



New insights into the Weichselian environment and climate of the East Siberian Arctic, derived from fossil insects, plants, and mammals[☆]

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Abstract

Multidisciplinary study of a key section on the Laptev Sea Coast (Bykovsky Peninsula, east Lena Delta) in 1998–2001 provides the most complete record of Middle and Late Weichselian environments in the East Siberian Arctic. The 40-m high Mamontovy Khayata cliff is a typical Ice Complex section built of icy silts with a network of large syngenetic polygonal ice wedges, and is richly fossiliferous. In combination with pollen, plant macrofossil and mammal fossils, a sequence of ca 70 insect samples provides a new interpretation of the environment and climate of the area between ca 50 and 12 ka. The large number of radiocarbon dates from the section, together with an extensive ¹⁴C database on mammal bones, allows chronological correlation of the various proxies. The Bykovsky record shows how climate change, and the Last Glacial Maximum in particular, affected terrestrial organisms such as insects and large grazing mammals. Both during the presumed “Karginsky Interstadial” (MIS 3) and the Sartanian Glacial (MIS 2), the vegetation remained a mosaic arctic grassland with relatively high diversity of grasses and herbs and dominance of xeric habitats: the tundra-steppe type. This biome was supported by a constantly very continental climate, caused by low sea level and enormous extension of shelf land. Variations within the broad pattern were caused mainly by fluctuations in summer temperature, related to global trends but overprinted by the effect of continentality. No major changes in humidity were observed nor were advances of modern-type forest or forest-tundra recorded, suggesting a major revision of the “Karginsky Interstadial” paradigm. The changing subtypes of the tundra-steppe environment were persistently favourable for mammalian grazers, which inhabited the shelf lowlands throughout the studied period. Mammal population numbers were lowered during the LGM, especially toward its end, and then flourished in a short, but impressive peak in the latest Weichselian, just before the collapse of the tundra-steppe biome. Throughout MIS 3 and MIS 2, the climate remained very favourable for the aggradation of permafrost. No events of regional permafrost degradation were observed in the continuous Bykovsky sequence until the very end of the Pleistocene.

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1. Introduction

The shallow shelf seas in the East Siberian Arctic (Laptev, East Siberian, Chukchi) are very recent. They

came into being only a few thousand years ago, in the early Holocene, when the dramatic rise of global sea-level resulted in the rapid inundation of the flat coastal plain (Bauch et al., 2001). Prior to that, during the Late Pleistocene regression, the East Siberian arctic marginal plain extended 400–700 km north, to about 78 °N, and incorporated all the present-day islands. Although wide-ranging geological and stratigraphic exploration of Pleistocene deposits had been done in the area by the USSR Geological Survey and other Russian researchers,

[☆]This paper is dedicated to the memory of Prof. Boris Yurtsev (15.03.1932–14.12.2004), a great Arctic botanist and a strong promoter of the tundra-steppe concept.

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and recently by international teams, the past environment of the shelf land remains essentially enigmatic and debatable, except for the almost unanimous opinion that it was never covered by glaciers (Sher, 1995). There is no clear knowledge about the dynamics of the environment on the shelf land during the global climatic variations. Even the last 50 ka, the period within the scope of radiocarbon dating, still raises many questions. For instance, how did the Late Weichselian climate cooling, corresponding to MIS 2 (the Last Glacial Maximum, named here Sartanian after the Sartan Glaciation of the Verkhoyansk Mountains) affect the environment and life in the high latitudes? Was the climate milder and vegetation richer in the Middle Weichselian (MIS 3) than today? Some researchers believe they were, and reconstruct shrub tundra (Alekshev, 1997) or even taiga forest (Igarashi et al., 1995) on the shelf land; they traditionally describe this period as a relatively warm “Karginian Interstadial”. Other students suggest that the vegetation of that time did not differ much from herb-dominated tundra or tundra-steppe of the “glacial” intervals; it should be noted, however, that real evidence is very poor and scattered (cf. Anderson and Lozhkin, 2001 for review). Another unsolved problem is the scale of the sea-level rise during MIS 3: the presumed “Karginian Transgression” (Saks, 1948; Lomachenkov, 1966; Kind, 1974), if it existed (cf. discussion in Astakhov, 2001), left almost no traces in the areas of the Laptev and East Siberian Seas.

