

Holocene tree line, permafrost, and climate dynamics in the Nenets Region, East European Arctic

Seija Kultti, Pirita Oksanen, and Minna Väliranta

Abstract: Pollen, stomata, and macrofossils in a lake core with a basal date of 9700 ¹⁴C BP were used to reconstruct past changes in climate and vegetation in the arctic tree line area, northeast European Russia. A peat profile was investigated to establish a chronology of mire initiation and permafrost development during the Holocene. Macrofossils show that tree birch was present in the study area at the beginning of the Holocene and stands of spruce became established shortly thereafter. However, pollen evidence suggests that almost 400 years passed before the area was occupied by a mixed spruce–birch forest, which lasted until ca. 5000 BP. Subsequently, the area reverted to forest–tundra. Paludification began ca. 9000 BP continuing at least until 5700 BP. The conditions were permafrost-free at least until 4500 BP. The latest permafrost aggradation phase is dated to the Little Ice Age. We interpret summer temperatures to have been ca. 3–4 °C higher between ca. 8900 and 5500 BP than at present, and the lowest temperature regime of the Holocene to have occurred between 2700 and 2100 BP.

Résumé : Du pollen, des stomates et des macrofossiles dans une carotte de fond de lac ayant une date de base de 9700 ¹⁴C avant le présent ont été utilisés pour reconstruire d'anciens changements dans le climat et la végétation dans la région de la ligne des arbres de l'Arctique, dans le nord-est de la Russie européenne. Un profil de tourbière à palse a été étudié pour établir une chronologie du début de la tourbière et du développement du pergélisol au cours de l'Holocène. Les macrofossiles montrent que des bouleaux étaient présents dans la région à l'étude au début de l'Holocène et que des peuplements d'épinette se sont établis peu de temps après. Toutefois, selon les évidences de pollen, il se serait écoulé environ 400 ans avant que la région ne soit occupée par une forêt mixte épinette–bouleau, laquelle a duré jusqu'à environ 5000 ans avant le présent. Par la suite, la région est redevenue une région forêt–toundra. La paludification a débuté vers 9000 ans avant le présent et a continué au moins jusqu'à 5700 ans avant le présent. Les conditions étaient libres de pergélisol au moins jusqu'à 4500 ans avant le présent. La plus récente extension de la zone de pergélisol date du Petit Âge Glaciaire. Selon nous, les températures durant l'été étaient de 3 à 4 °C plus élevées entre 8900 et 5500 ans avant le présent et les plus basses températures de l'Holocène seraient survenues entre 2700 et 2100 ans avant le présent.

[Traduit par la Rédaction]

Introduction

The circumpolar arctic is expected to experience a significant warming during the next few decades (IPCC 2001). The warming will have an effect on the location of the forest–tundra ecotone and the distribution of permafrost (Skre et al. 2002). Northward migration of forest zones in the extensive lowland areas of the Eurasian north may have a significant positive feedback on the warming climate (Foley et al. 1994; Betts 2000; Harding et al. 2002) and may cause a reduction of summer tundra pastures for reindeer herding. Thawing of permafrost could increase methane emissions and peat erosion in mires also resulting in positive feedbacks to the cli-

mate system (Gorham 1991). Permafrost collapse will affect the stability of urban, industrial, and transport infrastructure in arctic regions. Therefore, a better understanding of the amplitude and rate of vegetation and permafrost response to climate change is important.

Tree line history in the European Russian arctic has mainly been reconstructed with dated tree megafossils found north of present tree line. These megafossils indicate that birch and spruce tree lines advanced to the Barents Sea coastline between 9000 and 7000 BP and retreated to their present positions between 4000 and 3000 BP (Kremenetski et al. 1998; MacDonald et al. 2000b). However, it is difficult on the basis of mega- or macrofossils alone to discriminate

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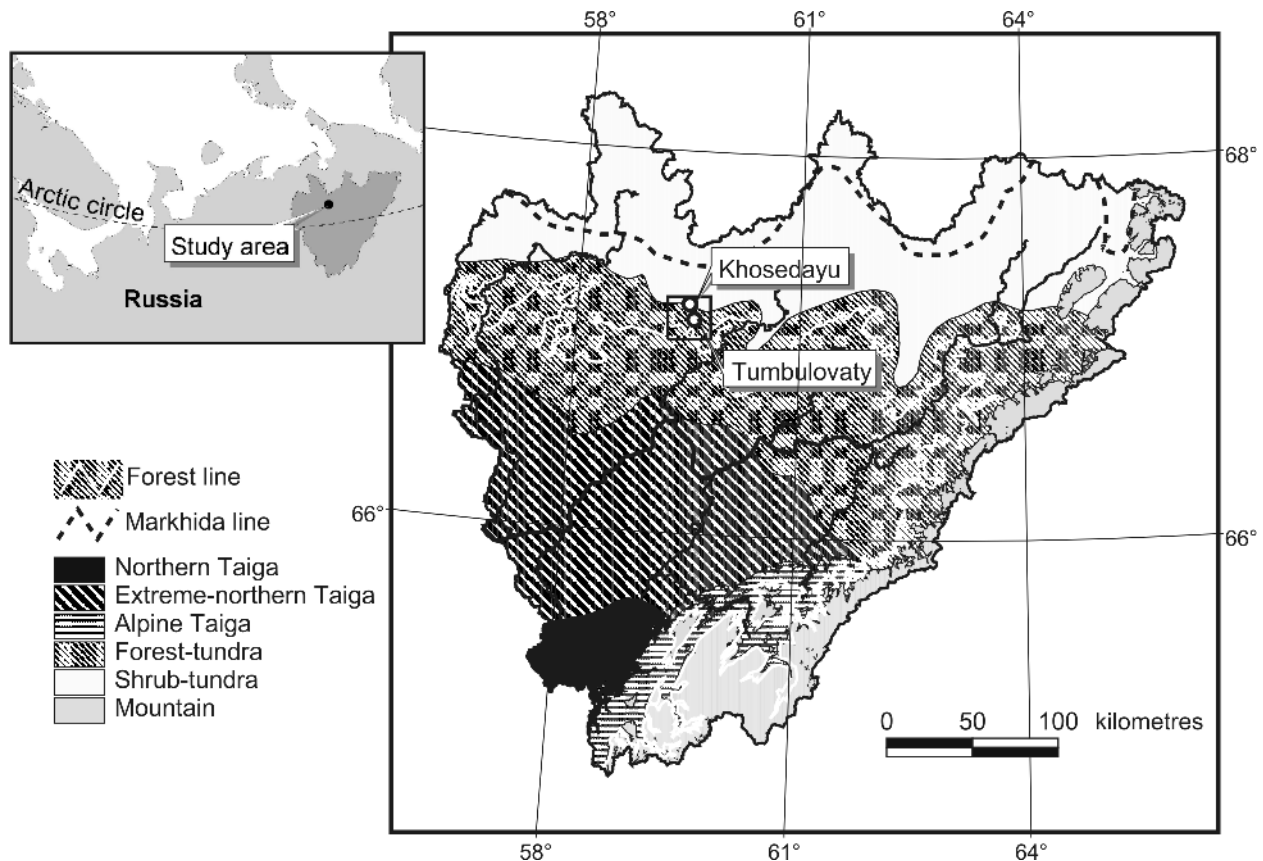
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S. Kultti¹ and M. Väliranta. Department of Geology, University of Helsinki, P.O. Box 64, Helsinki FIN-00014, Finland.
P. Oksanen². Arctic Centre, University of Lapland, P.O. Box 122, Rovaniemi FIN-96101, Finland.

¹Corresponding author (e-mail: seija.kultti@helsinki.fi).

²Present address: Department of Botany, Trinity College, Dublin 2, Ireland.

Fig. 1. Location of the study area in the Usa River basin, northeast European Russia. Morainic complexes of the Markhida line are after Mangerud et al. (1999). Vegetation zones are based on the map of the nature regions in Komi (Taskaev et al. 1996) and on vegetation classification of Virtanen et al. (2004). The forest-line was determined using satellite-image-based vegetation classification by Virtanen et al. (2004). The arctic tree line is formed by *Picea abies* and the alpine tree line by *Larix sibirica*. The study area depicted in Fig. 2 is also indicated (box on vegetation map, dot on inset map).



between forest-tundra and taiga zones (Hansen et al. 1996). The presence of individual trees can be confirmed from macrofossils but seldom from pollen data that reflect more broadly on the prevailing vegetation. Macrofossil evidence suggests that conifer tree line responded rapidly to warming climate at the beginning of the Holocene (e.g., Payette et al. 2002), but pollen evidence suggests, in many cases, that expansion of conifer forests occurred much later (e.g., Barnekow 1999; Gervais et al. 2002).

Permafrost began to aggrade in mires ca. 5000 BP in the present tundra, and ca. 3000 BP in the present forest-tundra and northern taiga (Oksanen et al. 2001; Väiranta et al. 2003; Oksanen et al. in press). The region is highly paludified (Kuhry et al. 2002), and permafrost is especially extensive in mires (Anonymous 1987). However, the permafrost history of the mires is poorly understood.

