Accepted Manuscript

Continental climate in the East Siberian Arctic during the last interglacial: implications from palaeobotanical records

Frank Kienast, Pavel Tarasov, Lutz Schirrmeister, Guido Grosse, Andrei A. Andreev

Please cite this article as: Kienast, Frank, Tarasov, Pavel, Schirrmeister, Lutz, Grosse, Guido, Andreev, Andrei A., Continental climate in the East Siberian Arctic during the last interglacial: implications from palaeobotanical records, *Global and Planetary Change* (2007), doi: 10.1016/j.gloplacha.2007.07.004

Continental climate in the East Siberian Arctic during the last interglacial: implications from palaeobotanical records

Frank Kienast[a], Pavel Tarasov[b], Lutz Schirrmeister[a], Guido Grosse[c], Andrei A. Andreev[a]

[a] Alfred Wegener Institute for Polar and Marine Research Potsdam, Telegrafenberg A43, 14473 Potsdam, Germany

[b] Free University Berlin, Institute of Geological Sciences, Palaeontology Department, Malteserstr. 74-100, Building D, Berlin 12249, Germany

[c] Geophysical Institute, University of Alaska Fairbanks, 903 Koyukuk Drive, Fairbanks Alaska 99775-7320, U.S.A.

Frank Kienast: fkienast@awi-potsdam.de

Tel. ++49 331 288 2100

Fax: ++49 331 288 2137

(Corresponding Author)

Pavel Tarasov: ptarasov@zedat.fu-berlin.de

Lutz Schirrmeister: lschirrmeister@awi-potsdam.de

Guido Grosse: ggrosse@gi.alaska.edu

Andrei A. Andreev: aandreev@awi-potsdam.de

Abstract

To evaluate the consequences of possible future climate changes and to identify the main climate drivers in high latitudes, the vegetation and climate in the East Siberian Arctic during the last interglacial are reconstructed and compared with Holocene conditions. Plant macrofossils from permafrost deposits on Bol'shoy Lyakhovsky Island, New Siberian Archipelago, in the Russian Arctic revealed the existence of a shrubland dominated by *Duschekia fruticosa, Betula nana* and *Ledum palustre* and interspersed with lakes and grasslands during the last interglacial. The reconstructed vegetation differs fundamentally from the high arctic tundra that exists in this region today, but resembles an open variant of subarctic shrub tundra as occurring near the tree line about 350 km southwest of the study site. Such difference in the plant cover implies that, during the last interglacial, the mean

1

summer temperature was considerably higher, the growing season was longer, and soils outside the range of thermokarst depressions were drier than today. Our pollen-based climatic reconstruction suggests a mean temperature of the warmest month (MTWA) range of 9-14.5 °C during the warmest interval of the last interglacial. The reconstruction from plant macrofossils, representing more local environments, reached MTWA values above 12.5 °C in contrast to today's 2.8 °C. We explain this contrast in summer temperature and soil moisture with a combination of summer insolation higher than present and climatic continentality in arctic Yakutia stronger than present as result of a considerably less inundated Laptev Shelf during the last interglacial.

Keywords: Last Interglacial; Arctic Siberia; Beringia; plant macrofossils; Laptev Sea level; tectonics

1. Introduction

During the late Quaternary, the Siberian Arctic experienced drastic climate changes with serious consequences for biocoenoses. In the course of the Holocene, the mammoth faunal complex became largely extinct probably in consequence of climate induced modifications of landscape and vegetation (Stuart et al., 2004). Northeast Siberia with its continental climate is regarded last refuge of such large herbivores as woolly mammoth (*Mammuthus primigenius*), woolly rhinoceros (*Coelodonta antiquitatis*), steppe bison (*Bison priscus*), and horse (*Equus* sp.) during the Holocene (Sher, 1991, 1997; Boeskorov, 2006). Consistently, the region is assumed to have been the main refuge of large grazers also during former interglacials (Sher, 1991, 1997; Stuart et al., 2004). The first scientist who found a link between mammoth fauna and steppe vegetation was Nehring (1890). During Pleistocene cold-stages, when continental, cold-arid climate conditions reached their maxima, the mammoth fauna formed together with the associated tundra-steppe vegetation an almost circumpolar organism community in the cold-arid climate zone - a zonal biome called mammoth steppe (Guthrie, 1990). The corresponding plant cover was the so-called tundra-steppe; vegetation co-dominated by steppe and tundra species and considered to be without modern analogue (Guthrie, 1990; Sher et al., 2005). Other approaches define tundra-steppe as landscape (Yurtsev, 1982, 2001), mosaic or complex (Kienast et al., 2005) of delimitable, yet associated modern plant communities that are today either characteristic of steppe or tundra zones and that currently still coexist in small refugia. The most continental, cold-arid climate conditions occurred during cold stages, when

huge water masses were frozen in northern ice sheets, resulting in a global sea level about 130 m lower than today.

At present, the vast and shallow Laptev and the East Siberian Seas have less than 30 m water depth over hundreds of kilometers in latitudinal extent. During the Weichselian cold stage (MIS 2, Sartan), these shelves were consequently dry land and underwent a tremendous transgression in the course of the Holocene (Romanovskii et al., 1998; Bauch et al., 2001). The increased oceanic influence on climate in high latitudes as result of the marine transgression is considered crucial for the formation of tundra vegetation during the Holocene (Frenzel, 1968; Crawford et al., 2003). Tundra in this context is regarded as a vegetation zone north of the boreal tree-line mainly composed of wetland plants. Tundra developed accordingly as result of increased precipitation and a decrease in summer temperature and evaporation. Soil paludification is, in the Arctic, additionally strengthened by the damming effect of perennially frozen ground.

Whereas the mammoth faunal complex and tundra steppe persisted during the former Quaternary warm stages presumably in their Siberian refugia, they largely perished in the Holocene. The overkill theory explains the disappearance of the mammoth faunal complex as the result of human hunting (e.g. Zimov, 2005; Haynes, 2007). After the extermination of mega herbivores, the lack of grazing pressure would accordingly result in a vegetation shift from grassland to tundra. According to the predator-prey equations of Lotka and Volterra, however, it is impossible that a predator extirpates its prey (Volterra, 1931). Palaeolithic and Mesolithic man in high latitudes was entirely dependent on game animals as agriculture was not yet developed and anyway impossible so far north. Humans could not eliminate their basic recourses before becoming extinct themselves. Hunters and large herbivores coexisted in arctic Siberia at least from 27,000 years BP (Pitulko et al., 2004) to about 12,000 years BP when the big animals disappeared over most of the mainland (Stuart et al., 2004). The remaining questions are 'why did the mammoth faunal complex not survive the current interglacial in contrast to all the others before?' and 'what makes the Holocene of all warm stages unique in the Arctic?'

This paper deals with the ancient vegetation existing in the northeastern Siberian Arctic during the Eemian Interglacial (MIS 5e, Kazantsevo) reconstructed on the basis of terrestrial plant macro remains preserved in frozen sediments of the Bol'shoy Lyakhovsky Island (73°20′N, 141°30′E), the New Siberian Archipelago, on the coast of the Dimitrii Laptev Strait (Fig. 1). We discuss the implications for interglacial environments, climate, and coast

3

line position in this highly sensitive arctic ecosystem in contrast to the current warm stage and in view of the forecasted anthropogenic warming.

Fig. 1

2. Study region

2.1. Geology

The New Siberian Islands separate the Laptev and the East Siberian Seas (Fig. 2), which are among the widest and shallowest shelf-seas worldwide. Due to their distance from precipitation source areas, they were not affected by large inland glaciations after the Middle Pleistocene (Alekseev, 1997; Hubberten et al., 2004). NE-Siberian arctic lowlands and shelves were consequently scarcely influenced by glacioisostatic lifts during that time. Instead, the whole region is characterised by active tectonics, indicated by high heat-flow values and intense seismicity (Drachev et al., 2003). As one of the few regions on the Earth's surface, sea-floor spreading there hits the edge of a continent (Fig. 2). At the Laptev Sea continental slope, the ultraslow-spreading Gakkel Ridge forms the end of the Atlantic-Arctic Mid-Ocean Ridge System and the boundary between the Eurasian and North American Plates. As result of the spreading process and the initial break-up of continents during the Cenozoic, the Laptev and western East Siberian Seas are a diffuse zone of ongoing extension including subsidence and formation of a series of deep basins within a complex horst and graben system (Fig. 2; Drachev, 2000; Drachev et al., 1998, 2003; Franke et al., 2000, 2001, 2004; Parfenov et al., 2001). Also the Lena River Delta is separated by an active N-S trending fault (Alekseev and Drouchits, 2004). The complicated tectonic setting is not yet fully understood. Initially continuing at the continental rise, the Gakkel Ridge spreading axis is cut-off at the transcurrent Khatanga-Lomonosov Fracture (Fig. 2), along which an eastward migration of the active rift zone connected with strike-slip faulting occurred (Drachev et al., 2003). The intense crustal deformation in the Laptev Sea region resulted in the redirection of the Lena River from its formerly western course along the current Olenyok River valley south of the Chekanovsky Ridge towards its modern northward course after the "Lena-Pipe" break through at the end of the Middle Pleistocene, thus shortly prior to the last interglacial (Alekseev and Drouchits, 2004). In the course of the Late Pleistocene, the eastward dislocation of the major Lena River run-off apparently continued within the Lena Delta from the west during marine isotope stages 5-3 to northwest during marine isotope stage 2 to the northeast and east during the Holocene (Schwamborn et al., 2002; Alekseev and Drouchits,

2004) illustrating the intensity of modern tectonic subsidence in the central part of the Laptev Shelf.

Fig. 2

Subsidence is in general largely compensated by sedimentation. Consisting of Cenozoic deposits, the sedimentary cover in the basins of the Laptev shelf ranges from 3 km to, in the grabens, 13 km (Franke et al., 2001) and resulted in a levelling of the tectonically dissected ground. When exposed during the Late Pleistocene regression stages, the Laptev Shelf and the adjacent coastal lowlands formed a common accumulation plain, where ice-rich permafrost sediments consisting up to 90 vol % of ice (Ice Complex) were deposited. This ice-bonded permafrost was approximately 40 m, in tectonically subsided portions of the shelf, up to 60 m thick (Romanovskii et al., 2000).

Ice-bonded permafrost is however climatically very susceptible. It was thus largely destroyed due to warming, precipitation increase, and submergence in the course of the Holocene. Due to the flat topography, the drainage system on the exposed shelf and the adjacent lowlands was poorly developed resulting in massive lake formation at the beginning of the Holocene (Romanovskii et al., 2000). Widespread lake formation is regarded as the cause of the excessive development of thermokarst, which almost completely destroyed the Ice Complex. Ice-bonded permafrost exists on the now inundated shelf currently only residually and diminishing near the coast and at shallow places of former Ice Complex islands (Romanovskii et al., 2004).

Bol'shoy Lyakhovsky Island (ca 4,600 km²) as part of a peneplained horst is largely occupied by rolling plains and low hills 30-50 m high (Aleksandrova, 1980). The deposits consist of Cenozoic sediments. Isolated heights with flat summits and cryoplanation terraces are typical of the New Siberian Archipelago. On Bol'shoy Lyakhovsky Island, several granite elevations reach up to 311 m a.s.l. They are regarded as remnants of a former plateau (Aleksandrova, 1980).

2.2. Climate

The Laptev Sea has fundamental influence on the modern climate of Bol'shoy Lyakhovsky Island, resulting in high cloudiness and fog frequency connected with low insolation and air temperature during the growing season (Fig. 3). The annual mean temperature is -15.1 °C at the nearby station Cape Shalaurova (location in Fig. 1, lower part) and scarcely differs from

values recorded in Kazache and Verkhoyansk (locations in Fig. 2) about 400 km south of the sea coast (Fig. 3, Rivas-Martínez, 1996-2004). In contrast, the mean temperature of the warmest month (MTWA, today July), which is crucial for plants, is only 2.8 °C opposite to 10.0 °C in Kazache and 13.9 °C in Verkhoyansk, documenting the impact of oceanicity. Increasing oceanicity towards the coast is also illustrated by the difference in mean temperatures of the coldest month (January), e.g. -32.2 °C at Cape Shalaurova compared to -36.4 °C in Kazache and -48.6 °C in Verkhoyansk (Fig. 3).

Fig. 3

The annual precipitation is only 253 mm (Rivas-Martínez, 1996-2004) owing to prevailing anticyclonal circulation in winter. Nevertheless, precipitation exceeds evaporation, which is also very low in consequence of cool summers. Thus, humid conditions prevail today. The humidity in the coastal lowlands and on the shelf islands is directly linked to their coastal position and the resulting oceanic influence today and is in contrast to cold stages, when the study region was farther inland (Romanovskii et al., 2000). Cool summers result in active layer depths of only 20-40 cm and low evaporation rates. Because of the non-permeability of permafrost, the active layer is wet; drainage is largely restricted to surface run-off.