One of the most intriguing facts about the past life on the shelf land is the abundance of fossil mammal bones, found over the coastal lowlands and on the shelf islands. Thousands of fossils of such grazing mammals as woolly mammoth, horse, bison, woolly rhino and others suggest the richness of the past fauna. Even one of the most stenotopic ungulates, saiga antelope, that now inhabits southern steppe and semi-desert, was able to live on what are now the Lyakhovskiy Islands. It seems difficult to blend this Late Pleistocene grazing assemblage with the modern Arctic environment. An abundance of grazing herbivores in high latitudes invites the assumption of some pasturable ecosystem, essentially different from modern tundra; in fact, a non-analogue environment. The concept of such an ecosystem, called “tundra-steppe”, was suggested by Tugarinov (1929), and successfully developed in Russia since then. Similar concepts emerged in North America under various names (“Arctic steppe”, “steppe-tundra”, or “mammoth steppe”). The critics of these concepts argue that the vegetation reconstructed from pollen data did not differ much from graminoid arctic tundra or even polar desert, and had such low productivity that it could not support populations of various grazers (Ritchie and Cwynar, 1982). The logical inference would be that the mammalian grazers did not live permanently in that environment, and either lived somewhere further south

and occasionally “visited” high latitudes, or lived here at a different time, i.e., that their fossils are not synchronous with this pollen record.

Such sceptical views have not been supported by the conveners of the great discussion on tundra-steppe in Beringia (Hopkins et al., 1982). They concluded that there was enough evidence confirming the presence of a diverse ungulate fauna in Beringia both during the “Duvanny Yar Interval” (i.e., MIS 2), and the Boutellier Interval (or Karginian, MIS 3) (Schweger et al., 1982). However, the nihilistic approach to the concept of a tundra-steppe biome as the favourable native environment for mammoth fauna is resilient (Colinvaux, 1996), and the main reason for that is our insufficient knowledge of the past environment in the Arctic and the details of its history and dynamics. The shelf lands of the Laptev and East Siberian Seas, due to their huge extent, extremely northern position, relative homogeneity of topography and geology and very rich fossil record, provide the best area to test these environmental concepts and, even more importantly, to get more detailed knowledge of variation of the tundra-steppe biome in space and time.

Critical new evidence on the Late Pleistocene environment of the Arctic shelf land has been obtained in the course of multidisciplinary paleoecological research under the German–Russian project “The Laptev Sea System 2000”. Here, we introduce some results of the field and lab research conducted in 1998–2002. One of the main objects was the continuous Late Pleistocene sequence exposed in the Mamontovy Khayata (MKh) cliff on the Bykovskiy Peninsula (east Lena Delta), where the first complete carcass of woolly mammoth (the “Adams’ Mammoth”) was found in 1799 (Fig. 1). After four seasons of field research, with a broad complex of geological and paleontological studies and an extensive programme of radiocarbon dating, this section provides the most complete record of the environmental and climatic history for the last 50,000 years in whole of Arctic Siberia. In this paper, we concentrate on biotic evidence from the record (mostly fossil insects, plants and mammals), which offers new perspectives on the problems raised above.

2. Material and methods

2.1. The study site

The 40-m high MKh cliff (Fig. 2) is built by ice saturated silts, sometimes fine silty sands, with a polygonal system of thick syngenetic ice wedges. This syncryogenic (i.e., turning into permafrost as it was deposited) sedimentary formation, containing up to 80–90% ice (both structure-forming and wedge ice) and usually called Ice Complex (IC), is extremely widespread