In this study, past changes in vegetation, permafrost, and climate near the present arctic tree line are inferred from pollen, stomata, macrofossil, and physico-chemical analyses in combination with radiocarbon dating. A lake core and a palsa profile are investigated in detail; additional information is presented from four other mire sites. Data on a radiocarbon-dated paleosol from the same area, published by Rusanova and Kuhry (2003), are used to assist climatic interpretation. The study area is situated both at tree line and in the transi-

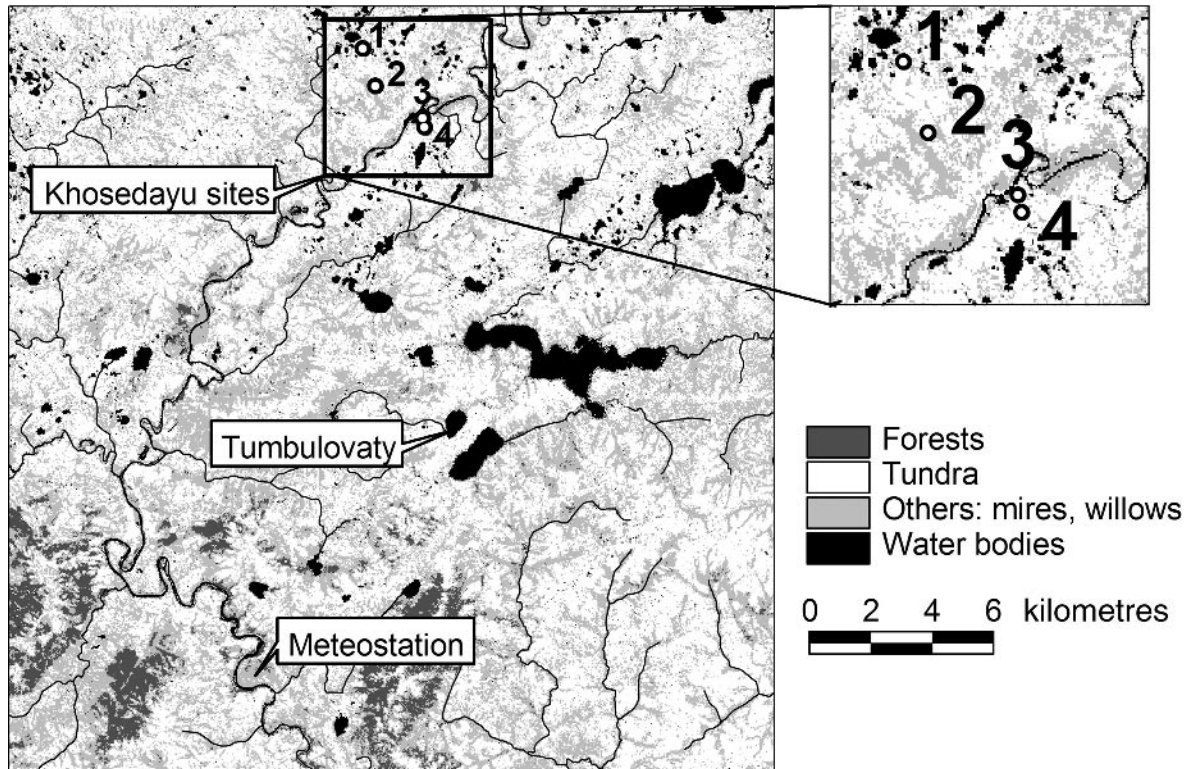
tion of the sporadic and discontinuous permafrost zones. Therefore, this sensitive area is suitable for studying past environmental changes with special emphasis on tree line and permafrost history.

Study area

The study area (Fig. 1) is situated ~50–70 km north of the Arctic Circle, in the Bol'shezemel'skaya Tundra, Nenets Autonomous District of the Arkhangelsk Region, northeast European Russia. The Bol'shezemel'skaya Tundra is bordered by the Ural Mountains in the east and by the Pechora River in the west. The region is characterized by extensive lowland, mainly varying between 80 and 150 m a.s.l. (above sea level), and by some river valleys. The study sites are near to the Khosedayu River (Fig. 2) in the Usa River drainage basin (Fig. 1). Peatlands and small lakes are abundant in the area.

According to Mangerud et al. (1999) and Svendsen et al. (1999), the area was not glaciated during the Late Weichselian (Valdai) glaciation. The Markhida Line (Fig. 1) that marks the southernmost limit of the Kara and Barents ice sheets, and is dated to Middle or Early Weichselian, is found ca. 30 km north of the area. The area is situated within the

Fig. 2. General vegetation types around the study sites based on the classification by Virtanen et al. (2004) and the meteorological station of Khoseda-Khard. Khosedayu sites: 1, peat plateau mire (KhPp); 2, tundra mire (KhTm); 3, palsa mire (KhPa, KhTp, KhFe); 4, paleosol site (Rusanova and Kuhry 2003). The lake core was collected from Lake Tumbulovaty.



Laya-Adzva lobe, which is probably of Early Weichselian or possibly Saalian age.

The study area is in the zone of widespread discontinuous permafrost, with 50%–90% of the ground permanently frozen (Oberman and Borozinetsh 1988). Permafrost is widespread in peatlands, but sporadic in mineral ground. The thickness of the active layer on palsas – peat plateaus is 30–50 cm. Some depressions between the palsas are also perennially frozen, with an active layer of 50–100 cm.

The study sites are situated in the northern part of the forest–tundra (Fig. 1). In this region, tree line coincides approximately with the 13.5 °C mean July isotherm (Virtanen et al. 2002) and with the transition zone from sporadic to widespread discontinuous permafrost (Oberman and Borozinetsh 1988).

Climate records (1961–1990) from the Khoseda Khard meteorological station (see Fig. 2 for location) show mean January and July temperatures of –21.0 °C and 13.4 °C, respectively. The mean annual temperature is –5.2 °C, and the annual precipitation is 441 mm.

The forest–tundra is a mosaic of forest, woodland, shrub, peatland, and tundra (Fig. 2). The upland plateau is generally treeless, while in sheltered river valleys spruce (*Picea abies* sl.) and some birch (*Betula pubescens*) are found. Within the forest–tundra ecotone, the proportion of forest cover varies from 60% in the south to < 3% in the north, and the canopy within the forest stands varies from 40% to 20% (Tarmo Virtanen, personal communication, 2003). The northernmost extensive forest stands are found just south of Lake Tumbulovaty (Fig. 2). North of this, only gallery forest are found along

the rivers, and individual trees on well-drained sandy upland soils, tens of kilometres further north (Lavrinenko and Lavrinenko 1999). Willow (*Salix* spp.) is abundant in river valleys and other depressions.

The forest of the extreme-northern taiga zone (Fig. 1) is composed mainly of spruce and birch, with pristine forest-stand canopy cover of 35%–60%. Pine (*Pinus sylvestris*) grows a few tens of kilometres south of the study area on peatland margins, and some stands are found on sandy soils along the shores of the western part of the Usa River.

Sediment samples were taken from Lake Tumbulovaty (67°07'N; 59°34'E; 115 m a.s.l.), which is situated on an upland plateau east of Khosedayu River (Fig. 2). The area is characterized by dwarf-shrub tundra with some peat deposits (15%). The nearest isolated spruce forest stands are found 5–6 km south of the lake, but some individual spruce trees are still found in a few locations to the north of the study area. The lake is relatively shallow, the depth varying between 1.2 m near the shoreline to 1.6 m in the middle. The sediment thickness in the middle is 2.8 m. Despite the water depth at the coring point being only 1.6 m, no signs of disturbance were detectable in the sediment. During spring in 1998 to 2000, the thickness of lake ice in the area surrounding the study sites varied between 0.8 and 1.2 m.

The primary site of interest in the study of permafrost dynamics was a small palsa mire (67°10'N; 59°30'E; 90 m a.s.l.), situated on the upper terrace of Khosedayu River (Fig. 2, site 3). The mire is treeless, but spruce grows in the nearby river valley. The biggest palsas in the mire are about 3 m high and up to 20 m in diameter. The edges of some

Table 1. Radiocarbon dates for Lake Tumbulovaty sediments and Khosedayu peat deposits.

Lab code	Dated material	Sample	$\delta^{13}\text{C}$	Age BP	Cal BP
Hel-4428	Bulk sediment	Tum 65–75 cm	–27.5	1890±130	1 850
Hela-519	<i>Betula</i> leaves, catkin scales and bark	Tum 85–90 cm	–29.8	2790±60	2 910
Hel-4429	Bulk sediment	Tum 140–150 cm	–30.8	6190±130	7 090
Hel-4430	Bulk sediment	Tum 233–243 cm	–32.4	8530±170	9 530
Hela-427	Wood in lake deposit	Tum 279 cm	–26.3	9700±125	11 170
UtC-10059	Rootlet peat	KhPa 5–10 cm	–28.0	–75±35	modern
UtC-8660	<i>Betula</i> , <i>Sphagnum</i> , <i>Carex</i> , <i>Equisetum</i>	KhPa 30–35 cm	–24.7	4570±50	5 300
UtC-8661	Wood in basal peat	KhPa 185–190 cm	–29.3	5705±40	6 490
UtC-8662	Organic mud	KhTp 4–6 cm	–28.3	1410±30	1 300
UtC-8663	Muddy sand	KhTp 64–66 cm	–27.9	160±30	190
UtC-10060	Rootlet peat	KhPp 10–14 cm	–27.3	380±30	470
UtC-8672	<i>Betula</i> twig	KhPp 52–54 cm	–29.0	4990±50	5 720
UtC-8673	<i>Betula</i> leaves and catkin scales	KhPp 194–199 cm	–29.5	8010±60	8 990
UtC-8665	Bulk peat	KhTm 154–155 cm	–30.6	9260±60	10 440

Table 2. Accumulation rates for Khosedayu peat deposits.

Profile code	Interval age (BP)	Interval age (cal BP)	Interval depth (cm)	Material type	Vertical (mm a ⁻¹)	Dry matter (g m ⁻² a ⁻¹)	Organic (g m ⁻² a ⁻¹)	Carbon ^a (g m ⁻² a ⁻¹)	Site characteristics
KhPa	0–4570	0–5300	0–32.5	Peat	0.06	16.9	14.0	6.9*	Palsa
KhPa	4570–5705	5300–6490	32.5–187.5	Peat + sand	1.22	214.2	161.5	79.3*	Treed fen
KhPp	0–380	0–470	0–12	Peat	0.27				Peat plateau
KhPp	380–4990	470–5720	12–53	Peat	0.09				Fen + palsa
KhPp	4990–8010	5720–8990	53–196.5	Peat	0.37				Fen
KhTm	0–9260	0–10440	0–154.5	Peat	0.15				Mire

^aEstimated based on KhFe.

palsas were calving into thermokarst ponds, the other side of which were overgrowing with new vegetation. Collapsing and completely collapsed palsas were observed, as well as embryonic palsas. Near to the edges of the mire, there are smaller *Sphagnum* hummocks (pounus) that are commonly frozen. In addition, some samples were taken from a peat plateau mire, situated ca. 3 km northwest of the Khosedayu palsa mire, on the dwarf-shrub tundra plateau, at 110 m a.s.l., and from a dry peat-covered tundra site, about 1 km northwest of the Khosedayu mire (Fig. 2, sites 1 and 2, respectively). The peat plateau mire was occupied by a large, level peat plateau, one side of which was calving into a thermokarst pond and the other side merged into a sandy plateau.