2.3. Vegetation

Owing to soggy soils, the vegetation of constantly wet places is frequent in the landscape together with snow bed and wetland communities. Due to its wetness, the soil temperature at these sites is decreased, resulting in low productivity, poor species diversity and the dominance of mosses. After the Circumpolar Arctic Vegetation Map (CAVM-Team, 2003), the study area is covered by moist tundra (G1) and sedge/grass, moss wetland (W1), both vegetation units characteristic of the northernmost, coldest bioclimatic subzones A and B. The moist tundra is composed of very low growing (5-10 cm) plants, mainly grasses, rushes, forbs, mosses, lichens, and liverworts in a single layer and a moderate coverage of 40-80 %. Wetland vegetation consists mainly of sedges, grasses and mosses.

The vegetation of Bol'shoy Lyakhovsky Island was described in detail by Aleksandrova (1980). The island is situated in the northern belt of the arctic tundra zone, where poor spotty tundra dominates with plant coverage of approximately 50 - 65% (Aleksandrova, 1980). At characteristic sites, *Alopecurus alpinus* (occupying 15% of the covered area) and *Salix polaris*

6

(up to 60%) prevail together with other arctic elements such as *Luzula confusa, Potentilla hyparctica, Ranunculus sulphureus*, and arctic poppies.

The absence of any boreal or subarctic floral element especially of subarctic shrubs such as *Betula exilis* or *Duschekia fruticosa* in zonal habitats is another characteristic feature for that region (Aleksandrova, 1980). Arctic dwarf and prostrate willows (*Salix polaris, S. nummularia*) are the only shrubby plants. In habitats with a thin snow cover, denuded tundra (15-40% coverage) with *Deschampsia brevifolia* and *Festuca brachyphylla* is the typical vegetation. *Dryas*-dominated tundra with up to 80% coverage occurs at places sheltered from wind and favored by exposition. Also *Salix reptans* is present at such sites. Polygonal wetland tundra with a peat layer up to 15 cm thick develops in lowland areas with stagnant moisture and poor drainage. In the low centers of polygons *Dupontia fisheri, Eriophorum polystachion, E. medium*, and the mosses *Drepanocladus revolvens, D. vernicosus* and *Calliergon sarmentosum* prevail. *Arctophila fulva* and *Carex stans* occur emerging in shallow depressions with stagnant water. Wetland vegetation with *Eriophorum scheuchzeri* and *Alopecurus alpinus* appears in thermokarst depressions. The elevations on Bol'shoy Lyakhovsky Island including Mount Khaptagai Tas (185 m a.s.l.) close to the study site can be divided in several vertical vegetation belts, (1) a lower belt with herb-moss tundra on skeletal-loamy soils, (2) impoverished mountain tundra on stony pioneer soils and debris, and (3) polar desert-like barrens on patterned stony ground (Aleksandrova, 1980).

3. Materials and methods

3.1. Study Site

A natural outcrop, made accessible by thermal and coastal erosion of ice-rich permafrost deposits on the southern coast of Bol'shoy Lyakhovsky Island (73°20´N, 141°30´E), was studied for plant macrofossils (Fig. 4). The outcrop consists of several thermo-erosional cirques and extends several km along the coast of the Dimitri Laptev Strait on both sides of the Zimov'e River mouth (Fig. 4). A thermo-erosional cirque is a steep, horseshoe-shaped headwall of a retrogressive thaw slump. Due to thermal erosion and ice wedge thawing, such a steep wall is divided into numerous thermokarst mounds. The sequence of up to *c*. 200 ka old permafrost deposits consists of frozen deposits of mid and late Quaternary origin (Fig. 4), described in detail in Schirrmeister et al. (2000, 2002) and Andreev et al. (2004b; Andreev et al., submitted).

The lowermost accessible unit was deposited under cold-stage conditions according to sediment characteristics (ice-rich, sandy silt) and pollen signature (typical tundra-steppe

spectra; Andreev et al., 2004b). A peat lens of about 30 m length and 1 m thickness trapped in these deposits was dated by the ^{230}Th/U rate reliably to 209 ± 3.4 ka BP (Schirrmeister et al., 2002). The sediments are thus of Saalian (Taz) origin. Above, there are freshwater deposits filling ice wedge casts, which according to stratigraphy (above the Saalian and below Weichselian cold stage deposits), pollen signature (clearly warm stage spectra) and dating (out of the range of the AMS method) formed during the Eemian interglacial (Andreev et al., 2004b). They indicate that, during the last warm stage analogous to the current one, thermokarst and thermal erosion were widespread in the arctic lowlands of NE Siberia resulting in lake formation. Early Weichselian (MIS 4, Zyryanian) floodplain deposits, Middle Weichselian (MIS 3, Karginian) Ice Complex deposits, AMS dated to *c*. 50-30 ka BP, and Holocene fluvial, alluvial, slope, and alas sediments, AMS dated to *c*. 9-3.7 ka BP (Andreev et al., submitted) partly underlain by taberits (formerly thawed, then refrozen taliks) complete the sequence. All units above the Eemian Interglacial sequence are penetrated by various types of ice wedges both epigenetic and syngenetic, in each unit of characteristic size, shape, and structure (Meyer et al., 2002). The described units are traceable across several km along the coastal outcrop.

Fig. 4

For the present study, the subprofiles L12+30 and R22+60, exposing Saalian (MIS 6, > 130 ky BP) and Eemian (MIS 5, *c* 130 kyr BP) deposits, were sampled for plant macrofossil studies (Figs. 4+5). The analysed sediments correspond to samples that were already used for pollen, chironomid, rhizopod, and beetle analysis (Andreev et al., 2004b). Another subprofile (R35) was earlier studied in fine stratigraphical details for pollen and chironomids (Ilyashuk et al., 2006). From this subprofile, we investigated plant macrofossils from the sample S9, 200 cm above sea level (Fig. 5), which corresponds to the warmest interval of that sequence according to pollen-based reconstructions. The macrofossil composition has been used for the reconstruction of the MTWA resembling Iversen (1944) to gain comparisons with results of pollen-based climate reconstructions. In parallel, a quantitative reconstruction of temperature and moisture conditions during the deposition period of the R35 section is provided using the published pollen record (Ilyashuk et al., 2006) and the best modern analogue (BMA) approach (Guiot, 1990). For detailed descriptions of pollen-climate reference data sets and calculation techniques used for the BMA reconstruction see Andreev et al. (2004a).

Fig. 5

3.2. Taphonomy and macrofossil preservation

The samples OS 49 to OS 52 and OS 58 (Fig. 5), originating from ice-rich deposits under the Eemian ice wedge casts and assumed to be of Saalian cold stage origin, correspond to Weichselian Ice Complex deposits in cryo-structure and macrofossil composition. They are syngenetically frozen and mainly consist of yellowish-grey silty sediments with a low addition of pebbles, gravel, peat inclusions, fine sand and plant detritus. The plant remains are very poorly preserved and reflect a low-diverse spectrum of plants, mainly arctic pioneer plants, halophytes, and unidentifiable grasses (Tab. 1), reflecting a poor tundra-steppe under cold and dry climate. Given their very poor preservation, we abstained from a detailed interpretation of Saalian macrofossil spectra.

In contrast, the studied last interglacial macrofossil assemblages are exceptionally well preserved and, composed of remnants of 100 vascular plant taxa, very diverse (Tab. 1+2). They were obtained from organic-rich sediments deposited in or above ice wedge casts. The sampled Eemian sediments were deposited in shallow lakes, indicated by the inclusion of freshwater organisms such as aquatic plants, ostracods, molluscs and dormant *Daphnia* eggs. The grain size distribution clearly proves a deposition in small bodies of standing water. Thus, the sediments are unaffected by fluvial deposition. The exceptional preservation of macrofossils also argues against long-distance transport. The deposition within ice wedge casts suggests rather that the small lakes or ponds were formed as a result of thermokarst processes. Due to the thermal erosion of terrestrial ice-rich permafrost sediments, terrestrial plant remains were incorporated into subaquatic deposits during lake formation. The preserved plant macrofossils are thus of both terrestrial and shallow freshwater origin. Another likely source of sediments is lateral transport into the existing lake by wind deposition, melt water run-off and slope ablation. Eemian lacustrine sediments could not be traced continuously along the whole coastal outcrop of about 4 km. There were, instead, several separate Eemian sequences about 3 km apart, deposited probably in two different small and shallow lakes each with a former size of probably several dozens to several hundred m (Fig. 2 in Andreev et al. 2004). Three Eemian lacustrine sequences (L12+30, R22+60 and R35) were studied palaeobotanically.

3.3. Laboratory techniques

The samples were taken from undisturbed frozen sediments and air-dried in the field. In the laboratory, 500 g of each sample were dispersed in water, sieved using several mesh sizes (0.25, 0.5, 1, and 2 mm), and dried. For sample S9 from the subprofile R35, only 180g were available. Identifiable plant remains, mainly seeds, fruits, scales, buds, and leaves, were picked under a binocular. Their identification to the most precise taxonomic level possible was based on a reference collection of seeds, fruits, and herbarium material taken during several expeditions in central and north Yakutia. Additionally, use was made of several identification keys and atlases. The nomenclature of identified vascular plants follows the 'Vascular Plants of Russia and Adjacent States' (Czerepanov, 1995). Many arctic taxa are phylogenetically very young. Speciation processes in such widespread arctic taxa as *Draba, Cerastium, Potentilla*, and *Papaver* sect. *Scapiflora* are still in progress, resulting in frequent hybridisation of related species, polyploidisation, apomictic reproduction and reticulate evolution (Brochmann et al., 1992; Brysting et al., 2007). In most cases, an identification of species within these genera or sections by seeds is impossible as is shown for *Draba* by Brochmann (1992). We abstained from identifying plant species within such genera or designated taxa with cf. (looks like a similar species) or s.l. (sensu lato, in a broad sense).

Tab. 1

Tab.2

4. The vegetation of the last interglacial

The last interglacial macrofossil assemblages (Tabs. 1+2) reflect a rich flora representing a wide spectrum of plant communities that obviously existed in a broad range of available habitats. These plant communities mirror an Eemian landscape and vegetation complex consisting mainly of subarctic shrub tundra interspersed with patches of grasslands, high-arctic pioneer and snow-bed communities as well as perennial and impermanent lakes that supported aquatic, littoral, and wetland vegetation.

Such a diverse vegetation complex clearly differs from the monotonous arctic tundra that exists today in the study area (chapter 2.3). Aleksandrova (1980) distinguishes the subarctic tundra from the arctic one by the presence of birch and alder shrub thickets and meadow communities. In contrast to today, plants typical of such birch and alder shrub thickets and grasslands were present during the Eemian and dominated the pollen spectra (Andreev et al., 2004b) and macrofossil assemblages (Tab. 1 & 2) from the study site; they document a

northward shift of climate and vegetation zones during that time. The species composition is similar in all Eemian assemblages and particularly the signature of the community composition does not differ within the Eemian sequence even though the abundance of certain plant species fluctuates. It is impossible however to distinguish between environmental and taphonomical reasons for such small scale fluctuations. Regarding their modern ecological requirements and habitats, it is obvious that most plant species might have occurred in several plant communities that existed coevally. While reconstructing the palaeovegetation, we kept in mind that plant communities merge into one another at habitat transition zones. Therefore, we discussed ecologically related plant communities jointly. The palaeo-communities reconstructed by macrofossils of their indicative plant species are subsequently discussed separately. Following Kienast (2006), the reconstruction of the Quaternary palaeo-vegetation is based on modern plant sociological grouping according to the principle of uniformitarianism. To make reconstructed plant communities comparable with modern ones, we described the palaeo-vegetation using higher syntaxa according to the international code of phytosociological nomenclature (Weber et al., 2000), and referred to descriptions in the Circumpolar Arctic Vegetation Map (CAVM-Team, 2003).