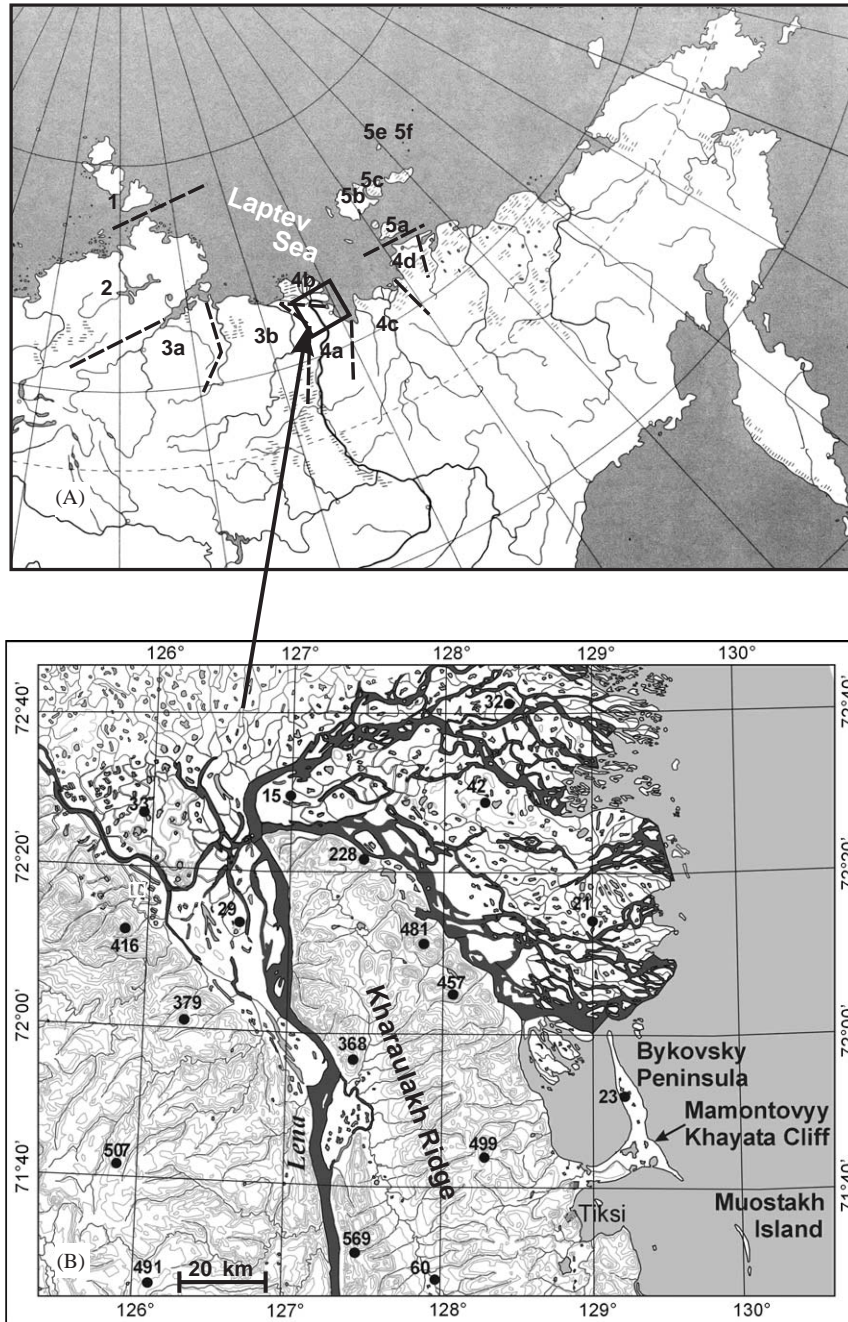


Fig. 1. Geographic position of the studied section. (A) The regions around the Laptev Sea, where the radiocarbon-dated mammal bones came from (cf. Appendix Table A1 in the online version of this paper and Fig. 7): 1—Severnaya Zemlya; 2—Taimyr; 3—Khatanga-Olenyok (3a—Khatanga; 3b—Anabar-Olenyok); 4—the Lena River-Dm. Laptev Strait (4a—the Lena River lower course; 4b—the Lena River Delta; 4c—Omoloy-Yana; 4d—Laptev Sea Coast (east)); 5—New Siberian Islands (5a—Bolshoy Lyakhovskiy Is.; 5b—Kotelniy and Bel'kovskiy Islands; 5c—Faddeevskiy Is.; 5e—Bennet Is.; 5f—Zhokhov Is.). (B) The study area. Numbered dots—elevation marks, and m above sea level.

in Northeast Siberia, and is famous for the abundance and excellent preservation of animal and plant fossils, representing the Mammoth Biome (Sher, 1997). Long-term debate on the origin and sedimentary environment of this formation is still ongoing, but more and more scientists are inclining to the idea, that IC is of polygenetic origin, and reflects a certain climatic situation rather than a particular depositional agent. It

is a product of generally very cold but highly continental climate, with intense cryogenic weathering and other permafrost processes and phenomena, that gave a similar appearance to deposits formed in various environments and under different factors (fluvial, aeolian, lacustrine, slope downwash, etc.).