Materials and methods

Sampling and dating

Fieldwork was carried out in summer 1998 (Khosedayu sites) and spring 2000 (Lake Tumbulovaty). The lake and unfrozen peat cores were collected with a Russian peat corer, and the palsa and peat plateau samples were taken from exposed profiles along the edges of thermokarst ponds. The samples were packed in plastic bags and stored in a freezer after transportation.

The Lake Tumbulovaty sediment sequence was dated by three conventional (Hel-) and two AMS (accelerator mass spectrometry) (Hela-) ¹⁴C assays (Stuiver and Polach 1977) at the Dating Laboratory of the University of Helsinki, Finland.

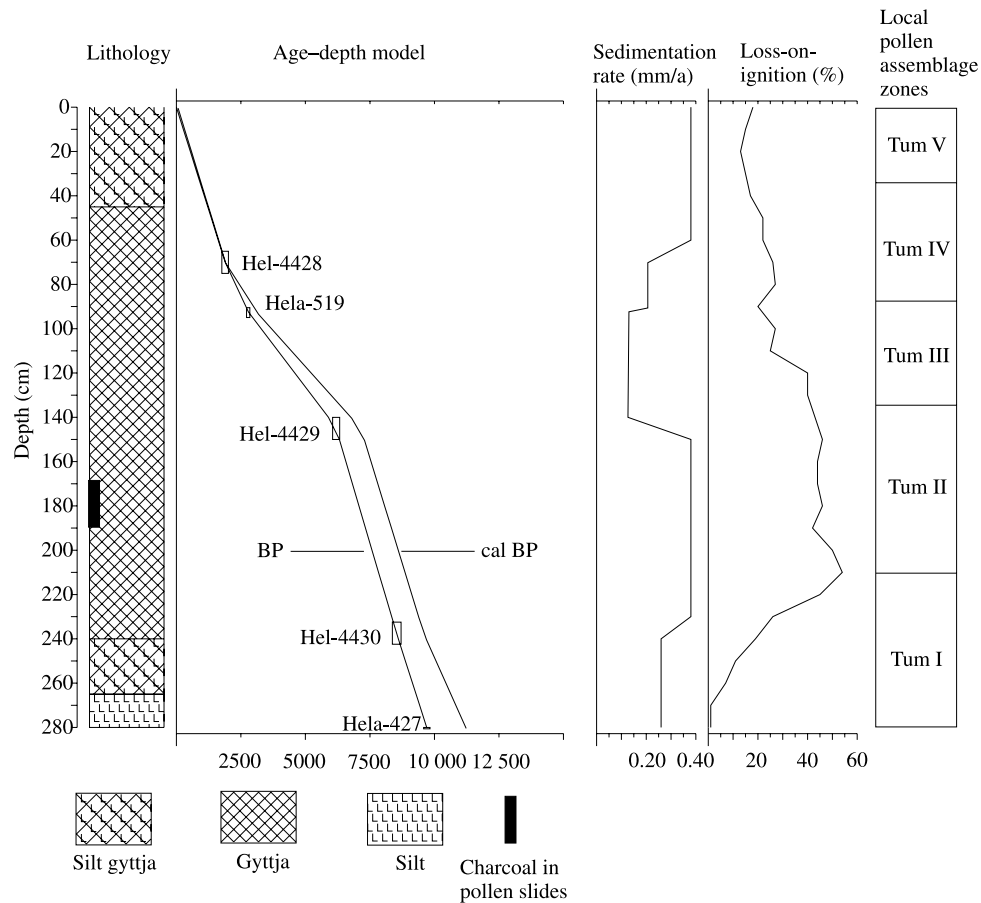
The peatland sites were dated by the AMS method at the Faculty of Science, University of Utrecht, The Netherlands (Table 1). Both bulk sediment and selected terrestrial macrofossils were used for dating. The dates were calibrated using the Calib4.1-program (Stuiver and Reimer 1993); the median values of the results were used. In the text, calibrated dates are denoted as “cal BP” and uncalibrated ages as “BP.” Accumulation rates are discussed based on calibrated ages (Table 2). Approximate ages between the dated horizons were calculated using linear interpolation.

Lake sediments

The lowermost part of the 2.8 m long lake sediment sequence core (280–265 cm) consists of silt, which grades into silt-gyttja at 265 cm. Between 240 and 45 cm, the sediment is brownish gyttja. Pieces of charcoal were found between 190 and 170 cm. The uppermost 45 cm is silt-gyttja. To define the organic content, a loss-on-ignition analysis (4 h, +550 °C) was carried out at 5–10 cm intervals (Fig. 3).

In the laboratory, the core was sampled at 5–10 cm intervals, and pollen samples (10 cm intervals) were treated by standard KOH, HF, and acetolysis methods (Fægri and Iversen 1989). For estimation of pollen concentrations, two *Lycopodium* tablets (Stockmarr 1971) were added to 0.5 cm³ samples of fresh sediment. The samples were mounted in glycerol and stained with safranin. A minimum of 300 terrestrial pollen grains per sample were counted. The total pollen sum of terrestrial plants is the basic sum used for the percentage calculations. The percentages of the spores and the aquatic pollen

Fig. 3. The lithology, age–depth model, sedimentation rate, loss-on-ignition values and local pollen assemblage zones from Lake Tumulovaty, northeast European Russia.



were calculated by adding the basic sum to the sum of the spores or to the sum of the aquatics, respectively. The pollen accumulation rates were calculated using the calibrated ^{14}C -ages. Conifer stomata found in the pollen slides were identified to the genus level with the help of reference slides. Pollen nomenclature is according to Moore et al. (1991), except in *Compositae tubuliflorae* and *Compositae liguliflorae*.

For plant macrofossil analysis, volumetric samples (30–50 cm³) were taken at 5 cm intervals. The sediment was then soaked in sodium pyrophosphate ($\text{Na}_4\text{P}_2\text{O}_7 \cdot 10\text{H}_2\text{O}$) solution overnight, or longer if needed, to break up the minerogenic matter. The sediment was sieved through a 125 μm mesh. *Betula* seeds were divided into three groups: tree birch, dwarf birch (only pure *Betula nana* seeds), and when reliable identification was not possible, birch. The identification of small pieces of conifer needles was based on stomata. The nomenclature is according to Hämet-Ahti et al. (1998) for vascular plants.

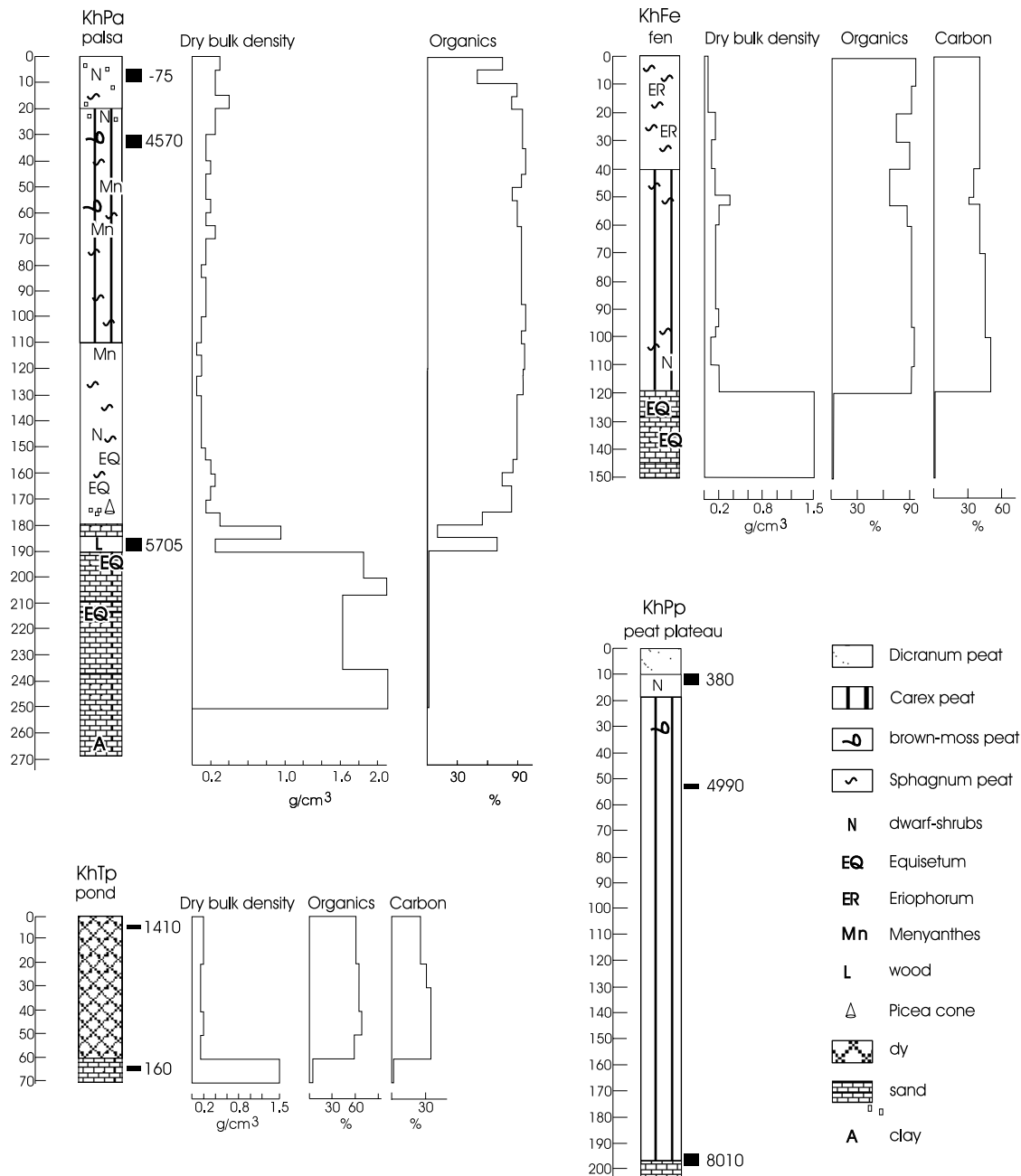
Mire deposits

Three peat profiles were investigated in the Khosedayu palsa mire (Fig. 2, site 3), on a 3 m high, lichen–moss covered palsa (KhPa), on a thermokarst pond (KhTp), and on a wet *Sphagnum* fen (KhFe). Their stratigraphy (Fig. 4) was described in the field. Samples were taken continuously every 5–10 cm from the whole depth of the profiles. The

organic deposit of the palsa (KhPa) is 190 cm thick and is underlain by sand with roots. A spruce log was located at the base (190–185 cm) of the peat profile. A second sand stratum was found at the 185–180 cm level. Above that, a spruce cone and charred wood were discovered in the peat. Further mineral grains within the peat were found at the 30 cm level. In the adjacent thermokarst pond (KhTp; Fig. 2, site 3), sand constitutes the lowermost sediment, and is overlain by a 60 cm thick sequence of organic sediment. The water depth was 2 m. The fen (KhFe) has a 119 cm peat layer above the basal sand.