4.1. Subarctic Shrub Tundra (Betulo-Adenostyletea Br.-Bl. et R. Tx. 1943, Vaccinio-Piceetea Br.-Bl. 1939)

According to the dominance of shrubs and especially the presence of tall shrubs like *Duschekia fruticosa* (synonym: *Alnus fruticosa)* and *Betula fruticosa* in the macrofossil record (Fig. 6), subarctic shrub tundra primarily constituted the plant cover at the study site during the last interglacial. Among low shrub species, *Betula nana* s.l., *Vaccinium vitis-idaea, Ledum palustre*, and *Empetrum nigrum* s.l. are preserved as macrofossils. The macro remains of *Betula nana* s.l. and *Empetrum nigrum* s.l. cannot be identified in finer detail. Probably they originate from the vicarious species *Betula exilis* and *Empetrum subholarcticum*, the only members of their respective species groups (artenkreis) in the study region (Aleksandrova, 1980; Tolmachev & Yurtsev, 1980; Cherepanov et al., 2000). The only feature of *B. exilis* differing from *B. nana s.str* is the existence of resinous warts on young twigs (Cherepanov et al., 2000). Differentiation by macrofossils is thus impossible. The reconstructed vegetation corresponds approximately to descriptions of low-shrub tundra (S2) typical of the southernmost arctic bioclimatic subzone E in the Circumpolar Arctic Vegetation Map (CAVM-Team, 2003). Today, the closest occurrence of that vegetation is about 350 km SW of the study site at the lower course of the Yana River. The abundance of tall shrubs,

alder in particular, points to the proximity of the tree line (CAVM-Team, 2003). *Duschekia fruticosa* was one of the most common taxa in the record, suggesting that the Siberian shrub alder was a principal constituent of the interglacial vegetation. This assumption is supported by the evidence of *Boschniakia rossica,* an uncommon Orobanchaceae that parasitises on *Duschekia fruticosa* (Fig. 6). The European shrub alder *Duschekia abnobetula* (synonym: *Alnus viridis*) is characteristic of subalpine forb and shrub vegetation (Betulo-Adenostyletea) in European mountains above the forest line, and at former forest sites after zoogenic disturbances (Pott, 1995). Corresponding habitats close to the polar forest line can be assumed for the closely related and ecologically similar *D. fruticosa* in northern Siberia.

Among forbs, typical of the herb layer of northern birch and alder shrublands and open forests in Siberia, we found *Moehringia laterifolia*, *Chrysosplenium alternifolium* and *Bistorta vivipara* (Dierßen, 1996; Malyschev and Peschkova, 2003). Several of the found crowfoot species (*Ranunculus propinquus, R. turneri*), occur there as well, albeit in particular under grazing influence (Dierßen, 1996).

Fig. 6

4.2. Steppe vegetation (Koelerio-Corynephoretea Klika ap. Klika & Nowák 1941, Festuco-Brometea Br. Bl. & R.Tx. 1943)

Although plants of shrub tundra dominate the record, steppe and meadow species are abundant in all studied samples as well (Fig. 7). The Eemian existence of steppes is indicated by plant macrofossils namely among dicotyledonous herbs, e.g. *Artemisia sp., Potentilla cf. arenosa, P. cf. stipularis, Rumex* subgen. *Acetosella*, *Androsace septentrionalis*, *Myosotis sp.* (the only species in NE-Siberia is *Myosotis asiatica)* and the sedges *Carex duriuscula* and *C. supina* s.l.. Due to their very long style, the fossil nutlets of *C. supina* seem to originate from the subspecies *C. supina ssp. korshinskyi* (Fig. 7.), but the subspecies that occurs today closest to the study site is the boreal-subarctic *C. supina ssp. spaniocarpa* (Meusel et al., 1965). Grasses are frequently proven, but could not be identified down to the species level. Steppe plants certainly reflect dry local habitat conditions. They are furthermore supported by disturbances, especially by grazing. Most of the proven species are also typical of sandy substrates. Depending on soil water regime and exposure, steppe communities likely formed mosaics with shrub thickets, saline *Puccinellia*-meadows, and Kobresietea-communities as known today from continental regions of high latitudes (Böcher 1954). Northern steppes often merge floristically in Kobresietea communities.

Fig. 7

4.3. Dry arctic upland vegetation (Carici rupestris - Kobresietea bellardii Ohba 1974)

Arctic upland communities are indicated by fossil remains of *Kobresia myosuroides, Dryas octopetala s.l., Potentilla cf. nivea, Minuartia arctica, Gastrolychnis involucrata, Lloydia serotina, Ranunculus affinis* and *Rhododendron* sp. (Fig. 7). The macro remains of *Dryas octopetala s.l.* probably come from *D. punctata,* which is the only *Dryas* species in the study region (Polozhij & Malyschev, 2004). The special feature of *D. punctata* leaves, a glandular upside of leaves (Polozhij & Malyschev, 2004), could not be detected on fossil leaf fragments. *Ranunculus affinis* (synonym: *R. pedatifidus*) is described from tundra steppe analogues at dry, south-facing pingo slopes in arctic Alaska (Walker et al., 1991). Kobresietea communities are cold-resistant and form the climax vegetation at relatively dry, exposed sites in the arctic and the alpine belt of mountains with a thin or no snow cover in winter. Their constituents are able to withstand great seasonal and even diurnal temperature fluctuations. Occurring in vegetation complexes with steppe and salt meadow communities (Böcher, 1954; Yurtsev, 1982), they are characteristic of continental regions within the Arctic under non-acidic soil conditions. Due to humidity, high arctic plants that are characteristic of non-acidic, dry habitats and little snow cover like *Kobresia myosuroides* are today rare in the Siberian Arctic and mainly restricted to mountainous regions.

4.4. Pioneer communities (Thlaspithea rotundifolii Br.-Bl. 1948, Stellarietea mediae R.Tx., Lohm. & Prsg. Ap. R. Tx. 1950) and snow bed vegetation (Salicitea herbaceae Br.-Bl. 1947)

Arctic pioneer plants including *Draba sp., Minuartia rubella,* and *Papaver* sect. *Scapiflora,* characteristic of fine debris at dry, exposed, frequently disturbed sites in the Arctic, are abundant in the studied interglacial deposits. Due to the conditions of arctic permafrost (wetness, fine-grained substrates, solifluction), however, most of the found arctic pioneer species possess a clear affinity to moist sites, and often occur also in snow-bed communities. The latter applies, among the found macrofossil species, especially to *Cerastium cf. beeringianum, C. cf. jenissejense, Gastrolychnis involucrata, Luzula confusa, Eutrema edwardsii,* and *Sagina intermedia*. They appear today both in arctic pioneer communities on circumneutral to base-rich, fine debris (the alliance Arenarion norvegicae within the class Thlaspithea rotundifolii) and in snow-bed vegetation on wet soils, influenced by solifluction (alliance Saxifrago-Ranunculion nivalis within the class Salicitea herbaceae, Dierßen, 1996;

13

Möller, 2000). Among the genera *Salix* and *Alopecurus,* which also were preserved as macrofossils, *Alopecurus alpinus, Salix polaris*, and *S. herbaceae*, are characteristic of snow-bed communities. Another moist site pioneer is *Descurainia sophioides,* whose seeds were evidenced continuously throughout the sequence of interglacial sediments partly in large quantities (Tab. 1). This weed is known for occupying exclusively moist, disturbed sites in high latitudes. After soil stabilization and the invasion of other plants, the species cannot compete and perishes (Mckendrick, 2000). It also occurs at animal burrows and in overgrazed areas. Its evidence may indicate frequent disturbances by animals. Consistently, faeces of rodents were frequently found in the studied deposits.

4.5. Wetland vegetation (Scheuchzerio-Caricitea nigrae (Nordh. 1936) R. Tx. 1937)

In the studied sediments, *Eriophorum polystachion, E. scheuchzeri, E. brachyantherum, Carex aquatilis, C.* sect. *Phacocystis, Juncus biglumis, Chrysosplenium alternifolium, Comarum palustre, Caltha palustris, Parnassia palustris, Ranunculus hyperboreus, R. lapponicus* and *Gastrolychnis violascens* represent sedge-dominated wetland communities. Such vegetation occurs on constantly wet soils above permafrost and played an important role in the Arctic during warm stages in contrast to cold stages when precipitation was low. The peat accumulation in wetland habitats during the last interglacial was obviously insufficient for the establishment of typical peat mire plants such as *Eriophorum vaginatum*.

We found many macrofossils of today extralimital, warmth-demanding wetland plants like *Parnassia palustris, Epilobium palustre*, *Comarum palustre, Eriophorum gracile,* and *Menyanthes trifoliata* (Fig. 8). They indicate, together with aquatics, shrubs, and steppe plants of likewise southern present distribution, Eemian summer mean temperatures distinctly higher than today. Also *Eriophorum brachyantherum* does not extent far beyond the arctic tree line (Aiken et al., 1999) and thus indicates summer-warm conditions.

4.6. Moist pastures and saline floodplain meadows (Molinio-Arrhenatheretea R. Tx. 1937, Juncetea maritimi Br.-Bl. 1931)

Numerous plants, typical of floodplain meadows, moist pastures or drained former fens including *Agrostis* sp., *Alopecurus* sp., *Deschampsia* sp., *Calamagrostis* sp., *Ranunculus propinquus* and *R. repens* have been preserved as macrofossils. Within the genus *Calamagrostis*, the meadow plants *C. langsdorffii, C. neglecta, C. holmii* and *C. angustifolia* occur in the study region today. Under slight saline influence and seasonally fluctuating groundwater level, *Puccinellia sp.* together with *Alopecurus* species (e.g. *A. arundinaceus, A.*

14

glaucus) may become dominant. Both genera were found in Eemian deposits at the study site. Occurring out of the range of periodical flooding, these saline meadows merge floristically into halotolerant, seasonally inundated littoral pioneer vegetation described in the next paragraph.

4.7. Littoral vegetation (Bidentetea tripartitae R. Tx. et al. ap. R. Tx. 1950)

Annual littoral pioneer vegetation including *Tephroseris palustris, Rorippa palustris, Stellaria crassifolia* and *Rumex maritimus* (Fig. 7) is characteristic of periodically inundated, nutrient rich, fine-grained soils at muddy littoral sites along margins of pools and lakes in various climate zones. This vegetation is supported by a seasonal alternation of inundation and drying up and frequent disturbances e.g. trampling by cattle. It is thus characteristic of lake shores that retreat in the course of the summer due to high evaporation. *Tripleurospermum hookeri, Gastrolychnis involucrata, Ranunculus hyperboreus* and *Rumex arcticus* are also characteristic of disturbed and fluctuating lake and sea shores, but they occur exclusively in the Arctic. *Tripleurospermum hookeri* (Fig 7) occurs also at moist places not covered by vegetation like fresh alluvium at the lower course of rivers and thermoerosional slopes, but it has a clear affinity to saline environments. Thus, its modern habitats are mainly moist, sandy places by the seashore (Aiken et al., 1999). High salt content in soils is also indicated by *Stellaria crassifolia* and *Rumex maritimus* (Fig 7), which are typical pioneers at muddy sea shore sites and otherwise at fluctuating shore lines of inland lakes under salt influence due to an arid climate (Hilbig, 1995). *Ranunculus hyperboreus* occurs in various communities within wetlands, salt marshes, snow beds and even pioneer vegetation (Möller, 2000) mainly at sites with waterlogged soils that may dry out in summer. This plant has a broad tolerance regarding salt concentration and is abundant in saline and non-saline situations. In northern Europe, *Ranunculus hyperboreus* is described as characteristic of steadily wet, humous, silty soils at shore sites of brackish brooks and at the sea shore (Dierßen, 1996).

4.8. Aquatic vegetation (Potamogetonetea R. Tx. & Prsg. 1942, Charetea fragilis Fukarek ex Krausch 1964)

Compared with the modern flora in this region, the aquatic flora from the last interglacial was very rich and included *Callitriche hermaphroditica, Potamogeton vaginatus, Myriophyllum spicatum, Batrachium sp., Nitella sp., Hippuris vulgaris, Sparganium hyperboreum* and *S. minimum* (Fig. 8). All these species indicate the presence of shallow

freshwater lakes and ponds with mesotrophic, circumneutral or slightly alkaline water under a boreal climate. Among the genus *Batrachium, B. eradicatum* advances today farthest to the north in Yakutia (Hulten and Fries, 1986). The plant is characteristic of stagnant waters particularly at temporarily disturbed, open riparian sites with fluctuating water levels (Ranunculion aquatilis, Dierßen, 1996). Fluctuating salt concentration and frequent disturbances highly support this *Batrachium* species (Dierßen 1996). Also *Hippuris vulgaris* and *Callitriche hermaphroditica* are typical of shallow, mesotrophic, limy, sometimes brackish ponds and lakes with fluctuating water level (Dierßen 1996). *Potamogeton vaginatus* is interpreted as an indicator of slight or fluctuating salt content correlated with aridity (Kienast et al., 2005).