The MKh IC section has been repeatedly studied for various, but mostly sedimentary, aspects (Tomirdiaro

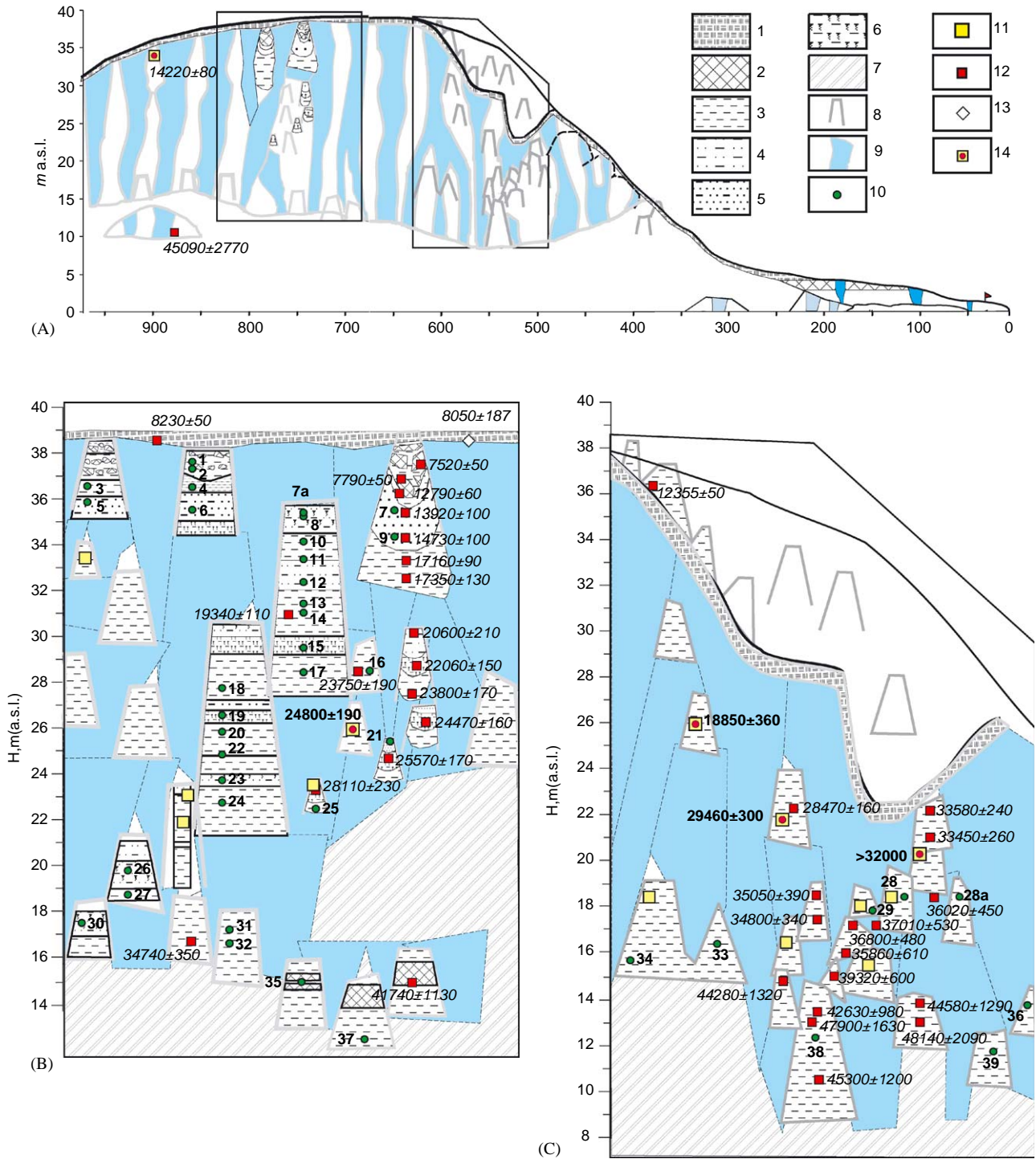


Fig. 2. MKh IC section. (A) General construction of the cliff and position of studied profiles; (B) MKh99-01 group of profiles; (C) MKh98 group of profiles. Two main combined profiles have been studied in most detail: MKh99-01 in the highest central part of the cliff, covering the interval of 39–22 m.a.s.l. (above sea level), and MKh98 in its NW wing, where the interval of 10–24 m.a.s.l. was covered. Additional local profiles were studied across the cliff. The lowest 10 m of the cliff are closed with frozen mud flows, and only small isolated outcrops with unclear stratigraphy could be studied in this part of the succession. For that reason, we concentrate here on the main part of the exposed section, i.e., 10–39 m a.s.l. 1—cover layer and modern soil; 2—peat; 3—silt; 4—sandy silt; 5—silty sand; 6—abundant grass rootlets; 7—colluvium and frozen mud; 8—baidzherakhs—residual (thermo-erosional) ground mounds; 9—ice wedges; 10—macrofossil samples; 11—mammal bones, found in situ; 12—AMS radiocarbon dates on plant remains; 13—conventional radiocarbon dates on bulk samples; and 14—radiocarbon-dated mammal bones.

et al., 1984; Kunitsky, 1989; Slagoda, 1993). Our recent work at the site was explicated with great detail in a series of reports (Siegert et al., 1999a, b; Sher et al., 2000, 2002b), presenting the geomorphology of the site, field descriptions of the section, lithology, permafrost features, sampling areas, and complete lists of various samples. These data, along with the results of age determinations, analysis of sedimentology, stable isotopes of ice wedges, the preliminary studies of organic fossils (pollen, plant macrofossils, testate amoebae, insects and mammals) were summarized in recent publications (Andreev et al., 2002; Meyer et al., 2002; Schirrmeister et al., 2002a, b; Siegert et al., 2002).