A dry lichen-covered peat plateau site was studied in the peat plateau mire (KhPp; Fig. 2, site 1; Fig. 4). 2–4 cm long samples were taken at every 10–20 cm. The peat deposit is 197 cm deep, and the bottom material is sand. A basal peat sample for dating was taken from the tundra mire (KhTm) at depth of 155 cm.

Subsamples of 8 cm³ were dried for 18 h at 95 °C and then ignited for 2 h at 550 °C, to determine dry bulk density and loss-on-ignition, respectively. The carbon content was measured with an Elemental Analyser, Model EA 1110 (CE Instruments). For macrofossil analysis, subsamples of 5 cm³ were heated in 5% KOH solution for deflocculation, and sieved through a 180- μm mesh. The amount of macrofossils was counted as volume percentages (mosses, epidermia, roots, etc.) or as number per 5 cm³ of sample (seeds, leaves of higher plants, etc.). The degree of decomposition was es-

Fig. 4. Stratigraphy, radiocarbon dates, and results of physico-chemical analyses of the mire sites from Khosedayu.

timated from the reciprocals of moss preservation classes (Janssens 1983); where 0 indicates intact plants and 5 fragmented leaf remains. Macrofossil abundance as cover value on a petri dish was estimated for each sample taking the top sample as a standard (100%) (Kuhry et al. 1992). Observations on vegetation-permafrost relationships in European mires (Oksanen 2002) and field observations on vegetation in the Khosedayu area were used to interpret permafrost dynamics from the peat macrofossil records.

Mire vegetation

Eleven stratified random vegetation quadrats 1 m² in area were described in the Khosedayu palsa mire (Table 3). Vegetation cover in percent is given for bottom, field, and shrub

layers. The depths to water table, permafrost table, and mineral ground were measured. pH was determined with test paper (Merck). Additional observations on vegetation were also made during the field work. Nomenclature follows Euroala et al. (1992) for *Sphagna*, Koponen (1994) for other mosses, and Hämet-Ahti et al. (1998) for vascular plants.

Results

Lake Tumbulovaty record

The organic content of the 2.8 m-thick sediment sequence of Lake Tumbulovaty varies between 1% and 54% (Fig. 3). Table 1 shows the radiocarbon dates. According to the basal date Hela -427 (9700 BP), sediment accumulation in Lake

Tumbulovaty started at the beginning of the Holocene. The sedimentation rates vary between 0.13 and 0.38 mm year⁻¹ (Fig. 3).

The pollen stratigraphy of Lake Tumbulovaty has been divided into five local pollen assemblage zones (Tum I–Tum V, Figs. 5, 6). The zonation is based on the changes in conifer and *Betula* pollen proportions. The same zonation is presented on the Lake Tumbulovaty macrofossil diagram (Fig. 7). Dates of the zone boundaries have been approximated from an age–depth model (Fig. 3) and have been rounded to the nearest 100 years.

Tum I: 280–230 cm (9700–8300 BP; 11 200 – 9300 cal BP)

The pollen percentages of *Betula* (60%–70%), Cyperaceae (5%–20%), and Gramineae are relatively high in this zone. The proportion of *Picea* is lower than 5% in the bottom half of the zone increasing gradually upwards, reaching ca. 20% at the upper border of the zone. The pollen accumulation rate (PAR) of *Betula* reaches a maximum (ca. 1000 grains m⁻²year⁻¹) within this zone. Pollen of *Juniperus* and *Salix* is abundant, and their maximum pollen percentages and PAR also occur in the zone. Total concentrations and total PAR are low (<20 000 grains cm⁻³, <500 grains m⁻²year⁻¹, respectively) in the lower half of the zone but increase rapidly upwards. The plant macrofossil record consists of *Betula* (both tree and dwarf type) and some unidentified conifer remains. Remains of *Salix* and aquatic plants, like *Potamogeton*, *Myriophyllum*, and *Nuphar* were also present. The bottom-most sign of conifers in the macrofossil record appeared at ca. 9000 BP, 10 200 cal BP (255 cm), and the first stoma of *Picea* appeared at ca. 8600 BP, 9600 cal BP (240 cm).

Tum II: 230–135 cm (8300–5500 BP; 9300–6300 cal BP)

The highest proportions of *Picea* pollen were found in this zone. Pieces of *Picea* needles were found in the lower and upper parts of the zone, and *Picea* stomata were found between 210 and 150 cm. The percentages of *Picea* pollen are > 35% at 230–150 cm, and the PAR of *Picea* is ca. 300 grains cm⁻²year⁻¹. Both the percentages and PAR of *Picea* were lower in the upper part of the zone. Pollen of *Typha latifolia* was found at 180 cm. *Typha* sp. seeds were found at 210–180 cm, but *Typha* seeds cannot be identified to the species level, unlike its pollen. In addition to abundant *Betula* remains (mainly tree *Betula* seeds), several aquatic plants (*Potamogeton*, *Myriophyllum*, *Callitriche*, and *Nuphar*) dominate the macrofossil record.

Tum III: 135–95 cm (5500–2900 BP; 6300–3100 cal BP)

Betula dominates the pollen spectrum. At the lower boundary of the zone, the proportion of *Picea* pollen was below 30%. *Artemisia* pollen appeared at the lower boundary of the zone, and it is found, upwards, through the rest of the sequence. The proportion of *Pinus* pollen was ca. 5%, or less. Pieces of *Picea* needles were present in the macrofossil assemblage at 125–120 cm. *Betula* macrofossils were present, but in smaller quantities than in the lower zones, and tree *Betula* seeds were only found in the lower part of the zone. Among aquatics, remains of *Potamogeton* were the most abundant, but *Callitriche*, *Ranunculus* Sect. *Bathracium*, and *Myriophyllum* were also found.

Tum IV: 95–35 cm (2900–1000 BP; 3100–1000 cal BP)

The proportion of *Pinus* pollen is over 10% throughout the whole zone. *Betula*, *Picea*, *Salix*, Cyperaceae, Gramineae, and *Artemisia* are present. The relative share of non-arboreal pollen (NAP) is ca. 20%. Macrofossil remains of conifers were found at two levels; bark and (or) other tissues at 90 cm and an unidentified needle at 50 cm. *Betula* remains were present in the macrofossil assemblage. It is notable that between 85 and 75 cm hardly any macrofossils were found, only a few remains of *Carex*. This coincides with a minimum of *Betula* PAR (<60 grains cm⁻² year⁻¹), as well as a minimum of total PAR (<150 grains cm⁻² year⁻¹). There were no macrofossils of aquatic plants above 85 cm.

Tum V: 35–0 cm (1000 BP – present; 1000 cal BP – present)

The proportion of *Pinus* is below 10% at the lower boundary of the zone. Concentrations and PAR of *Betula* and *Picea* show slightly higher values compared with the previous zone. The relative share of NAP reaches 30%. Spores of *Equisetum*, Polypodiaceae, and *Sphagnum* increase. *Betula*, *Carex*, and *Ledum palustre* are present in the macrofossil assemblages.

Modern vegetation in Khosedayu River area

The results of the vegetation survey are given in Table 3. The typical palsa and peat plateau vegetation consists of lichens, mosses *Polytrichum strictum*, *Dicranum elongatum*, and *Pleurozium schreberi* and dwarf-shrubs. *D. fuscescens* s. lato (*D. flexicaule* Brid.) was encountered on a palsa. *Sphagnum fuscum* is present in small quantities. Slightly more moisture-demanding species grow on the slopes of palsas, such as *S. capillifolium* and *S. russowii* and on the lower parts also *S. angustifolium*, *S. lindbergii* and *Polytrichum commune*. The most common species on both frozen and non-frozen smaller hummocks are *S. fuscum* and *S. capillifolium*. *P. commune*, *Pleurozium schreberi*, *D. elongatum*, *Calamagrostis lapponica*, and *Salix glauca* were also encountered on them. *Sphagnum balticum* is found on their edges. In wet flarks, *S. lindbergii* and *S. riparium* are abundant; sometimes brown-mosses, *Drepanocladus aduncus*, *Calliergon stramineum*, and *Sarmentypnum sarmentosum* prevail instead. The field layer of flarks consists mainly of sedges, *Carex rariflora*, *C. aquatilis*, *C. rostrata*, and *Eriophorum*. *Potentilla palustris* is found in pools. Gullies between palsas and the mineral edge of the mire are occupied by *Salix lapponum* bushes.

Khosedayu peat records

Figure 4 shows the results of physico-chemical analyses of two peat profiles and a thermokarst pond sediment. The mean dry bulk density in the peat profiles (KhPa, KhFe) was 0.17 g cm⁻³, and the average organic content of dry peat was 80%. The average carbon content (KhFe) in dry organic matter of peat was 49.1%. The corresponding values for pond mud (KhTp) were 0.17 g cm⁻³, 64% and 47.9%, respectively. Table 1 shows the radiocarbon dates. The dates of the upper layers of palsa and peat plateaus are obtained from bulk rootlet peat, because macrofossil remains are sparse in these layers. The date of the 5–10 cm level of the palsa KhPa gives a negative result, indicating that the surface is modern. The ages of the bottom (60 cm) and surface sediment of the thermokarst pond KhTp are reversed, signifying mixed material.