Fig. 8

5. Environmental and climatic implications

5.1. Summer mean temperature and tree line

The dominance of *Betula nana s.l.* and in particular of *Duschekia fruticosa* together with a high proportion of other boreal species in the studied macrofossil assemblages are indicative of the immediate vicinity of the tree line during the Eemian. Such species combination is today characteristic of the southern belt of the subarctic tundra adjacent to the tree line (Aleksandrova, 1982; CAVM-Team, 2003). In this context, we must note however that a strict latitudinal succession of vegetation belts presumably did not exist during former warm stages in the way we know it from the recent plant cover in northern Eurasia. Instead, boreal forests have been more open and insular in character and formed mosaics with grasslands (Frenzel, 1968; Sher, 1991; Lozhkin and Anderson, 1995). Today, the main constituent of coniferous forests in northern Yakutia is larch (*Larix dahurica*). Owing to their situation very far north, larch forests might have been replaced at today's Bol'shoy Lyakhovsky Island during the last interglacial by shrub thickets mainly composed of shrub birches and alders. The absence of macrofossil proof, however, does not mean the complete absence of larch in the whole study region during the Eemian, because *Larix* occurred north of its present distribution in the Pleistocene even during cold stages as is evidenced by macrofossils in a mammoth stomach at 74°N on the Taymyr Peninsula dated about 21 ky BP (Mol et al., 2006). The growth of trees in the north is supported by a continental climate and, respectively, inhibited by paludification due to rising oceanic influence in favour of wetland tundra (Crawford et al., 2003). As revealed by the relatively high proportion of plants indicating

16

unsteady or low moisture and high evaporation, the conditions for the survival of trees during the Eemian were much better than today. They indicate the existence of dry and well drained sites in the study area. The establishment of trees and tall shrubs at the arctic tree line depends on the availability of well-drained sites (Lloyd et al., 2003). It is inferred from pollen data that an open *Larix–Betula* forest existed at the nearby Yana Lowland during the last interglacial (Lozhkin and Anderson, 1995). *Larix* pollen was found in low quantites also in the studied sequence (Andreev et al., 2004b). It must be noted that larch pollen is in general underrepresented in sediments. No larch macro remains were found; larch was thus locally absent. Its former presence in the region is possible however; but it was rare then and there were no closed forests. The larch occurred, according to Sher (1991), spatially very restricted in north Siberia during the Eemian Interglacial. Accordingly, birches were the main constituents of woods. Despite the lack of macrofossil evidence, the occurrence of tree birches on today's Bol'shoy Lyakhovsky Island during the last interglacial cannot be completely excluded because most of the few found *Betula* catkin scales that were found were poorly preserved and thus did not allow an exact identification. The discrimination of shrub alder and tree birch nutlets is very difficult without wings, because nutlet shapes of shrub alder and tree birch scarcely differ (Fig. 6) in contrast to fruit bodies of dwarf and tree birches (Van Dinter and Birks, 1996). Venation and the edges of fossil leaf fragments leave no doubt that there coexisted at least three different shrubby species of Betulaceae with similar nutlets (Fig. 6) – *Duschekia fruticosa, Betula fruticosa* and *B. nana*. Tree birch pollen was found in a small quantity in the examined Interglacial sequence (Andreev et al. 2004b).

At the nearest modern occurrence of the subarctic shrub tundra above described on the lower course of the Yana River, the mean temperature of the warmest month (MTWA) reaches 10-12.5 °C (VMGO, 1980), a value that can be expected for our study site during the Eemian. Using the best modern analogue (BMA) approach, the calculation of modern climate values based on a set of 1,173 surface pollen samples from northern Eurasia (Tarasov et al., 2005) suggests a MTWA of 10 to 15 °C, for pollen assemblages with an average percentage of 30-40% *Duschekia fruticosa* pollen. Such a percentage of shrub alder is characteristic of our studied Eemian samples (Andreev et al., 2004b). The presumably immediate vicinity of the tree line shifts supposed MTWA values towards 12 °C, the minimum for trees (Lozhkin and Anderson, 1995).

The macrofossil finding of numerous warmth-demanding, today extralimital plant species especially among aquatic and wetland plants is another indicator of mean summer temperatures much higher than today. Aquatic and wetland plants are regarded as especially

17

good temperature indicators since they are independent of exposition and the altitude of the sun (Iversen, 1954).

In the following, we present a compilation of plants that occurred in the studied region during the Eemian and whose northernmost distribution limit is considerably farther south today (Tab. 3). Steppe plants are excluded from that compilation due to their affinity to extrazonal habitats, which can be climatically favoured by declination and exposition and thus do not reflect the macroclimate. Also *Potamogeton vaginatus* was excluded because, according to Rebristaya et al. (1995), arctic occurrences of that boreal aquatic are evidently due to fluvial transport of its fragments northward. The northernmost genuine occurrence in Yakutia according to Krasnoborov (1988) is on the Vilyuy River, Central Yakutia, where the MTWA exceeds 17.5 °C. A climatic interpretation of the modern distribution of that plant is very difficult, however, since it is obviously associated with other environmental factors, in particular with brackish waters.

For the reconstruction of the MTWA, we considered the modern distribution of plants exclusively within Yakutia for the following reasons.

- The degree of continentality must be comparable within the considered region because the response of plants to certain climate parameters, like the MTWA, depends on their interaction with other climate parameters such as the period of snow cover, the percentage of sunshine duration, humidity etc.

- The genetic diversity and thus climatic adaptability of plant species in high latitudes vary considerably in different parts of their distribution area. In contrast to western Eurasia, Yakutia was climatically always continental throughout the Quaternary and was not covered by large inland ice sheets. Within a glacial–interglacial cycle, the climate in eastern Siberia consequently did not change as radically as in the more oceanic western regions of Eurasia, where northern plants had to deal with range losses and increasing continentality due to ice sheet formation (Kienast, 2006). Yakutian plants are therefore relatively stable in their genetic configuration. The high percentage of polyploid species among arctic plants in oceanic West Eurasia contrasts with the flora of the Yakutian refuge areas and is a distinct indicator of the frequent isolation and subsequent fusion of very small populations in consequence of glaciations (Murray, 1995). Allopolyploidy, as a strategy against gene pool impoverishment due to the founder effect, results in broader genetic variability among plants. Polyploid plants therefore possess a broader climatic tolerance. In contrast, the genetic diversity of Yakutian plants is smaller and their

18

climatic indication is more precise than those of their more western, often polyploid conspecifics.

Plant distribution depends to a large degree on continentality. The borders of Yakutia's mainland correspond well with the sphere of the northern ridges of the Siberian anticyclone in winter and, respectively, with greatest continentality in northern Eurasia. In contrast, the adjacent Taymyr Peninsula is already influenced by the subpolar low pressure trough and the Chukotka Peninsula is under control of monsoonal activity, both resulting in higher winter precipitation – a precondition for ice sheet formation during cold stages.

Tab. 3

From the climate values at the northernmost modern occurrences of extralimital plants listed in table 3, we are able to estimate an MTWA of at least 12.5 °C under the given conditions of continentality. The reconstruction is based on the assumption that the MTWA is the major climate factor that limits plant growth in this region. Winter temperature is irrelevant since it decreases even further southwards due to the Siberian High. Also other climate parameters such as precipitation do not change dramatically over large distances there (VMGO, 1980).

A reconstructed MTWA of 12.5 °C (*c.* 10 °C higher than today) far exceeds previous pollen-based estimates of MTWA deviations, which ranged between 4 and 5 °C (Frenzel et al., 1992; Andreev et al., 2004b; CAPE-Last Interglacial Project, 2006). For a comparison of our macrofossil-based climate interpretation and to get a more regional picture, we additionally performed a quantitative pollen-based BMA reconstruction of thermal and moisture conditions during the last interglacial from the 4-m long R35 section (Fig. 9), which is assumed to represent the complete development of a thermokarst lake in the course of the last interglacial (Ilyashuk et al., 2006). The results (Fig. 9) confirm that the study region experienced summers substantially warmer than present. Accordingly, the BMA reconstructions reflect, in the lower part of the R35 record, probable MTWA values of 6-10 °C, thus about 3 to 7 °C warmer than present. Later, the MTWA dropped to 4-6 °C. From sample S9 at 200 cm a.s.l., which reflects the warmest interval in the R35 section (Fig. 9), the studied macrofossils indicate that the MTWA reached 12.5 °C or even higher values (Figs. 6-8, Tab. 3), shifting the confidence interval within the reconstructed BMA range of 9-14.5 °C towards the upper limit. Although the Eemian summers were noticeably warmer than at present, the reconstructed values of GDD5 (growing degree days, annual sum of mean-day

temperatures above 5 °C) were lower than 350 °C except for the sample S9 at 200 cm a.s.l.. This value is regarded as the lower limit for the growing of boreal tree species (Prentice et al., 1992). According to the reconstructed GDD5 values close to the tree growth limit, the tree line might have been very close to the sampling site during the last interglacial optimum. This conclusion is in agreement with our qualitative interpretation of the plant macrofossil assemblages above in this chapter.

Warm summers with an MTWA of up to 12 °C were also reconstructed for today's mainland coast of the Laptev Sea during the last cold stage, especially during the Middle Weichselian Interstadial (Kienast et al., 2005). The vegetation during that time was characterised, however, by extensive absence of subarctic shrubs. We interpret this difference as the result of significantly lower precipitation during the last cold stage and, in particular, of deficient snow cover in winter, which is crucial for the survival of subarctic shrubs, including shrub birches (Kaplan, 2001).

Fig. 9

5.2. Water balance

Our pollen-based reconstruction for the older part of the R35 alas lake record (Fig. 9) suggests similar to present annual precipitation sums, e.g. 200-300 mm/yr in comparison with a modern value of 253 mm/yr (Rivas-Martínez, 1996-2004). The presence of grassland vegetation such as steppe and meadow communities and arctic *Kobresia* meadows during the last interglacial, however, represents a fundamental difference to the constantly wet and monotonous modern wetland tundra (chapter 2.3) because it indicates that locally dry habitat conditions must have existed, probably connected with increased evaporation. This result confirms that the current humidity in the arctic coastal lowlands of Yakutia is a function of low evaporation due to low temperature and is not the result of high precipitation. The small content of Ericales pollen in the studied interglacial deposits is correlated with considerably drier conditions than today (Andreev et al., 2004b), also suggesting that evaporation, due to warming, greatly increased. Later in the lake's history, the precipitation decreased to 150-200 mm/yr (Fig. 9).

The open character of the NE-Siberian interglacial shrublands and their coexistence with grasslands could also have been the consequence of grazing by large herbivores. The Eemian dominance of *Duschekia fruticosa* might be an indication of certain grazing pressure. South of the polar and below the alpine timber line, shrub alder replaces trees at grazed places. There,

it is regarded as an indicator of potential forest sites (Pott, 1995). Some crowfoot species (*Ranunculus propinquus, R. repens*) are typical of the herb layer in northern forests particularly under grazing influence but occur otherwise mainly in moist pastures (Dierßen, 1996). *Ranunculus propinquus* (synonym: *Ranunculus borealis*) is considered a northern race of the pasture weed *R. acris* (Cherepanov et al., 2000). Also several wetland plants such as *Carex aquatilis*, *Deschampsia* sp., *Agrostis* sp. (e.g. *A. canina* s.l.) and *Caltha palustris* tolerate grazing and appear in wet pastures too. The presence of herbivores during the last interglacial is furthermore indicated by coprophilous fungi spores (Andreev et al., 2004b). A grazing impact by large herbivores during the last interglacial is thus probable. Steppes and floodplain meadows formed potentially important food resources for herbivorous mammals.

Kobresia myosuroides is also supported by grazing but mainly by little or no snow cover in winter (Dierßen, 1996). However, snow bed vegetation, indicating locally thick snow cover, was also present. In contrast to *Duschekia fruticosa*, the presence of *Betula nana s.l.* depends on sufficient snow cover (Aleksandrova, 1980). Together with the evidence of chionophobic plants like *Kobresia myosuroides* and *Potentilla nivea*, this result might indicate a very variable snow cover depending on topography. Precipitation comparable to today can be interpreted as a sign of a locally thick snow cover explaining the presence of the subarctic shrubs, especially *Betula nana s.l.*, which requires a snow cover higher than 15 cm for surviving the extremely cold arctic winters (Kaplan, 2001).

Species of aquatic and wetland vegetation were also important components in the Eemian macrofossil records. However, they do not reflect necessarily wet climate conditions but might indicate the former existence of shallow lakes and seasonally inundated depressions, which formed as result of intense thermokarst and thermoerosional processes. Melting of the extremely ice-rich permafrost deposits occurred at the study site also during the Eemian Interglacial (Andreev et al., 2004b). The pioneer character of aquatic and littoral vegetation indicates water level fluctuations and seasonal lakeshore retreat due to high evaporation rather than excessive wetness. Similarly, the former occurrence of *Puccinellia sp.* and the halophytic littoral plants *Stellaria crassifolia, Rumex maritimus*, *Rorippa palustris* and *Tripleurospermum hookeri* reflect seasonal water level oscillations and salt accumulation as a result of high evaporation. Also most of the found aquatics are tolerant of brackish waters, disturbances, and lake level fluctuations. The floral composition in arctic Yakutia during the Eemian, containing *Puccinellia sp., Rumex maritimus*, *Stellaria crassifolia, Callitriche hermaphroditica,* and *Potamogeton vaginatus*, was partly resembled the Weichselian cold stage, when the climate was extremely continental and more arid (Kienast et al., 2005).

