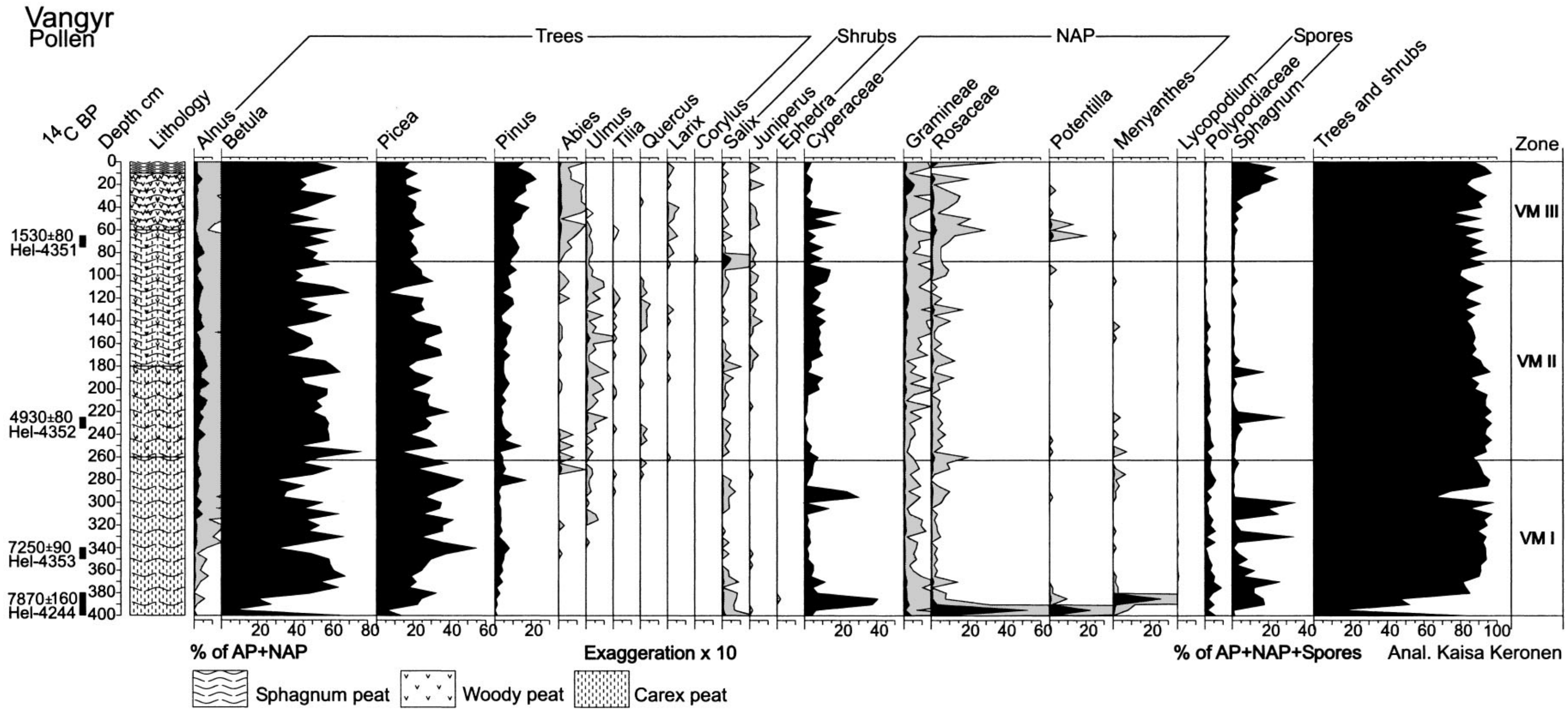

Figure 11 Relative pollen diagram of selected taxa from Vangyr Mire, northeast European Russia

2001). The present data suggest that spruce reached the present alpine conifer tree-line at least 500 yr earlier than the present arctic tree-line. However, even though spruce is able to immigrate rapidly following a climatic warming, there was a time lag between the first scattered immigrants and the development of dense spruce forest.

At Mezhgornoe Lake the phase of mixed conifer forest lasted until ca. 5500–4500 yr BP. The highest density of dated tree megafossils in northern Russia occurs between 9000 and 7500 yr BP (Kremenetski *et al.*, 1998; MacDonald *et al.*, 2000), at the same time as the *Picea* needles were found in the Mezhgornoe Lake sediment. A maximum in spruce forest density occurred in the polar Ural Mountains between 8000 and 4500 yr BP (Surova *et al.*, 1975), which corresponds well with the present results. The increased proportion of *Abies* pollen between 160 and 100 cm (7000–4500 yr BP) suggests that the forest was composed mainly of Siberian fir mixed with spruce. This implies lowering of the altitudinal vegetation belts (Fig. 4). The larch tree-line forest was established in the Mezhgornoe Lake area during the late Holocene. Increasing proportions of *Abies* and *Larix* pollen in the the Vangyr Mire record also corroborates a gradual altitudinal lowering of the forest belts after ca. 5500 yr BP.