Table 3. Khosedayu palsa mire, vegetation survey.^a

Relévé	Palsa dry	Palsa dry	Palsa slope	Gully between palsas	Hummock mire edge	Palsa embryo	Remnant pool of a palsa	Pool beside collapsing palsa	Fen pool	Filling pond fen	Gully palsa – sandy hill
pH	3.5	3.5	3.9	6.2	4.0	5.0	6.2	6.0	6.1	5.9	6.3
Water depth	—	—	20	23	35	—	0	3	0	10	5
Depth of permafrost	37	50	30	100	—	40	—	(45)	—	—	—
Depth of mineral ground	190	?	?	?	30	?	> 120	> 120	60	> 120	2
% bottom layer											
<i>Polytrichum strictum</i>	10	3			+						
<i>Dicranum elongatum</i>		3									+
<i>Dicranum fuscescens</i>	2		2								
<i>Pleurozium schreberi</i>	10	3	4								
<i>Sphagnum fuscum</i>	5		20		55						
<i>Hepaticopsisida</i>		1	1		+						
Lichens	73	65	5								88
Bare + litter		25									
<i>Sphagnum capillifolium</i>			30		40						
<i>Sphagnum russowii</i>			15	20							5
<i>Sphagnum lindbergii</i>			15			(99)		95			
<i>Polytrichum commune</i>			7	15	5						
<i>Pohlia nutans</i>			+	+							
<i>Sphagnum angustifolium</i>				65							
<i>Sarmentypnum sarmentosum</i>						(1)					
<i>Drepanocladus aduncus</i>							100				
Water								5	15		
<i>Sphagnum riparium</i>									85	100	
<i>Sphagnum fimbriatum</i>											5
<i>Aulacomnium palustre</i>											+
<i>Rhizomnium pseudopunctatum</i>											+
% field layer											
<i>Arctostaphylos alpina</i>	2										
<i>Empetrum nigrum</i>	20	15	5	1	10						
<i>Rubus chamaemorus</i>	10	4	40	15	20						90
<i>Betula nana</i>	5	12	10	15	3						25
<i>Ledum palustre</i>	20	15		+							
<i>Vaccinium vitis-idaea</i>	10	1	1		2						1
<i>Vaccinium uliginosum</i>		8	3	15	3						
<i>Vaccinium oxycoccos</i>				2	2						
<i>Carex</i> sp.				8	1	(25)					
<i>Carex rariflora</i>								10			
<i>Eriophorum</i> sp.						(20)		3	10		

Table 3 (concluded).

	Palsa dry	Palsa dry	Palsa slope	Gully between palsas	Hummock mire edge	Palsa embryo	Remnant pool of a palsa	Pool beside collapsing palsa	Fen pool	Filling pond fen	Gully palsa – sandy hill
<i>Carex aquatilis</i>							1			30	
<i>Carex lapponica</i>									3		
Poaceae											3
<i>Rubus arcticus</i>											+
% shrub layer											50
<i>Betula nana</i>											

Note: + indicates presence of < 1%, — indicates not present. Percentages between brackets indicate mainly dead plants; depth of permafrost between brackets refers to an ice lens.

^aAnalyses done by P. Oksanen and M. Väliranta.

Three basal dates of peat deposits are at 9260 BP, 10 440 cal BP (Utc-8665); 8010 BP, 8990 cal BP (Utc-8673); and 5705 BP, 6490 cal BP (Utc-8661). The average vertical accumulation in peat profiles (KhPa, KhPp) has been 0.22 mm year⁻¹, and the average carbon accumulation has been 21.0 g m⁻² year⁻¹ (Table 2).

Figure 8 shows the plant macrofossil record for profile KhPa. The zonation is based on botanical and physico-chemical properties of the profile.

KhPa 0, >190 cm (>5700 BP, >6500 cal BP)

Few macrofossils were found in this zone and these were mainly roots of *Equisetum* and Cyperaceae. The extent of decomposition was high. Some pieces of *Equisetum* epidermia, leaves of *Sphagnum*, and samaras of an unidentified type of *Betula* were found. Charcoal was regularly present in small amounts. Fungal sclerotia were observed.

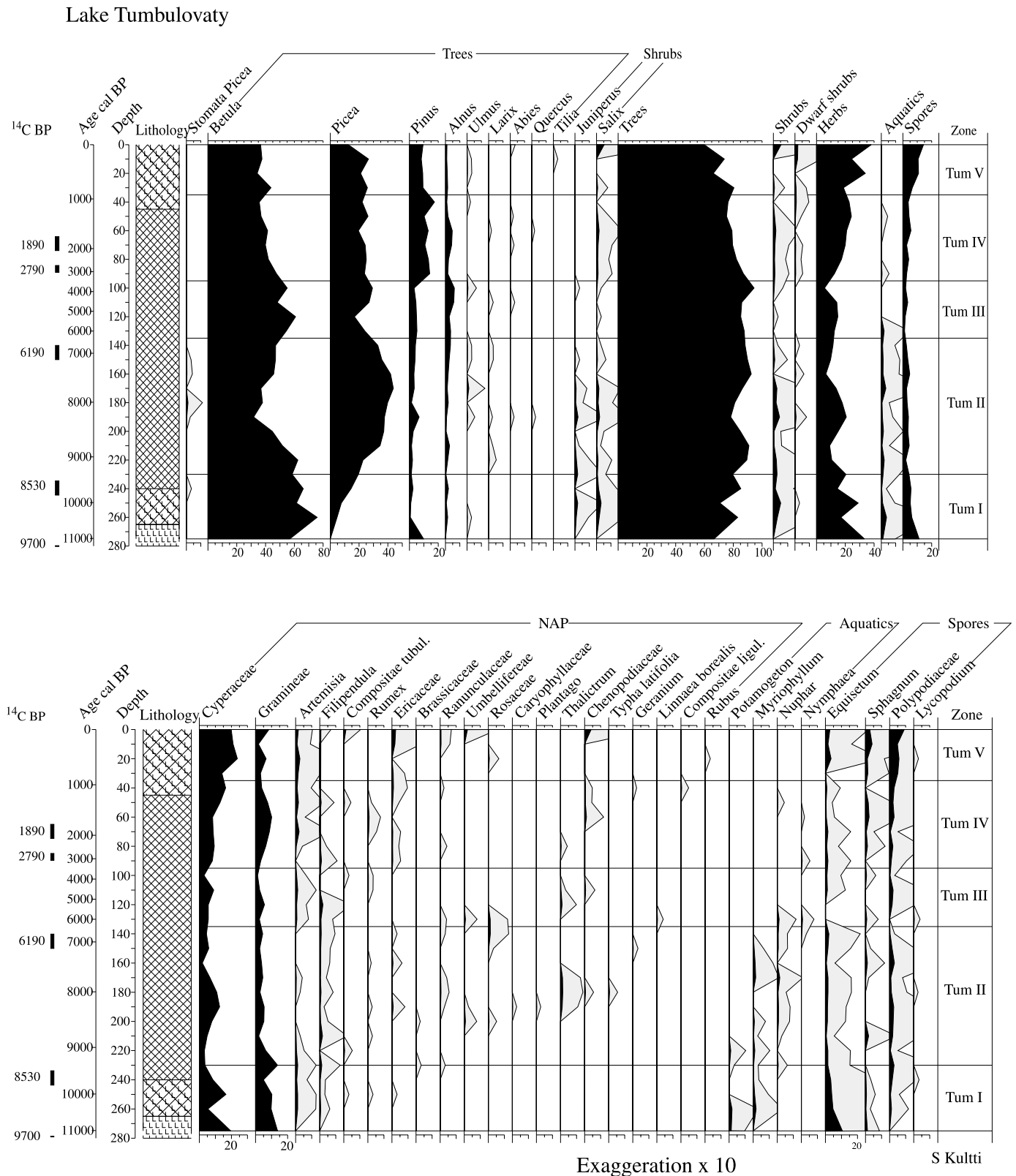
KhPa A, 190–110 cm (5700–5100 BP, 6500–5900 cal BP)

Macrofossil abundance rapidly increases upwards in this unit, from rather low to average. In the lowermost layers the remains were almost entirely decomposed, but at higher levels, they are relatively well preserved. In the basal peat layer the main contributor was *Polytrichum* (50%). *Aulacomnium*, *Pleurozium*, and *Sphagnum squarrosum* were found in minor quantities. In the subsequent sand layer, the amount of *S. squarrosum* remains exceeded those of *Polytrichum*. *Calliergon* s.l. (cf. *Sarmentypnum*) was also present. Fungal sclerotia were abundant in these lowermost strata. Some charcoal particles were present. In the subsequent peat layer, the prevailing mosses were initially *Polytrichum* cf. *commune* (30%) and *Calliergon cordifolium* (40%), soon replaced by *Sphagnum squarrosum* (≤50%) and later on by *S. teres* (≤95%). *Betula* remains, predominantly from trees, were abundant from the beginning of the zone. Up to 15 *Picea* needles per sample were found, and remains of *Carex* and *Equisetum* were regularly encountered. Among herbs, cf. *Potentilla*, Rosaceae, and *Menyanthes* were recognized.

KhPa B, 110–20 cm (5100–4500 BP, 5900–5100 cal BP)

This material was moderately decomposed. Macrofossil abundance was particularly high at the 45–30 cm level but low above this. The moss species most regularly present was *Sphagnum riparium* (≤80%), but at some stages other mosses dominated: *S. balticum* (≤50%), *S. annulatum* (≤50%), *Warnstorfia fluitans* (≤60%), *Calliergon stramineum* (≤30%), and, in the topmost layer, *S. subsecundum* (≤40%) and *W. procera* (≤35%). *Scheuchzeria* was present from the beginning of the zone with *Sphagnum riparium*, but it was especially abundant at 90–75 cm, accompanying *S. balticum*, *S. annulatum*, and *W. fluitans*. In the latter half of the zone, *Scheuchzeria* was mostly absent, while *Equisetum*, not present earlier in the zone, reappeared. *Carex* seeds (mainly the triangular type) and epidermia were commonly found throughout the zone, but they were especially abundant in the latter half (up to 100 seeds per sample). Rosaceae seeds were common. The uppermost remains of *Picea* needles were encountered in the lower part of the zone. *Betula* remains were common; some pieces of them were recognized as belonging to the tree type (*B. pubescens*).