6. Discussion

To sum up, today's Bol'shoy Lyakhovsky Island was characterised during the last interglacial by dominating subarctic shrub tundra interspersed with grasslands and shallow lakes, which formed due to thermokarst processes. The macrofossil floral composition indicates climate conditions in summer about 10 °C warmer than today, connected with an extended growing season, high evaporation and locally thin snow cover in winter. How is such a climatic difference especially in the MTWA between two succeeding warm stages possible?

6.1. Changes in solar insolation

Due to systematic variations in the Earth's orbital parameters, the summer insolation over the Arctic (north of 66°N) between 130,000 and 127,000 years ago exceeded the current insolation by 13% or 45 Wm^{-2} (CAPE-Last Interglacial Project, 2006). The MTWA values during that time are estimated 4-5 °C higher than present over most arctic lands resulting in an advance of larch taiga northward close to the current arctic coasts of Yakutia (CAPE-Last Interglacial Project, 2006). The strong thermal response of the Arctic in contrast to lower latitudes cannot be explained by the insolation increase alone but is presumed to be the result of positive feedbacks such as quicker deglaciation and reforestation at the start of the warm stage, smaller sea ice cover, and lower albedo, all due to more intense influx of warm Atlantic water into the Arctic (CAPE-Last Interglacial Project, 2006). The latter would amount to a greater oceanic influence, thus more precipitation and a lower seasonal temperature gradient. Increased oceanicity is, however, incompatible with such high summer temperature and intense evaporation as indicated by the palaeovegetation at the Laptev Strait. As is obvious at the tree-line retreat during the current warming connected with paludification in oceanic regions of the north (Crawford et al., 2003), boreal forests, which advanced there north to the arctic coasts during the Eemian, are now rather inhibited by rising oceanicity. Increased oceanicity would result in thicker snow cover, thus later snow melt and shortened growing season, thus higher albedo due to extended snow cover, less insolation owing to denser cloud cover, and less sensible in favour of latent heat. To explain the higher Eemian summer warmth in the Laptev Sea region, we suggest instead that the arctic warming due to the increase in northern hemisphere insolation was boosted by more intense continentality.

6.2. Continentality

Continentality frequently yields a clear sky, thus more direct insolation, thinner snow cover, earlier snow melt, lower albedo, less energy demands for melting of snow, heating of water, and evaporation and consequently considerably more sensible warmth in summer (compare Guthrie, 2001). Our results reflect an MTWA ca 10 °C warmer than present and a moderate precipitation that at least does not exceed the high evaporation, which might be the result of warming. These comparatively continental climate conditions at our coastal study site are, however, incompatible with a former location at the sea. The warming in the Arctic during the last interglacial happened rapidly and reached its peak during the earliest part of that warm stage (CAPE-Last Interglacial Project, 2006). Also during the Holocene, the initial stage was the warmest of that interglacial at least in the non-glaciated areas of the Arctic, visible at the northward advance of the tree-line during the Early Holocene in arctic Siberia (Kremenetski et al., 1998; Macdonald et al., 2000). *Duschekia fruticosa* shrub tundra occurred at the New Siberian Archipelago for a short time early in the Holocene as proven by macroremains on Kotel'ny Island, dated to 9920±180 ^{14}C years BP, and on Bol'shoy Lyakhovsky Island, dated to 9220±175 ^{14}C years BP (Kremenetski et al., 1998) indicating a rapid summer warming at the very beginning of the current warm stage. Such an intense temperature rise thus occurred obviously when increased insolation in the northern hemisphere coincided with persisting continentality due to still exposed shelves. The huge Holocene transgressions, which established oceanic influence in the north, occurred only later as result of delayed northern hemisphere ice sheet decay and the resulting global sea-level rise.

A northward displacement of the Polar Front is assumed to have taken place during the last interglacial (CAPE-Last Interglacial Project, 2006). This could be due to the expansion of the Asian anticyclone during the Eemian preventing the intrusion of Atlantic air masses into the Siberian mainland and shifting the Polar Front northward. The strength of the Asian anticyclone depends on the size of the landmass above it forms. Thus, the increased continentality at the Laptev Sea Shelf during the last interglacial suggests that at that time it was significantly less inundated than now.

6.3. Coast line position and tectonics

As mentioned above, the Laptev and East Siberian shelves are among the regions of the world most affected by the Holocene global sea level rise, which caused a southward transgression there of up to 800 km. Coast line shifts including warm stage transgressions are believed to have taken place also during former glacial/interglacial cycles, deduced from the modern bathymetry and global sea level fluctuations. Accordingly, the Eemian global sea

level exceeded the current one by 5.5-6 m (Chappell et al., 1996; Dumas et al., 2006). But there are no marine deposits known at the continental Laptev Sea coast dated to the last interglacial (Romanovskii et al., 1998). In arctic Siberia, evidence of Eemian transgressions exists in fact only on the Taymyr and Chukotka Peninsulas (Kind & Leonov, 1982; Brigham-Grette et al., 2001). Between the Lena and Kolyma Rivers, Eemian marine deposits were only reported from the northern coast of Kotel'ny Island (Alekseev, 1997). The sequence 8-9 m a.s.l. at the Reshetnikovaya River, described by Alekseev (1997), consists of sandy deposits with a thickness of 1-2 m interbedded between two layers of terrestrial sediments and containing the marine bivalves *Hiatella arctica, Astarte borealis*, and *Sipho togatua*. Its grain size composition points to a deposition close to the beach and the low thickness of the sediments might be the result of a short term inundation. The underlying, also sandy deposits contain shrub and other plant remains; the marine sequence itself includes pollen of *Betula* sect. *nanae* (15-21%), *Betula* sect. *fruticosae* (1-3%), and *Duschekia fruticosa* (20-25%), thus a spectrum of clearly interglacial signature and revealing that our reconstructed subarctic shrub tundra existed even on today's Kotel'ny Island ca 76°N (Alekseev, 1997).

Kleiber et al. (2001) detected a seismic unit in a Quaternary marine succession at the Western Laptev Sea Shelf edge containing layered sediments indicative of a sea level high stand, albeit with increasing thickness towards the continent. The latter implies higher input of particulate material originating from the Laptev Shelf and thus a coastline during that sea level high stand considerably further north than today. The authors interpreted that non-dated unit to be deposited during the Middle Weichselian (Karginian) Interstadial, but it might be of Eemian origin as well.

The isolated marine deposits on the northern coasts of the Kotel'ny, Fadeyevsky, and Novaya Sibir Islands (Ivanenko, 1998) suggest that the north-coast of the New Siberian Archipelago was Yakutia's northernmost continental coastline during the maximum transgression of the last interglacial. Consequently, if the New Siberian Islands were part of the mainland at that time, the shelf must have been elevated in contrast to today. Thus, a shelf subsidence must have taken place beneath the current sea level after the Eemian but prior to the Holocene global sea level high stand. As described above (chapter 2.1.), the Laptev Shelf region undergoes an intense tectonic spreading, which results in a rapid subsidence – a process that has been, so far, possibly underestimated in Quaternary coast line reconstructions of that extremely shallow epicontinental sea. The current mean rate of shelf subsidence connected with spreading is calculated to be 0.5 to 2 mm/year (Nikonov, 1977). This mean rate is however considerably increased in the numerous rifts within the shelf (Fig. 2, Nikonov,

1977). When we take into account an average subsidence rate of 2 mm per year during the last 130,000 years, the Weichselian permafrost bottom - that is the last interglacial ground surface - was 26 m higher than today. Such an altitude would result in a shift of the continental coast line at the longitude of Cape Svyatoy Nos more than 400 km to the north taking into account an Eemian sea level 6 m above the current one (Fig. 1). In this case, Bol'shoy Lyakhovsky Island would have been as far inland as Verkhoyansk today; the climatic influence of the sea would have been dramatically lower (compare Fig. 3).

There is another peculiarity of the Laptev Shelf that has to be considered regarding the extreme Holocene transgression. Owing to its exceptionally high ice content, the sedimentary cover that accumulated on the subaerically exposed Laptev Shelf and in the coastal lowlands of northeast Siberia during the last cold stage – ice-bonded permafrost - is climatically very susceptible and was abraded quickly at the start of the current warm stage. The compensation of subsidence by sedimentation was therefore only transient. In subsided areas of the shelf, the former lower boundary of the Ice Complex is currently below the sea level. Already beginning before the transgression about 13-11 ka BP, the initial melting of the Ice Complex caused an irregular subsidence of the ground surface by several dozen m (Romanovskii et al., 2000). The resultant thermokarst depressions, frequently including shallow lakes, occupy today 80 to 90% of the surface in the coastal lowlands and on shelf islands (Romanovskii et al., 2000). In tectonically subsided areas directly adjacent to the sea, the thermokarst depressions gave way to thermokarst lagoons causing a jagged coastline that became, due to its greater effective length, object to intensified thermal erosion, wave action, and resultant coastal erosion taking place after about 7-8 ka BP (Romanovskii et al., 2000). From this time on, precipitation escalated and entailed further intensified thermal erosion (Romanovskii et al., 2000). Simultaneously, sea water temperatures rose significantly as indicated by marine diatom records and resulted in the reduction of the coast-protective sea ice cover (Romanovskii et al., 2000). In consequence of thermokarst intensification, the rapid marine transgression continued in northeast Siberia after 7 ka BP despite the decelerated global sea level rise.

Thus, the combination of ongoing tectonic subsidence and very quick thermal destruction of the frozen Weichselian sedimentary cover during the Holocene possibly resulted in a transgression that was unique in extent and environmental consequences during the Quaternary.

6.4. Environmental consequences of the Holocene marine transgression

Available paleobotanical records confirm former assumptions that the recent monotonous NE Siberian coastal lowland tundra, poor in diversity and productivity, seems to be an exceptional phenomenon during the Quaternary (Frenzel, 1968). During the last warm stage by contrast, a diverse subarctic shrubland existed, reflecting warm summers and high evaporation, thus climate conditions that indicate continentality. Comparable vegetation and climate occurred in NE Siberia also during the Early Holocene before the marine transgression took place (Kremenetski et al., 1998, Kienast et al., 2005). The current oceanic influence, resulting in low summer mean temperature and small evaporation in the NE Siberian arctic coastal lowlands, is thus obviously connected with the Holocene Laptev Sea advance and if it really did not occur during former warm stages, it might possibly be a reason for mammoth extinction. As pointed out in the introduction, arctic Yakutia was the most important refuge of mammoth fauna and tundra steppe during interglacials due to its permanent continentality. When oceanic influence expanded far into the former mainland, xerophilous biota had to retreat south into the steppes or perished. Some adaptable herbivores, such as the reindeer were able to adapt. Xerophytic plants survived in small Yakutian refugia mainly in the rain shadow of mountains and in remaining areas of extreme continentality.

The Laptev Shelf inundation, however, might have had global consequences. Due to the greater landmass in Pleistocene, the then expanded Siberian High, which is the dominant Northern Hemisphere anticyclone during winter, reliably prevented the intrusion of atlantic air masses in winter and probably pushed the Polar Front northward. This influence would have affected not only NE Siberia but also other parts of northern Eurasia and partly even Alaska, decreasing precipitation and cloudiness there. After the Holocene weakening of the Asian Anticyclone in north Siberia associated with a marine transgression by 400 km compared with the Eemian, oceanic influence resulted in humidification and paludification of northern Eurasia and the alteration of ecosystems towards wetland tundra replacing boreal forests, grasslands, and shrublands.

When we transfer the cognitions into the near future to evaluate the risk of enduring modern global warming for landscape and vegetation in NE Siberia, we must assume accelerated melting of ice-rich permafrost due to the forecasted rise in annual mean temperature, sea level and precipitation (ACIA, 2004) all destructive to permafrost. In the Siberian lowlands, accelerated thermal erosion would result in further subsidence and intensified marine transgression. Large amounts of fossil carbon, currently trapped in permafrost, would be released (Walter et al., 2006) and the predominantly anaerobic environment in paludificated soils would result in the formation of huge amounts of methane, both possibly entailing

positive feedbacks on global warming. The humidification would probably cause an advance of wetlands and a further retreat of boreal forests southward as can be already observed in more humid regions (Crawford et al., 2003).

7. Conclusions

1. Plant macrofossils preserved in frozen deposits of former thermokarst lakes reveal that subarctic shrub tundra, interspersed with grasslands and lakes, existed on today's Bolshoy Lyakhovsky Island during the last interglacial.

2. Macrofossils of warmth-demanding shrubs and aquatic plants, occurring farther south today, indicate that local mean temperatures of the warmest month were at least 12.5 °C, thus *c*. 10 °C higher than today at that time.

3. Pollen-based reconstructions yield regional MTWA values between 9 and 14.5 °C and mean annual precipitation of 200-300 mm in comparison to 253 mm today.

4. Judging by the presence of steppes and *Kobresia*-meadows, which indicate locally dry habitats, as well as by floodplain meadows and littoral pioneer vegetation, which suggest fluctuating lake levels, evaporation was very high, as is confirmed by the former existence of halophytic plants.