Lake-level changes in Lake Mezhgornoe

The results suggest a low water-level or even a limnotelmatic contact at the coring point in the beginning of the Holocene. The sediment is minerogenic (loss-on-ignition is 6%) and the organic matter consists mainly of remains of terrestrial mosses, *Betula* and *Carex* seeds, together with *Equisetum* and herbs of moist environments. The low concentration of Cladocera and diatoms, as well as the occurrence of many broken diatom frustules and the presence of terrestrial diatom taxa also point to a low water-level or even temporarily dry conditions. Probably the trophic state was relatively high, as indicated by the moss and herb species found in the samples and by the rising inferred TP.

Apparently, the water-level started to rise ca. 9500 yr BP. Aquatic macrofossils and Cladocera thriving in eutrophic lakes (*Bosmina longirostris* and *Chydorus sphaericus*) suggest a littoral environment at the coring point. The relatively high trophic state is also shown by the inferred TP.

The disappearance of aquatic plant remains, together with an increase in planktonic *Bosmina (Eubosmina)* at 230 cm (ca. 9000 yr BP) suggest a further rise in the water-level at the coring point. The data therefore show a typical succession from a telmatic/shore environment, through a low-water littoral area towards pelagic conditions. The *Bosmina (Eubosmina)* maximum lasts until 170 cm (ca. 7500 yr BP), but on the basis of the present results it remains unclear if a drier period followed.

Inferred climate

As tree birch had already established in the Mezhgornoe lake area at the onset of the Holocene at higher altitudes than today, the climate was at least as warm as today. Mixed mountain taiga was established locally at ca. 9500–9000 yr BP. On the basis of the modern climate and forest limits, this indicates that summer temperatures at that time must have been at least 2°C higher than today, but probably even higher, because the middle Holocene vegetation suggests a slight cooling to temperatures at least 2°C warmer than today (see below).

These results support earlier studies that suggest an early Holocene summer thermal maximum in northern Russia. The finds of *Typha latifolia* in the western Pechora basin indicate a regional thermal optimum before 8200 cal. yr BP (Paus, 2000). The same is shown by the maximum density of tree birch megafossils ca. 9000–8000 yr BP, found in the Barents Sea coast (Kremenetski *et al.*, 1998; MacDonald *et al.*, 2000). Pollen studies in Novaya Zemlya (Serebryanny *et al.*, 1998) indicate amelioration of climate at the onset of the Holocene. A chironomid record from the Lena River area suggests warmer temperatures than today between 10 000 and 6000 yr BP (Porinchu and Cwynar, 2002). According to MacDonald *et al.* (2000) summer temperatures in the Pechora region were ca. 4°C warmer than today between ca. 9000 and 4000 yr BP.

Evidence of the early Holocene climatic optimum in the Arctic regions has also been found in Canada (Ritchie *et al.*, 1983; Pellatt *et al.*, 1998) and in the Scandes Mountains (Kullman and Kjällgren, 2000). However, most of the results from northern Fennoscandia and the Kola peninsula suggest a relatively cool early Holocene (Korhola *et al.*, 2000; MacDonald *et al.*, 2000; Seppä and Birks, 2001; Gervais *et al.*, 2002). This may be explained by the North Atlantic ocean–atmosphere circulation system that influenced the climate prevailing in Fennoscandia and Kola Peninsula.

The early Holocene thermal maximum in northern Russia probably can be explained as follows. According to Milankovich theory summer insolation was at its highest at the onset of the Holocene (COHMAP Members, 1988). Glacio-eustatic sea-level rise enabled warm North Atlantic and Pacific waters to penetrate the Arctic at the beginning of the Holocene. In addition, the decreased albedo as a result of the reduced sea-ice cover (Koç *et al.*, 1993; deVernal and Hillaire-Marcel, 2000; Lubinski *et al.*, 2001; Ivanova *et al.*, 2002), as well as the expansion of evergreen forests over the former tundra, had a positive feedback on the warming climate.

The vegetation at Mezhgornoe Lake (550 m a.s.l.) during the middle Holocene (7000–4500 yr BP) resembles the present vegetation at Vangyr Mire (300 m a.s.l.). This suggests summer temperatures at least 2°C warmer than today during the middle Holocene. Siberian fir and larch became prominent in the mixed mountain taiga, suggesting a slight cooling compared with the previous period. Kremenetski *et al.* (1998) and McDonald *et al.* (2000) reached similar conclusions from studies of tree megafossils on the Barents Sea coast.

The withdrawal of the mixed mountain taiga starting at ca. 5500–4500 yr BP reflects gradually cooling conditions towards the late Holocene when the establishment of larch forest took place at the alpine tree-line at Mezghornoe Lake. It is difficult to establish an exact chronology for this period owing to uncertainties in the dates (see above). The data show no indication of the medieval warm period or the Little Ice Age in the area. The low temporal resolution of the study may be responsible for this.

The biostratigraphy of Mezhgornoe Lake suggests that soon after the Pleistocene–Holocene transition moisture increased and lake development began. At first, the rise of lake-level was rather slow, but between 9500 and 7500 yr BP the region experienced high effective moisture conditions when precipitation must have exceeded evaporation.

To conclude, our results from the pre-Polar Urals show an early Holocene warming, as is the case in many other studies from Arctic regions. Trees seem to appear earlier at the alpine tree-line than at the arctic tree-line in the lowlands. The hypsithermal phase lasted until ca. 5500–4500 yr BP. Lake-level changes suggest a moist early Holocene until ca. 7500 yr BP.

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