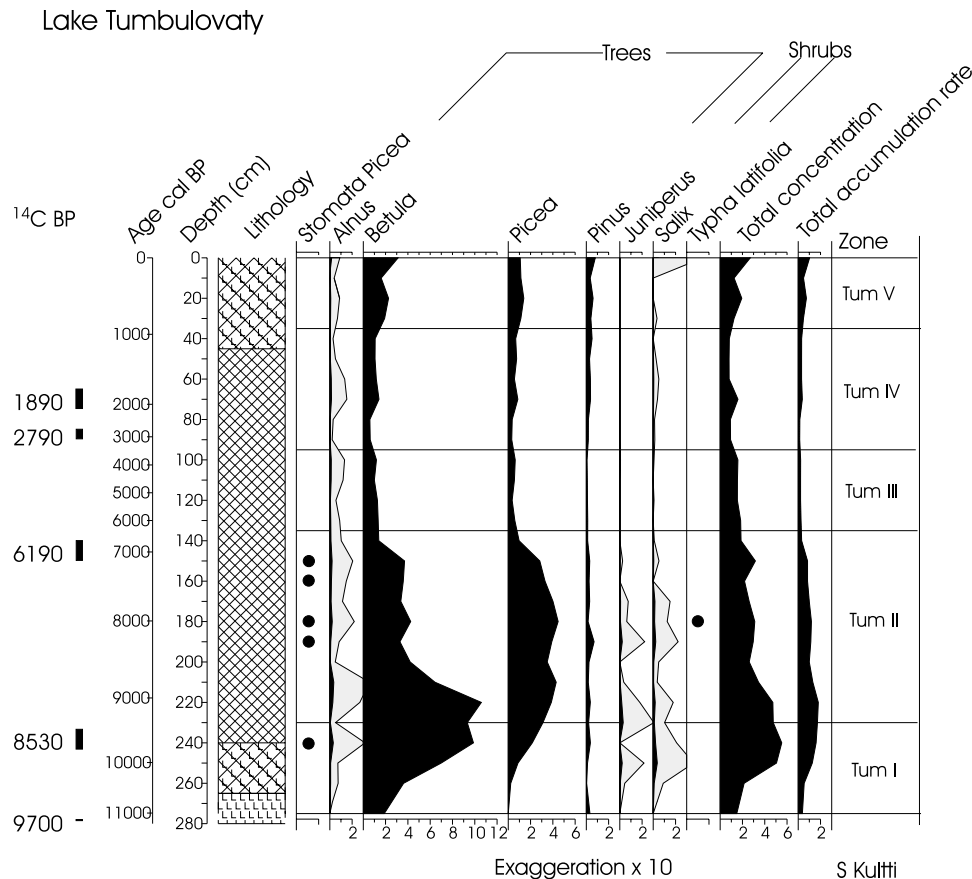
Fig. 5. Relative pollen diagram including conifer stomata record for Lake Tumbulovaty, northeast European Russia. Sediment (lithology) symbols as in Fig. 3.



KhPa C, 20 – 0 cm (<<4500 BP, <<5100 cal BP)
 In the lower half of the zone, peat was highly humified and composed mainly of unidentified organic material (≤50%)

and roots of *Cyperaceae* and shrubs. Some wood and bark were present, and a few leaves of *Polytrichum* and *Sphagnum*, pieces of *Eriophorum* epidermia, and fungal sclerotia were

Fig. 6. Pollen accumulation rates of selected taxa, total concentration, and accumulation rate, for Lake Tumbulovaty, northeast European Russia. The incidence of *Picea stomata* and *Typha latifolia* are shown with black dots. The scale bar for accumulation rate is $\times 100$, for total concentration $\times 10\,000$, and for total accumulation rate $\times 1000$. Sediment (lithology) symbols as in Fig. 3.



found. The second half was well decomposed, but macrofossil abundance was greater than lower in the zone. The peat was mainly formed by roots of shrubs. Leaves and other remains of *Ledum*, *Andromeda*, *Vaccinium*, and *Betula nana* were also common. Among mosses, *Polytrichum strictum*, *Dicranum elongatum*, and *Pleurozium* were found. Lichen remains were present. A piece of Cyperaceae epidermis was encountered.

Some samples of the site KhPp were scrutinized for macrofossils (not plotted). Remains of tree *Betula* were encountered at the bottom of the core. A change into more decomposed and compacted peat occurred at the 53 cm level, which has been dated to 4990 BP, 5720 cal BP (UtC-8672). Above that, *Drepanocladus* s.l. – Cyperaceae peat was found. Between 14 and 10 cm, the peat was mainly composed by roots and unrecognized organic material. The uppermost 10 cm was *Dicranum* cf. *fuscescens* – lichen – rootlet peat.

Discussion

Vegetation history in the arctic tree line area

The pollen and macrofossil records of Lake Tumbulovaty reflect relatively open birch woodland accompanied by willow, dwarf birch, juniper, and some herbs at the very beginning of the Holocene. The macrofossil evidence shows that tree birch was growing in the present lowland tundra as early as 9700 BP (11 200 cal BP). The oldest megafossil of tree birch in the Lower Pechora region has previously been dated

to 9440 BP (Kremenetski et al. 1998) and from the nearby Rogovaya River peat site to 9420 BP (10 640 cal BP) (Oksanen et al. 2001).

On the basis of the first stoma of *Picea* (240 cm), the expansion of spruce to the study area took place by 8600 BP (9600 cal BP) at the latest, but probably as early as 9000 BP (10 200 cal BP) on the basis of the first conifer needle, even though it was not possible to identify this to the genus level. Stomata from the Ortino area, east of the Pechora Delta, indicate spruce expansion there around 9000 BP (10 200 cal BP) (Kaakinen and Eronen 2000). The age of the oldest dated megafossil of spruce in the Bol'shezemel'skaya Tundra is 8560 BP (Kremenetski et al. 1998; MacDonald et al. 2000b). A combined pollen and macrofossil analysis from Lake Mezghornoe (Kultti et al. 2003), on the western slopes of the Ural Mountains, indicates spruce expansion to the present alpine tree line at ca. 9500 BP (10 900 cal BP). It suggests that the time difference between spruce migrations to the present alpine and arctic tree lines has been ca. 700–1300 years, depending on whether the first signs of conifer in the Lake Tumbulovaty macrofossil record were spruce or not.

Lake Mezghornoe is situated ca. 170 km south of Lake Tumbulovaty. On the basis of this distance, the migration rate of spruce has been established at ca. 0.13–0.25 km year⁻¹, if a direct northward migration is assumed. However, Lake Mezghornoe is situated in the Ural Mountains, where spruce

Fig. 7. Plant macrofossil diagram for Lake Tumbulovaty, northeast European Russia. Sediment (lithology) symbols as in Fig. 3.