5. The simplest explanation of such high summer temperature and evaporation in contrast to the current warm stage is strong continentality superimposed by increased summer insolation as result of changed orbital parameters of the Earth.

6. Since increased continentality is incompatible with the immediate adjacency of the Laptev Sea and owing to the lack of marine deposits in the study region, a much less advanced marine transgression during the last interglacial may be supposed.

7. Due to the greater northward extent of the Siberian landmass, the Siberian anticyclone was larger and resulted in greater continentality around the Bol'shoy Lyakhovsky Island area.

8. The excessive Holocene marine transgression in NE Siberia was thus possibly a unique event within the Quaternary and resulted from tectonic extension and subsidence of the extremely shallow Laptev Sea Shelf.

9. The most recent enormous marine transgression had serious climatic consequences in this highly sensitive refugial ecosystem, entailing weakening continentality connected with increased precipitation and cloudiness, thus lower insolation and summer temperature and shortened growing season.

10. The resultant alteration of northern ecosystems towards modern wetland tundra possibly caused the disappearance of the mammoth steppe and the rise of modern tundra.

Acknowledgements

References

ACIA, 2004. Impacts of a Warming Arctic: Arctic Climate Impact Assessment. Cambridge University Press, Cambridge.

Aiken, S.G., Dallwitz, M.J., Consaul, L.L., McJannet, C.L., Gillespie, L.J., Boles, R.L., Argus, G.W., Gillett, J.M., Scott, P.J., Elven, R., LeBlanc, M.C., Brysting, A.K. and Solstad, H., 1999. Flora of the Canadian Arctic Archipelago: Descriptions, Illustrations, Identification, and Information Retrieval. Online Database, http://www.mun.ca/biology/delta/arcticf/_ca/index.htm.

Aleksandrova, V.D., 1980. The Arctic and Antarctic: their division into geobotanical areas. Cambridge University Press, Cambridge.

Alekseev, M.N., 1997. Paleogeography and geochronology in the Russian eastern Arctic during the second half of the quaternary. Quaternary International, 41-42: 11-15.

Alekseev, M.N. and Drouchits, V.A., 2004. Quaternary fluvial sediments in the Russian Arctic and Subarctic: Late Cenozoic development of the Lena River system, northeastern Siberia. Proceedings of the Geologists' Association, 115(4): 339-346.

Andreev, A., Tarasov, P., Schwamborn, G., Ilyashuk, B., Ilyashuk, E., Bobrov, A., Klimanov, V., Rachold, V. and Hubberten, H.-W., 2004a. Holocene paleoenvironmental records from Nikolay Lake, Lena River Delta, Arctic Russia. Palaeogeography, Palaeoclimatology, Palaeoecology, 209(1-4): 197-217.

Andreev, A.A., Grosse, G., Schirrmeister, L., Tarasov, P.E., Meyer, H., Kuzmina, S.A., Novenko, E.Y., Bobrov, A.A., Ilyashuk, B.P., Kuznetsova, T.V., Krbetschek, M. and Kunitsky, V.V., 2004b. Late Saalian and Eemian palaeoenvironmental history of the Bol'shoy Lyakhovsky Island (Laptev Sea region, Arctic Siberia). Boreas, 33(4): 319-348.

Andreev, A., Grosse, G., Schirrmeister, L., Kuznetsova, T. V., Kuzmina, S. A., Bobrov, A. A., Tarasov, P. E., Novenko, E. Yu., Meyer, H., Derevyagin, A. Yu., Kienast, F., Bryantseva, A., Kunitsky, V. V., (submitted). Weichselian and Holocene palaeoenvironmental history of the Bol'shoy Lyakhovsky Island, New Siberian Archipelago, Arctic Siberia. Boreas.

Bauch, H.A., Mueller-Lupp, T., Taldenkova, E., Spielhagen, R.F., Kassens, H., Grootes, P.M., Thiede, J., Heinemeier, J. and Petryashov, V.V., 2001. Chronology of the Holocene transgression at the North Siberian margin. Global and Planetary Change, 31(1-4): 125-139.

Böcher, T.W., 1954. Oceanic and continental vegetational complexes in Southwest Greenland. Meddelelser om Grønland, 148(1): 1-336.

Boeskorov, G.G., 2006. Arctic Siberia: Refuge of the Mammoth fauna in the Holocene. Quaternary International, 142-143: 119.

Brochmann, C., 1992. Pollen and seed morphology of Nordic Draba (Brassicaceae): phylogenetic and ecological implications. Nordic Journal of Botany, 12 (6): 657-673.

Brochmann, C., Soltis, P.S., Soltis, D.E., 1992. Recurrent formation and polyphyly of Nordic polyploids in Draba (Brassicaceae). American Journal of Botany, 79 (6): 673-688.

Brysting, A.K., Oxelman, B., Huber, K.T., Moulton, V., Brochmann, C., 2007. Untangling complex histories of genome merging in high polyploids. Systematic Biology, 56 (3): 467-476.

Busunova, I.O., Gladkova, V.N., Saikonnikova, T.I., Petrovsky, V.V., Rebristaya, O.V., Taraskina, N.N., Tikhomirov, V.N. and Yurtsev, B.A., 1984. Droseraceae-Rosaceae. Arkticheskaya Flora SSSR, 9/1. Nauka, Leningrad, 333 pp.

CAPE-Last Interglacial Project, M., 2006. Last Interglacial Arctic warmth confirms polar amplification of climate change. Quaternary Science Reviews, 25(13-14): 1383-1400.

CAVM-Team, 2003. Circumpolar Arctic Vegetation Map, Conservation of Arctic Flora and Fauna (CAFF) Map no. 1. U.S. Fish and Wildlife Service, Anchorage, Alaska.

Chappell, J., Esat, T., McCulloch, M., Pillans, B., Omura, A., Pandolfi, J. and Ota, Y., 1996. Reconciliation of late Quaternary sea levels derived from coral terraces at Huon Peninsula with deep sea oxygen isotope records. Earth and Planetary Science Letters, 141(1-4): 227-236.

Cherepanov, S.K., Kozhanchikov, V.I., Matsenko, A.Y., Petrovskiy, V.V., Rebristaya, O.V., Skvortsov, A.K., Tolmachev, A.I., Volkova, Y.V. and Yurtsev, B.A. (Editors), 2000. Salicaceae-Ranunculaceae. Flora of the Rusian Arctic, III. J.Cramer, Berlin, Stuttgart, 472 pp.

Crawford, R.M.M., Jeffree, C.E. and Rees, W.G., 2003. Paludification and forest retreat in northern oceanic environments. Annals of Botany, 91 (Spec. Iss. Jan.): 213-226.

Dierßen, K., 1996. Vegetation Nordeuropas. Eugen Ulmer Verlag, Stuttgart, 838 pp.

Drachev, S.S., 2000. Laptev Sea rifted continental margin: Modern knowledge and unsolved questions. Polarforschung, 68(1-3): 41-50.

Drachev, S.S., Kaul, N. and Beliaev, V.N., 2003. Eurasia spreading basin to Laptev shelf transition: Structural pattern and heat flow. Geophysical Journal International, 152(3): 688-698.

Drachev, S.S., Savostin, L.A., Groshev, V.G. and Bruni, I.E., 1998. Structure and geology of the continental shelf of the Laptev Sea, Eastern Russian Arctic. Tectonophysics, 298(4): 357-393.

Dumas, B., Hoang, C.T. and Raffy, J., 2006. Record of MIS 5 sea-level highstands based on U/Th dated coral terraces of Haiti. Quaternary International, 145-146: 106-118.

Franke, D., Krüger, F. and Klinge, K., 2000. Tectonics of the Laptev Sea - 'Moma `Rift' Region: Investigation with Seismologic Broadband Data. Journal of Seismology, 4(2): 99-116.

Franke, D., Hinz, K. and Oncken, O., 2001. The Laptev Sea Rift. Marine and Petroleum Geology, 18(10): 1083-1127.

Franke, D., Hinz, K. and Reichert, C., 2004. Geology of the East Siberian Sea, Russian Arctic, from seismic images: Structures, evolution, and implications for the evolution of the Arctic Ocean Basin. Journal of Geophysical Research B: Solid Earth, 109(7).

Frenzel, B., 1968. Grundzüge der pleistozänen Vegetationsgeschichte Nord-Eurasiens (Basic principles of the Pleistocene vegetation history of North Eurasia). Franz Steiner Verlag, Wiesbaden.

Frenzel, B., Pécsi, M. and Velichko, A.A., 1992. Atlas of paleoclimates and paleoenvironments of the northern hemisphere, Late Pleistocene - Holocene. Gustav Fischer, Budapest-Stuttgart, 153 pp.

Guiot, J., 1990. Methodology of the last climatic cycle reconstruction in France from pollen data. Palaeogeography, Palaeoclimatology, Palaeoecology, 80(1): 49-69.

Guthrie, R.D., 1990. Frozen Fauna of the Mammoth Steppe. University of Chicago Press, Chicago, 323 pp.

Guthrie, R.D., 2001. Origin and causes of the mammoth steppe: a story of cloud cover, woolly mammal tooth pits, buckles, and inside-out Beringia. Quaternary Science Reviews, 20(1-3): 549-574.

Haynes, G., 2007. A review of some attacks on the overkill hypothesis, with special attention to misrepresentations and doubletalk. Quaternary International, 169-170: 84-94.

Hilbig, W., 1995. The Vegetation of Mongolia. SPB Academic Publications, Amsterdam.

Hubberten, H.W., Andreev, A., Astakhov, V.I., Demidov, I., Dowdeswell, J.A., Henriksen, M., Hjort, C., Houmark-Nielsen, M., Jakobsson, M. and Kuzmina, S., 2004. The periglacial climate and environment in northern Eurasia during the Last Glaciation. Quaternary Science Reviews, 23(11-13): 1333-1357.

Hulten, E. and Fries, M., 1986. Atlas of North European Vascular Plants (North of the Tropic of Cancer). Koeltz, Königstein.

Ilyashuk, B., Andreev, A., Bobrov, A., Tumskoy, V. and Ilyashuk, E., 2006. Interglacial history of a palaeo-lake and regional environment: a multi-proxy study of a permafrost deposit from Bol'shoy Lyakhovsky Island, Arctic Siberia. Journal of Paleolimnology, 35(4): 855-872.

Ivanenko, G.V., 1998. Map of Quaternary Deposits, S-53-55 (New Siberian Islands), State Geological Map of the Russian Federation (New Series). St. Petersburg Cartographic Factory VSEGEI, St. Petersburg.

Iversen, J. 1944. Viscum, Hedera und Ilex as Climate Indikators. Geol. Fören. Förhandl. Stockholm 66. 463-483.

Iversen, J., 1954. The Late-glacial flora of Denmark and its relation to climate and soil. Danmarks Geologiske Undersøgelse, II(80): 88-118.

Kaplan, J.O., 2001. Geophysical Applications of Vegetation Modelling, Lund University, Lund.

Kienast, F., Schirrmeister, L., Siegert, C. and Tarasov, P., 2005. Palaeobotanical evidence for warm summers in the East Siberian Arctic during the last cold stage. Quaternary Research, 63(3): 283-300.

Kienast, F., 2006. Arctic Vegetation History - Eurasia. Encyclopedia of Quaternary Science, Elsevier, Vol. 3: 2422-2434.

Krasnoborov, I.M., 1988. Lycopodiaceae-Hydrocharitaceae. Flora Sibiri, 1. Nauka, Novosibirsk, 199 pp.

Krasnoborov, I.M. and Malyshev, L.I., 2003. Salicaceae - Amaranthaceae. Flora of Siberia, 5. Science Publishers, Inc., Enfield (NH), USA, 305 pp.

Kremenetski, C.V., Sulerzhitsky, L.D. and Hantemirov, R., 1998. Holocene History of the Northern Range Limits of Some Trees and Shrubs in Russia. Arctic and Alpine Research, 30(4): 317-333.

Lloyd, A.H., Yoshikawa, K., Fastie, C.L., Hinzman, L., and Fraver, M., 2003. Effects of Permafrost Degradation on Woody Vegetation at Arctic Treeline on the Seward Peninsula, Alaska. Permafrost and Periglacial Processes, 14: 93–101.

Lozhkin, A.V. and Anderson, P.M., 1995. The Last Interglaciation in Northeast Siberia. Quaternary Research, 43(2): 147-158.

MacDonald, G.M., Velichko, A.A., Kremenetski, C.V., Borisova, O.K., Goleva, A.A., Andreev, A.A., Cwynar, L.C., Riding, R.T., Forman, S.L. and Edwards, T.W.D.,

2000. Holocene Treeline History and Climate Change Across Northern Eurasia. Quaternary Research, 53(3): 302-311.

Malyschev, L.I. and Peschkova, G.A., 2003. Portulacaceae-Ranunculaceae. Flora of Siberia, 6. Science Publishers, Enfield, New Hampshire, USA, 301 pp.