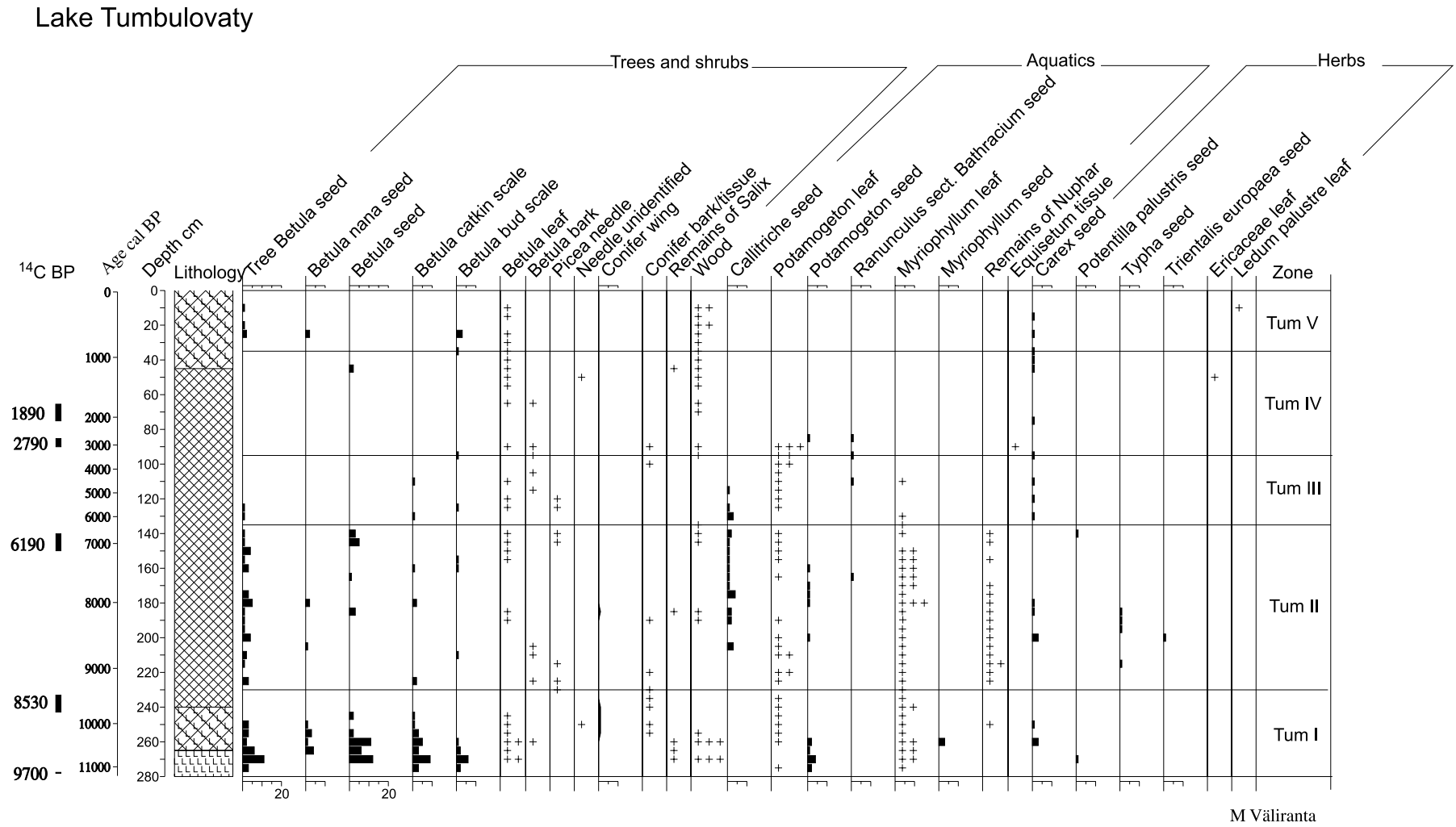
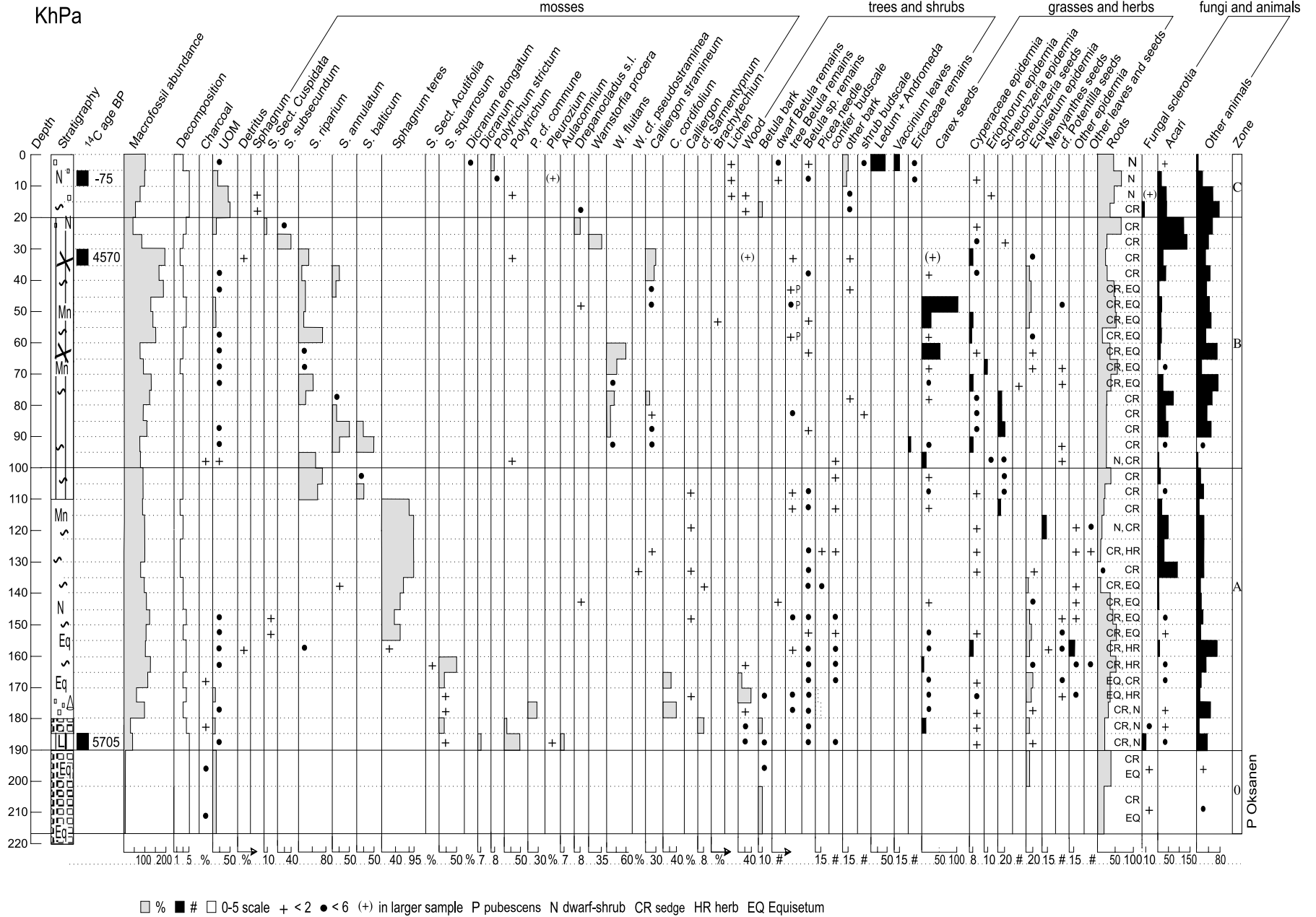


Fig. 8. Plant macrofossil diagram for palsa KhPa, northeast European Russia. Stratigraphic symbols as in Fig. 4.



conceivably could have had a migration lag compared with lowland areas at the same latitudes. Therefore, the actual migration rate probably was lower, although our estimate is analogous to the results of the migration rate of *Picea* spp. from eastern Canada (0.2–0.4 km year⁻¹, Payette et al. 2002). According to Kaakinen and Eronen (2000), mixed spruce forest was established in the Ortino area soon after 9000 BP (10 200 cal BP). Although Ortino is situated further north than Lake Tumbulovaty, spruce had migrated there at the same time or even earlier than to our study site. Ortino is situated next to the River Pechora, which may have provided a faster migration route for spruce. However, additional dated sites are needed before more reliable estimates of migration rates or routes can be provided.

A time lag can also be seen between the first signs of conifers (stomata and macrofossils) and the increased *Picea* pollen percentages and accumulation rates. According to the PAR and percentages of *Picea* that reflect the regional thickness of a forest, the highest density of spruce occurred between 8300 and 6000 BP (9300 and 6400 cal BP). This suggests a 300–900-year time lag between the first arrival of spruce and the development of closed mixed spruce–birch forests. Combined pollen and macrofossil studies from the Abisko area, Northern Sweden, indicate a time lag as long as 2200 years between the first pine trees and the dense pine forest in the early Holocene (Barnekow 1999), while a combined stomata and pollen study from the Kola Peninsula indicates a ca. 1000-year time lag (Gervais et al. 2002). Reasons for the “delayed” closed forest phase can be, e.g., climate, seedling conditions, and poorly developed soils.

The first mire inception in the area is recorded at 9260 BP, 10 440 cal BP (UtC-8665), in the early Holocene (Table 1). The result is identical with another forest–tundra site, the Rogovaya River (ca. 80 km southeast of the study area) with basal mire deposit dates of 9420–9250 BP, 10 640 – 10 440 cal BP (Oksanen et al. 2001). Two other basal peat samples from Khosedayu are dated to 8010 BP, 8990 cal BP (UtC-8673) and 5705 BP, 6490 cal BP (UtC-8667). They represent paludification of birch and mixed spruce–birch forest, respectively.

No longer than 20 years ago, the northernmost distribution area of *Typha latifolia* within Komi covered mainly the southern taiga zone. During the last two decades, it has moved northwards along the Vorkuta railway, so that today, it is also present in the middle taiga zone (Olga Lavrinenko, Personal communication, 2001). Therefore, the presence of *T. latifolia* between 7800 and 7000 BP (8800 and 8000 cal BP) in the Lake Tumbulovaty record suggests that middle or even southern taiga conditions prevailed in the study area at that time.

The pollen proportions and PAR of *Picea* in the Lake Tumbulovaty record start to decrease after 6100 BP (7000 cal BP) and *Picea* needles are absent after ca. 4600 BP. After about 5000 BP (5700 cal BP), no evidence of spruce was found in the Khosedayu palsa peat profile (KhPa). The increased mineral content in the peat profile after 4500 BP (5100 cal BP) reflects more open conditions, where the vegetation is no longer capturing sand. This suggests a gradual withdrawal of the mixed spruce–birch forest, which corresponds well with the tree megafossil data from the region

(Kremenetski et al. 1998; MacDonald et al. 2000b). Simultaneous withdrawal of the mixed conifer forest was also detected in the Ortino area from the Pechora lowland (Väliranta et al. 2003) and from Mezghornoe at the alpine tree line (Kultti et al. 2003). In the Kola Peninsula, northwestern Russia, as well as in other parts of Fennoscandia, the withdrawal of mixed conifer forest has been dated from ca. 6000–4000 BP (6800–4500 cal BP) (e.g., Hyvärinen 1975; Davydova and Servant-Vildary 1996; Seppä 1996; Kremenetski et al. 1997; Barnekow 1999; MacDonald et al. 2000a; Snyder et al. 2000; Gervais et al. 2002; Seppä et al. 2002).

Macrofossils suggest that spruce was at least sporadically present in the vicinity of Lake Tumbulovaty until 3000 BP (3200 cal BP). This is corroborated by a macrofossil study from the Rogovaya River peat plateau, where spruce needles were found until 2800 BP (2900 cal BP) (Oksanen et al. 2001). Furthermore, a paleosol date from Khosedayu implies that a forest stand persisted at the site until ca. 3000 BP (Rusanova and Kuhry 2003). Low PAR and decreased percentages of *Picea* suggest only scattered tree stands, in an environment that resembled the present-day forest–tundra ecotone, survived in the study area.

Between 3000 and 1000 BP (3200 and 900 cal BP) pollen accumulation rates were at their minimum, and macrofossils in the lake sediment are scarce. In view of the fact that pine is not growing close to the study area today, we can assume that the higher proportion of *Pinus* pollen during this phase is due to a decreased local pollen rain, which increases the representation of *Pinus* pollen. However, PAR of *Pinus* also increases slightly simultaneously with *Sphagnum* after 80 cm, a phenomenon reported in other pollen studies from south of the study area (Kultti et al. 2003; Sarmaja-Korjonen et al. 2003). Because pine presently grows mainly around mires, increased PAR of *Pinus* may reflect increased paludification in the area. The lack of plant macrofossils, and very low pollen accumulation rates, as well as the presence of *Artemisia* and *Salix* between 2700 and 2100 BP (2800 and 2100 cal BP), suggest that tree density was less than at present, and the forest line was probably further south than today. However, scattered remains of tree birch and conifers reappear in the macrofossil record after 1400 BP (<50 cm), indicating the presence of some sporadic birch trees and conifers in the vicinity of Lake Tumbulovaty.

A new phase of tree growth around 1000 BP is suggested by wood remains dated from a paleosol in presently unforested ground at the Khosedayu site (Rusanova and Kuhry 2003). At the same time, PAR and percentages of *Betula* and *Picea* increase slightly, which might be interpreted as the forest line moving towards the study area again at 1000 BP. Subsequently the species assemblage corresponds to present-day plant communities in the area.

Permafrost history of mires at the arctic tree line area

In the Khosedayu palsa (KhPa), a sample at 35–30 cm, below a stratigraphic change into more decomposed and compacted peat, is dated to 4570 BP (5300 cal BP). Until that time, the site was a wet, mesotrophic fen, and tree birch was growing nearby. The macrofossil assemblages indicate that the site was permafrost-free. Furthermore, the presence of *Scheuchzeria palustris* suggests that the environment was

different from the modern one. This species does not grow in the present forest–tundra of northeastern Europe (Tolmachev et al. 1995), and though it is common in northern Fennoscandia and the northern taiga of Russia (Tolmachev et al. 1995; Hämet-Ahti et al. 1998), it is only once reported from a palsa mire (Boch and Solonevich 1965; Alekseeva 1974). Peat accumulation in young peatlands is often rapid (Oksanen 2002), which corroborates the exceptionally high rate in the zones A and B of KhPa (5700–4600 BP, 6500–5300 cal BP), 79.3 g C m⁻² year⁻¹, 1.22 mm year⁻¹). The macrofossil assemblage (e.g., *Sphagnum subsecundum*, *Warnstrofia procera*) between 30 and 20 cm indicates non-permafrost conditions. Tree macrofossils are absent. Furthermore, mineral material is found in the peat implying increased erosion in the nearby landscape. The distinct increase in dry bulk density and decomposition of peat is probably an effect of later permafrost aggradation at the site.

A significant drying occurred after the 20 cm level, as indicated by a very high decomposition level and the presence of fungal sclerotia and shrub remains. A new type of vegetation (e.g., *Polytrichum strictum*, *Dicranum elongatum*, lichens) is found beginning from the 15 cm level, characteristic for a palsa. Since the 10–5 cm layer gives a modern age, it must be assumed that the recent palsa stage is very young, at maximum a few hundred years old. The organic accumulation rate in KhPa after 4600 BP is very low and identical with the rate obtained from mature peat plateau stages from the Rogovaya River (7 g C m⁻² year⁻¹), where peat accumulation ceased at about 1500 BP (1360 cal BP) (Oksanen et al. in press). The low rate suggests that some layers may have been eroded away from the profile. Erosion is common on mature palsas (e.g., Salmi 1972), and older palsa deposits are preserved only occasionally (Oksanen 2002).

The peat plateau profile KhPp is similar to the palsa KhPa: a stratigraphic change (at 53 cm) to more compacted peat is dated to 5000 BP, 5700 cal BP (UtC-8672), but the botanical composition does not indicate the presence of permafrost until much later. A change from *Drepanocladus* s.l. – Cyperaceae peat to rootlet – *Dicranum* cf. *fuscescens* peat occurs near the 14–10 cm level. The youngest date is from 14–10 cm, giving an age of 380 BP, 470 cal BP (UtC-10060). The vertical peat accumulation rate of KhPp between 5000 and 400 BP is very low (0.09 mm year⁻¹), which could indicate former erosive phases as also interpreted for KhPa.

It seems that both the recent permafrost stages at sites KhPa and KhPp developed during the Little Ice Age or, at KhPa, even later. Possibly older palsa forming phases existed at the sites, but their deposits have been eroded away. Aggradation and degradation cycles belong to the nature of permafrost mires (Seppälä 1988), and recent palsas (or peat plateaus) are rarely older than 2000 BP (Oksanen 2002). More sites and dates are needed to trace the first permafrost aggradation in the area. The first recorded Holocene permafrost aggradation in northeast European Russia took place at 4800 BP (5500 cal BP) at Ortino in the modern tundra (Väliranta et al. 2003). At the same latitude as Khosedayu, in the Rogovaya River, initial permafrost aggradation took place at 3100–2800 BP, which is simultaneous with another dating from Ortino (Väliranta et al. 2003) and with the first incipient permafrost in the modern northern taiga at Usinsk

(Oksanen et al. in press). Furthermore, much younger palsa aggradation dates have been obtained in the region; four ages between 600 and 100 BP have been obtained (Oksanen et al. 2001; Oksanen, unpublished data).

Climatic interpretation

The prevailing tree birch woodland in the study area at the beginning of the Holocene suggests that the climate was more favourable for tree birch than it is today. However, climatic interpretation is difficult because this vegetation type is absent from Northeast European Russia at present. Spruce immigration as early as 9000 BP indicates that conditions at least as warm as at present prevailed.

The presence of *Typha latifolia* in Lake Tumbulovaty at ca. 7800–7000 BP (8800–8000 cal BP) indicates an early Holocene hypsithermal interval. *T. latifolia* has also been found from the western Pechora Basin (Paus 2000). Those finds were dated to > 8900–8300 BP (10 000 – 9360 cal BP) (Paus 2000). Andreev et al. (2001) found *T. latifolia* pollen from lake sediment in the Yugorski Peninsula (northeast of Lake Tumbulovaty), and they proposed an age of 6000–5500 BP (6800–6300 cal BP) for this particular stratigraphic layer. According to Ritchie et al. (1983), the presence of *T. latifolia* pollen in lake sediment indicates a local source, because the pollen grain is relatively heavy. Compared to the current distribution area of *T. latifolia*, its more northern distribution in the early and middle Holocene (8900–5500 BP, 10 000 – 6300 cal BP) suggests that summer temperatures in Northeast European Russia have been up to 3–4 °C higher than at present.

The permafrost aggradation in the study area took place after 4500 BP (5100 cal BP), and at this time *Scheuchzeria palustris* disappears from the peat records. The present southern border of permafrost is found ca. 100 km south of the study area, and the present northern distribution limit of *S. palustris* follows approximately the same latitude (Tolmachev 1974). This suggests 2 °C higher mean annual temperatures in the study area until 4500 BP (5100 cal BP).

The withdrawal of mixed forest at ca. 5000 BP (5700 cal BP) can be assumed to have resulted from gradual climatic cooling and (or) related changes in soil hydrology, paludification, and permafrost conditions. Two cooling phases can be detected from the present data: the first at ca. 5000 BP (5700 cal BP) and the second at ca. 3000 BP (3200 cal BP). These cooling phases are corroborated by permafrost aggradation in the region during these periods (Oksanen et al. 2001; Väliranta et al. 2003; Oksanen et al. in press). Increased minerogenic content in Lake Tumbulovaty after 5000 cal BP and sand in the Khosedayu palsa peat might be related to a cooling of the climate, which resulted in deforestation, soil erosion, and redeposition of sand by aeolian activity. Increased aeolian activity during the Late Holocene is corroborated by a buried paleosol at the Khosedayu site (Rusanova and Kuhry 2003), as well as sand layers in Ortino 1 and Ortino 2 peat profiles (Kaakinen and Eronen 2000; Väliranta et al. 2003).

The Tumbulovaty record reflects decrease in tree abundance density between 3000 and 1000 BP, which suggests a lower temperature than at present. Furthermore, the record suggests that the coldest period during the Holocene occurred between 2700 and 2100 BP (2800 and 2100 cal BP).

This is corroborated with renewed permafrost aggradation on the Rogovaya peat plateau (Oksanen et al. 2001). The peat representing this age at Khosedayu has probably eroded or decomposed from the palsa (KhPa) and peat plateau (KhPp) sites.

Simultaneous cooling events can also be found from the reconstructed sea-surface temperatures (SST) in the North Atlantic. Major cooling events in SST at 5800 cal BP and 2800 cal BP have been observed in the records from the Norwegian Sea (Calvo et al. 2002). These events are proposed to be the result of changes in thermohaline circulation of the North Atlantic Ocean (Bond et al. 1997; Calvo et al. 2002). In SST reconstructions from the north Icelandic shelf a prominent cooling is detected around 2800 cal BP, and then a gradual decrease again between 2400 and 1300 cal BP (Jiang et al. 2002). It seems that the middle and late Holocene cooling events indicated in this study are analogous with the reconstructed drop in SST in the North Atlantic.

Subsequent warming during the Medieval Warm Period can be seen in the pollen and macrofossil records, as well as in the palaeosol in the Khosedayu site with woody fragments dated to ca. 1000 BP (Rusanova and Kuhry 2003). The Little Ice Age cold period cannot be distinguished in the lake sediment record, whereas new permafrost aggradation during this time has been detected in both the Khosedayu area and the Rogovaya area (Oksanen et al. 2001).

Conclusions

At the very beginning of the Holocene, open birch woodland dominated in the study area. The expansion of spruce took place at 8600 BP (9600 cal BP), at the latest. According to the pollen evidence, the optimum of the mixed conifer forest occurred between 8700 and 6200 BP (9800 and 7100 cal BP). During that time, southern or middle taiga conditions prevailed in the study area. Evidence from the Lake Tumbulovaty and Khosedayu palsa (KhPa) suggests that taiga prevailed in the study area until ca. 5000 BP. After that the area was occupied by forest-tundra, where both spruce and tree birch were sporadically present. The second phase of decreasing forest cover can be seen at ~3000 BP. Pollen and macrofossils from Lake Tumbulovaty suggest that tundra vegetation prevailed in the area between 3000 and 1000 BP. After that, forest-tundra similar to present invaded.

Both studied palsas have developed recently, probably during the Little Ice Age or even later. However, due to the possibility of eroded peat layers, older permafrost aggradation cannot be ruled out. The peat records imply that permafrost-free conditions have prevailed at the study sites at least until ca. 4900–4500 BP.

The study area experienced an early and middle Holocene hypsithermal (8900–5500 BP), when the summer temperatures were up to 3–4 °C higher than at present. Two cooling phases were detected from the present data: the first at ca. 5000 BP and the second at ca. 3000 BP. The lowest temperatures prevailed in the area between 2700 and 2100 BP. The Medieval Warm Period (at ca. 1000 BP) and the Little Ice Age have also been distinguished.

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