McKendrick, J., 2000. Northern Tansy Mustard fills a niche. Agroborealis, 32(1): 15-20.

Meyer, H., Dereviagin, A., Siegert, C., Schirrmeister, L., Hubberten, H.-W., 2002. Palaeoclimate Reconstruction on Big Lyakhovsky Island, North Siberia—Hydrogen and Oxygen Isotopes in Ice Wedges. Permafrost and Periglacial Processes 13: 91–105.

Mol, D., Tikhonov, A., van der Plicht, J., Kahlke, R.-D., Debruyne, R., van Geel, B., van Reenen, G., Pals, J.P., de Marliave, C. and Reumer, J.W.F., 2006. Results of the CERPOLEX/Mammuthus Expeditions on the Taimyr Peninsula, Arctic Siberia, Russian Federation. Quaternary International, 142-143: 186-202.

Möller, I., 2000. Studien zur Vegetation Nordwestspitzbergens. Dissertation Thesis, Universität Hamburg, Hamburg, 202 pp.

Mühr, B., 2000. Das Klima in Chatanga. In: Klimadiagramme weltweit, Online database, http://www.klimadiagramme.de/Asien/chatanga.html.

Murray, D.F., 1995. Causes of Arctic plant diversity; origin and evolution. In: F.S. Chapin III and C. Körner (Editors), Arctic and Alpine Biodiversity. Springer, Berlin.

Nikonov, A.A., 1977. The Holocene and contemporary movements of the Earth crust. Nauka, Moscow, 240 pp.

Parfenov, L.M., Prokopiev, A.V. and Spektor, V.B., 2001. The Surface Relief and the History of its Formation. In: L.M. Parfenov and M.I. Kuzmin (Editors), Tectonics, geodynamics, and Metallogeny of the Sakha Republic (Yakutia). MAIK "Nauka/Interperiodica", Moscow, pp. 12-32.

Peshkova, G.A., 1996. Geraniaceae-Cornaceae. Flora Sibiri, 10. Siberian Publishing Firm RAN, Novosibirsk, 253 pp.

Pitulko, V. V., Nikolsky, P. A., Girya, E. Yu., Basilyan, A. E., Tumskoy, V. E., Koulakov, S. A., Astakhov, S. N., Pavlova, E. Yu., Anisimov, M. A., 2004. The Yana RHS Site: Humans in the Arctic before the Last Glacial Maximum. Science, 303: 52-56.

Pott, R., 1995. Die Pflanzengesellschaften Deutschlands. Eugen Ulmer, Stuttgart, 622 pp.

Prentice, I.C., Cramer, W., Harrison, S.P., Leemans, R., Monserud, R.A. and Solomon, A.M., 1992. A global biome model based on plant physiology and dominance, soil properties and climate. Journal of Biogeography, 19(2): 117-134.

Rebristaya, O.V., Skvortsov, A.K., Tolmachev, A.I., Tsvelev, N.N. and Yurtsev, B.A., 1995. Polypodiaceae-Graminae. Flora of the Russian Arctic, 1. The University of Alberta Press, Edmonton, Alberta, 330 pp.

Rivas-Martínez, S., 1996-2004. Climate diagrams, Worldwide Bioclimatic Classification System. Phytosociological Research Center, Spain. Online database, http://www.globalbioclimatics.org/plot/ru-mys-s.htm

Romanovskii, N.N., Gavrilov, A.V., Tumskoy, V.E., Kholodov, A.L., Siegert, C., Hubberten, H.W. and Sher, A.V., 1998. Environmental Evolution in the Laptev Sea Region during Late Pleistocene and Holocene. Polarforschung, 68: 237-245.

Romanovskii, N.N., Hubberten, H.W., Gavrilov, A.V., Tumskoy, V.E., Tipenko, G.S., Grigoriev, M.N. and Siegert, C., 2000. Thermokarst and land-ocean interactions, Laptev sea region, Russia. Permafrost and Periglacial Processes, 11(2): 137-152.

Romanovskii, N.N., Hubberten, H.W., Gavrilov, A.V., Tumskoy, V.E. and Kholodov, A.L., 2004. Permafrost of the east Siberian Arctic shelf and coastal lowlands. Quaternary Science Reviews, 23(11-13): 1359-1369.

Schirrmeister, L., Kunitsky, V.V., Grosse, G., Meyer, H., Kuznetsova, T.V., Kuzmina, S.A., Tumskoy, V.E., Dereviagin, A., Akhmadeeva, I. and Syromyatnikov, I., 2000.

Quaternary deposits of Bol'shoy Lyakhovsky Island. Reports on Polar and Marine Research, 354: 113-168.

Schirrmeister, L., Oezen, D. and Geyh, M.A., 2002. ^{230}Th/U Dating of Frozen Peat, Bol'shoy Lyakhovsky Island (Northern Siberia). Quaternary Research, 57(2): 253–258.

Schwamborn, G., Rachold, V. and Grigoriev, M.N., 2002. Late Quaternary sedimentation history of the Lena Delta. Quaternary International, 89(1): 119-134.

Sher, A.V., 1991. Problems of the last interglacial in Arctic Siberia. Quaternary International, 10-12: 215-222.

Sher, A.V., 1997. A Brief Overview of the Late-Cenozoic History of the Western Beringian Lowlands. In: M.E. Edwards, A.V. Sher and R.D. Guthrie (Editors), Terrestrial paleoenvironmental studies in Beringia, Proceedings of a joint Russian-American Workshop, June 1991. The Alaska Quaternary Center, Fairbanks, Alaska, pp. 3-6.

Stuart, A.J., Kosintsev, P.A., Higham, T.F.G. and Lister, A.M., 2004. Pleistocene to Holocene extinction dynamics in giant deer and woolly mammoth. Nature, 431(7009): 684-689.

Tarasov, P., Granoszewski, W., Bezrukova, E., Brewer, S., Nita, M., Abzaeva, A. and Oberhänsli, H., 2005. Quantitative reconstruction of the last interglacial vegetation and climate based on the pollen record from Lake Baikal, Russia. Climate Dynamics, 25(6): 625-637.

Tolmachev, A.I. & Yurtsev, B.A., 1980. Geraniaceae-Scrophulariaceae, Articheskaya Flora SSSR, Vol. 8. Nauka, Leningrad, 333 pp.

Van Dinter, M. and Birks, H.H., 1996. Distinguishing fossil Betula nana and B. pubescens using their wingless fruits: Implications for the late-glacial vegetational history of western Norway. Vegetation History and Archaeobotany, 5(3): 229-240.

VMGO, Voeikov Main Geophysical Observatory, 1980. Climatic Atlas of Asia. In: WMO and UNESCO (Editors). Goscomgidromet USSR, Gidrometeoizdat, Leningrad.

Volterra, V., 1931. Lecons sur la théorie mathématique de la lutte pour la vie. Gauthier-Villars, Paris, 231pp.

Walker, M.D., Walker, D.A., Everett, K.R., Short, S.K., 1991. Steppe Vegetation on South-Facing Slopes of Pingos, Central Arctic Coastal Plain, Alaska, U.S.A. Arctic and Alpine Research, 23(2), 170-188.

Weber, H.E., Moravec, J., Theurillat, J.-P., 2000. International code of phytosociological nomenclature. Third edition. Journal of Vegetation Sciences 11, 739–768.

Yurtsev, B.A., 1982. Relics of the xerophyte vegetation of Beringia in Northeastern Asia. In: D.M. Hopkins, J.V. Matthews-Jr., C.E. Schweger and S.B. Young (Editors), Paleoecology of Beringia. Academic Press, New York, pp. 157-177.

Yurtsev, B.A., 2001. The Pleistocene "Tundra-Steppe" and the productivity paradox: the landscape approach. Quaternary Science Reviews, 20(1-3): 165-174.

Zimov, S.A., 2005. Pleistocene Park: Return of the Mammoth's Ecosystem. Science, 308: 796-798.

Figure and table captions

Figure 1; Location and bathymetry of the Laptev Sea and situation of the study site on the south coast of the Bol'shoy Lyakhovsky Island. Upper part derived from the National Geophysical Data Center (NGDC), NOAA Satellite and Information Service, available at http://www.ngdc.noaa.gov/mgg/global/.

Figure 2; Tectonic situation of the Lapev Sea Shelf. As a continuation of the Gakkel Ridge, the Laptev Sea forms a zone of extension (upper part). The consequence of extension is intense subsidence and formation of a series of deep basins (light grey areas in the lower part). Lower part derived from Drachev et al. (1998).

Figure 3; The impact of the Laptev Sea on regional climate. The satellite photo was taken in early summer on the 16th of July 2003, when the Laptev Sea was still covered with sea ice. It illustrates the cooling effect of the sea during the growing season. In the lower part, the climate diagrams of Verkhoyansk, Kazachye, and Cape Shalaurova show a decreasing seasonal temperature gradient and increasing precipitation towards the sea coast. The annual mean temperature in contrast scarcely differs between the three locations.

Climate diagrams from Rivas-Martínez (1996-2004), Photo: Terra, 1040 UTC (NOAA/NESDIS). http://www.ssec.wisc.edu/~gumley/modis_gallery/images/Arctic_20030716_1040_250m.jpg

Figure 4; Photos of the studied coastal outcrop (upper part) and scheme of the Late Pleistocene sediment sequence (lower part). The reddish signature illustrates Eemian warm stage deposits. The yellow bars mark the studied parts of the sequence. Photos: left- L. Schirrmeister, right- V. Tumskoy.

Figure 5; Schemes of the studied subprofiles, ice wedge casts in Saalian ice-rich permafrost filled with organic-rich lacustrine sediments, and locations of macrofossil and, at R35, pollen sampling.

Figure 6; Macrofossils with sample number (compare figure 5) and reference material of subarctic shrub tundra indicator plants. **1-4 *Duschekia fruticosa*;** 1a- *Duschekia fruticosa,* fossil leaf fragment (L12+30, OS 56), 1b- *D. fruticosa*, recent leaf fragment, 2- *D. fruticosa,* catkin scale, both sides (R35, S9), 3- *D. fruticosa,* fossil nutlet, both sides (R35 S9), 4- *D. fruticosa,* two different modern nutlets, 5- Betulaceae, two different fossil wingless nutlets

(L12+30 OS, 56), 6- *Betula platyphylla*, modern nutlet, 7- *Betula fruticosa*, two different modern nutlets, **8-10+13 *Betula nana s.l.,*** 8- *Betula exilis*, two different modern fruits, 9- *Betula nana s.l.,* fossil nutlet, both sides (R35, S9), 10- *Betula nana s.l.*, fossil catkin scale, both sides (R35, S9), **11-12+7 *Betula fruticosa*** 11- *Betula fruticosa*, fossil catkin scale, both sides (L12+30, OS 57), 12a- *Betula fruticosa*, fossil leaf fragment (L12+30, OS 56), 12b- *Betula fruticosa*, modern leaf fragment, 13a- *Betula nana s.l.*, fossil leaf fragment (L12+30, OS 56), 13b- *Betula exilis*, modern leaf fragment, 14- *Moehringia laterifolia*, seed, both sides (L12+30, OS 57), 15- *Boschniakia rossica*, seeds five times magnified compared to the other macroremains in this figure, left: fossil (L12+30, OS 56), right: modern, 16a+b- *Ledum palustre*, fossil capsule including seeds (R22+60, OS 53), both sides, 17- *Vaccinium vitis-idaea*, fossil leaf, both sides (R35, S9), 18- *Vaccinium vitis-idaea*, fossil seed, both sides (R22, OS 53), 19- *Empetrum nigrum* s.l. fossil seed, both sides (L14, OS 56), 20- *Ledum palustre*, fossil leaf fragments, underside (R22, OS 53).

Figure 7; Macrofossils of plants indicative of low or fluctuating moisture. **1-4 plants of dry arctic upland**, 1- *Kobresia myosuroides*, nutlet from two sides (R22+60, OS 53), 2- *Potentilla cf. nivea*, fruit, both sides (R22+60, OS 53), 3- *Ranunculus affinis,* two different nutlets (L12+30, OS 57), 4- *Minuartia arctica***,** seed, both sides (R22+60, OS 53), **5-8 steppe plants**, 5- *Artemisia* sp., achene, both sides (L12+30, OS 57), 6- *Carex* cf. *supina* ssp. *korshinskyi*, nutlet, two-sided (L12+30, OS 56), 7- *Rumex acetosella*, 7a- nutlet, 7b- detail of pericarp (L12+30, OS 56), 8- *Potentilla cf. stipularis*, fruit, both sides (R22+60, OS 53), **9-13 plants representative of shrinking lakes or salt accumulation due to high evaporation**, 9- *Puccinellia* sp., fruit from two sides (R35, S9), 10- *Rumex maritimus*, nutlet, both sides (L12+30, OS 57), 11- *Rorippa palustris*, seed, two-sided (L12+30, OS 57), 12- *Stellaria crassifolia*, seed from both sides (L12+30, OS 57), 13- *Tripleurospermum hookeri*, achene from two sides (L12+30, OS 57), 14- *Descurainia sophioides*, seed from both sides (L12+30, OS 56).

Figure 8; Fossil diaspores of aquatics and temperature-indicative wetland plants with sample numbers. 1- *Myriophyllum spicatum*, mericarp, 1a- ventral, 1b- basal, 1c- lateral (R35, S9), 2- *Hippuris vulgaris*, two sides of the fruit (L12+30, OS 57), 3+4- *Callitriche hermaphroditica*, two different mericarps, each two-sided (L12+30, OS 57), 5- *Sparganium minimum*, fruit, two-sided (R22+60, OS 53), 6- *Sparganium hyperboreum*, fruit, two-sided (R22+60, OS 53), 7- *Nitella* sp., oospore, two-sided (R22+60, OS 53), 8- *Batrachium* sp., nutlet, both sides

34

(R22+60, OS 53), 9- *Comarum palustre*, fruit, both sides (L12+30, OS 57), 10- *Eriophorum brachyantherum*, achene, both sides (L12+30, OS 56), 11- *Epilobium palustre*, two sides of the seed (L12+30, OS 57), 12- *Potamogeton vaginatus*, fruitstone, both sides (R22+60, OS 53), 13- *Menyanthes trifoliata*, seed fragment, 13a+13b lateral view, 13c- magnified surface pattern (L12+30, OS 56), 14- *Parnassia palustris*, seed with characteristically loose testa, two sides (L12+30, OS 57).

Figure 9: Climate of the last interglacial (MIS 5e) derived from the R35 pollen record (Ilyashuk et al. 2006) from Bol'shoy Lyakhovsky Island. (A) The mean temperature of the warmest month (MTWA), (B) annual precipitation (PANN), (C) annual sum of the growing-degree-days above 5°C (GDD5) and (D) moisture index (ratio of actual to potential evapotranspiration) are reconstructed using the best modern analogue approach and reference surface pollen data set from northern Eurasia, as described in Tarasov et al. (2005). Most probable values (open circles) are based on the weighted average of the 10 best modern analogues. Horizontal lines indicate confidence intervals taken from the climatic distribution of the selected analogues. Vertical lines illustrate modern values. From sample no. 9, shaded in pale grey, macrofossils were studied in addition to pollen analysis to compare the mean July T- reconstructions gained from both proxies. Note modern values (Rivas-Martínez, 1996-2004) for comparison: MTWA: 2.8 °C; PANN: 253 mm; GDD5: 0.

Tab. 1. (following pages). List of identified macrofossils from the subprofiles L12+30 and R22+60 (compare fig. 5). The grey columns represent macrofossil records dated to the last (Eemian) interglacial.

Tab. 2. List of identified macrofossils from the sample S9 taken in 200 cm a.s.l. at subprofile R35 (compare fig. 5) and classification into plant communities.

Tab. 3. Northernmost Yakutian distribution of selected Eemian macrofossil taxa from the Bol'shoy Lyakhovsky Island (compare figs. 6-8) and mean temperature of the warmest month (MTWA) at their modern northern range limits. Note that the current MTWA at the study site is 2.8 °C (Rivas-Martínez, 1996-2004).

Tab.1

Subprofile Nr	R22+60							L12+30			
Sample Nr	OS-49	OS-50	OS-51	OS-52	OS-53	OS-54	OS-55	OS-58	OS-56	OS-57	OS-60
Agrostis sp.							1			6	
Alopecurus sp.					4	1	4			20	
Androsace septentrionalis L.						1				1	
Artemisia sp.					1					5	
Asteraceae sp.					2						
Batrachium sp.					1						
Betula fruticosa Pall.									3	1	
Betula nana L. *s.l.*					2	5			3	2	1
Betula sp.									3		
Betulaceae									>100	>100	19
Bistorta vivipara (L.) S.F. Gray					9				1		
Boschniakia rossica (Cham. & Schlecht.) B. Fedtsch.						1					
Calamagrostis sp.										3	
Callitriche hermaphroditica L.					2	1	2		5	49	8
Caltha palustris L. s.l.									8	2	
Carex aquatilis Wahlenb.						2					
Carex duriuscula C.A. Mey.					8				24	5	1
Carex Sect. Phacocystis Dumort.					c. 70	5	5		>200	>100	17
Carex sp.					6				16	>100	5
Carex supina Willd. ex Wahlenb.*s.l.*					30		1		61	40	
Carex cf. Sect.Temnemis (Rafin.) V. Krecz										3	
Caryophyllaceae sp.			3							21	
Cerastium cf. beeringianum Cham. & Schecht.					40	9	5			13	
Cerastium cf. jenissejense Hult.					4						
Cerastium cf. regelii Ostenf.								c. 100			
Chenopodiaceae sp.		2									
Chenopodium sp.	4		10	2							
Chrysosplenium alternifolium L.							1		15	5	1
Comarum palustre L.					2				9	24	
cf. Corydalis sp.									28	x	
Cyperaceae sp.									2		
Deschampsia sp.					7		4			31	
Descurainia sophioides (Fisch. ex Hook.) O.E. Schulz					2	16	13		39	63	3
Draba sp.	54	2	40		>100	>100	30	5	ca 80	>100	3
Dryas octopetala L. *s.l.*					6	6	1				1
Duschekia fruticosa (Rupr.) Pouzar					26	9	1		77	c. 50	58
Empetrum nigrum L. *s.l.*					9				3	1	1
Epilobium davuricum Fisch. ex Hornem.										16	
Subprofile Nr	R22+60							L12+30			
Sample Nr	OS-49	OS-50	OS-51	OS-52	OS-53	OS-54	OS-55	OS-58	OS-56	OS-57	OS-60
Epilobium palustre L.									11	8	
Eriophorum brachyantherum Trautv. & C.A. Mey.					1				3	1	
Eriophorum cf. gracile Koch					1						
Eriophorum polystachion L.					1				1	1	
Eriophorum scheuchzeri Hoppe							1		11	8	

	R22+60							L12+30			
Subprofile Nr											
Sample Nr	OS-49	OS-50	OS-51	OS-52	OS-53	OS-54	OS-55	OS-58	OS-56	OS-57	OS-60
Eriophorum sp.							1		2	7	
Eutrema edwardsii R. Br.					4						
Fabaceae sp.											1
Festuca sp.		46									
Gastrolychnis involucrata s.l. (Cham. & Schlecht.) A.& D. Löve					5	1				5	
Gastrolychnis violascens s.l. Tom.										1	
Hippuris vulgaris L. *s.l.*									2		2
Juncus biglumis L.					8	10	11		13	5	1
Kobresia myosuroides (Vill.) Fiori					3				1	1	
Ledum palustre L.					29	4	1		5	7	
cf. Lesquerella arctica (Wormsk. ex Hornem.) S. Wats.					1						
Lloydia serotina (L.) Reichenb.							1				
Luzula confusa Lindeb.						1			7	2	
Luzula cf.wahlenbergii Rupr.										5	
Menyanthes trifoliata L.									2		1
Minuartia arctica (Stev. ex Ser.) Graebn.					2						
Minuartia rubella (Wahlenb.) Hiern						34	3		1	3	1
Moehringia laterifolia (L.) Fenzl.										1	
Myosotis sp.										1	
Nitella sp.					1						
Oxycoccus microcarpus Turcz. ex Rupr.										1	1
Papaver Sect. Scapiflora Reichenb.			1		73	15	4		10	2	
Parnassia palustris L.										1	
Poa sp.		17			12	16	1	2	13	>100	
Poaceae sp.	22	>100	c. 30		17	24		4	26	>100	
Potamogeton vaginatus Turcz.					16	4	1		9	6	2
Potentilla cf. arenosa (Turcz.) Juz.					c. 80			10		21	6
Potentilla cf. hyparctica Malte			6		c. 100	18	9	23		23	7
Potentilla cf. nivea L.					28	4		c. 100	1	1	
Potentilla cf. stipularis L.					28	5			5	21	
Potentilla sp.			1			40		30		>100	
Puccinellia sp.	22	27	14		45	12	9	1	15	>100	1
Ranunculus cf. affinis R. Br.					14	1			6	8	1
Ranunculus hyperboreus Rottb.					1				2	3	
Ranunculus lapponicus L.					9				2	1	2
Ranunculus propinquus C.A. Mey						1			2		
Ranunculus repens L.					1						
Rhododendron sp.						1					
Rorippa palustris (L.) Bess.									17	25	
Rumex arcticus Trautv.										2	
Rumex maritimus L.										2	
Rumex subgen. Acetosella (Meisn.) Rech.									1		
Sagina intermedia Fenzl ex Ledeb.						1					

Species								
Salix sp.			15			c. 50	c. 30	5
cf. Saxifraga hieracifolia Waldst. & Kit.		5						
Sparganium hyperboreus Laest.			1					2
Sparganium minimum Wallr.			1					
Stellaria crassifolia Ehrh.						2	6	
Stellaria sp.			1			3		
Taraxacum cf.ceratophorum (Ledeb.) D.C.	1							
Tephroseris palustris (L.) Reichenb.			1				3	
Thymus sp.						1		
Tripleurospermum hookeri Sch. Bip.			3				2	
Vaccinium vitis-idaea L.			8	1	1		1	

Tab. 2

Taxon	Number	Vegetation
Myriophyllum spicatum L.	2	**Aquatics**
Potamogeton sp.	5	
Batrachium sp.	2	
Eriophorum scheuchzeri Hoppe	1	**Wetland communities**
Epilobium palustre L.	4	
Carex Sect. *Phacocystis* Dumort.	44	
Juncus biglumis L.	9	
Betula nana s.l. L.	12	**Subarctic shrub tundra**
Duschekia fruticosa (Rupr.) Pouzar	c.50	
Ledum palustre L.	6	
Vaccinium vitis-idaea L.	2	
Ranunculus hyperboreus Rottb.	1	**Sporadicly dry riparian sites**
Tephroseris palustris (L.) Reichenb.	c.50	
Puccinelia sp.	23	**Floodplain meadows**
Ranunculus cf. affinis R. Br.	17	
Artemisia sp.	2	**Xerophytic communities**
Rumex subgen. Acetosella (Meisn.) Rech.	4	
Carex duriuscula C.A. Mey.	3	
Potentilla cf. arenosa (Turcz.) Juz.	c.60	
Potentilla cf. stipularis L.	>100	
Oxyria digyna (L.) Hill.	2	**Arctic upland and pioneer vegetation**
Papaver Sect. *Scapiflora* Reichenb.	27	
Minuartia rubella (Wahlenb.) Hiern	9	
Cerastium cf. beeringianum Cham. & Schlecht.	63	
Draba sp.	>100	
Descurainia sophioides (Fisch. ex Hook.) O.E. Schulz	7	
Salix sp.	27	**Without clear indication**
Poaceae sp.	>100	
Carex sp.	2	
Alopecurus sp.	6	
Caryophyllaceae sp.	2	
Primulaceae sp.	1	

Tab. 3

Taxon	Northernmost distribution in Yakutia	Source of distribution map	MTWA at the northern-most occurrence
Duschekia fruticosa	At the confluence of Kotuy and Kheta Rivers (~71,8 °N)	(Krasnoborov and Malyshev, 2003)	Between 10 and 12.5 °C isotherms (VMGO, 1980)
Batrachium sp.	Lower Yana River (71°N)	(Malyschev and Peschkova, 2003)	10 °C (VMGO, 1980)
Betula fruticosa	Lower Lena River (~71,2°N)	(Krasnoborov and Malyshev, 2003)	Between 10 and 12.5 °C isotherms (VMGO, 1980)
Betula nana s.l.	Western bank of the Khatanga Bay (~74,5°N)	(Krasnoborov and Malyshev, 2003)	6 °C (VMGO, 1980)
Callitriche hermaphroditica	North of the Alazeya River (~68,6°N)	(Peshkova, 1996)	>12,5 °C (VMGO, 1980)
Menyanthes trifoliata	Settlement Khatanga (~72°N)	(Hulten and Fries, 1986)	12,4 °C (Mühr, 2000)
Moehringia laterifolia	Near the settlement Chokurdakh (70°37'N)	(Cherepanov et al., 2000)	10 °C (Rivas-Martínez, 1996-2004)
Myriophyllum spicatum	Upper Yana River (~67,5°N)	(Hulten and Fries, 1986)	>12.5 °C (VMGO, 1980)
Parnassia palustris	Lower Olenyok River, southern Lena Delta (~72°20'N)	(Busunova et al., 1984)	Between 7.5 °C and 10 °C isotherms (VMGO, 1980)
Sparganium hyperboreum	Lower Yana River near Kazachye (70°45'N)	(Krasnoborov, 1988)	10 °C (Rivas-Martínez, 1996-2004)

48