Because of the polygonal system of thick ice wedges, the MKh cliff sediment could not be studied in a single continuous profile. Instead, the network of frozen thermo-erosional mounds (baidzherakhs) offered an opportunity to combine their particular profiles, 2–6 m high each and instrumentally correlated by altitude, in a more or less continuous succession (Fig. 2B and C; Figs. 3 and 4). The stratigraphy of the MKh IC section is relatively simple. The bedding is close to horizontal, which is evidenced by a generally good correlation between ^{14}C dates and altitude, with possibly only minor dipping at the flanks of the hill. The erosional unconformities seem to be rare and of local importance, without a major re-structuring of the polygonal ice-wedge system. The sediment is mostly fine-grained sandy silt, occasionally silty sand, more or less uniform, with varying organics content, including fine plant detritus and macroscopic plant remains. Among the latter, the most common are in situ thin rootlets of herbaceous plants; in some layers woody roots and twigs of small shrubs are rather abundant; sometimes, moss stems can be seen. These kinds of plant remains have mostly been used for the AMS dating. Autochthonous peat is rare, and forms a few lenses in the lower part of the studied sequence. There is cyclic variation in the concentration of thin rootlets and woody roots (Sher et al., 2002b). The increase of variation in some geochemical parameters, such as organic carbon content and C/N ratio (Siegert et al., 2002) in the middle part of the section (10–28 m a.s.l.) can be related either to climatic fluctuations, or to less stable sedimentary conditions. The latter seems more likely, as these variations are correlated with the grain size of the sediment. Abundance of green algae colonies through the whole section and occurrence of freshwater ostracodes suggest that water was the main depositional agent of the MKh IC, although contribution from other agents, such as aeolian and slope processes, cannot be ruled out.

Currently, the MKh site is situated in the grass/herb and moss-dominated tundra, with dwarf shrubs extending above the moss surface for not more than 10 cm. Single bushes of willow up to 50 cm high and dwarf birch can be found in wind-protected sites only. The

open ground surface is rare. In the Russian nomenclature, this environment corresponds to the typical tundra subzone. The climate is severe and locally strongly affected by the coastal position of the site. Mean July air temperature (T) is not higher than 7°C (Tiksi), or even as low as 4.3°C (Muostakh Island 30 km SE of the MKh cliff); January T is about -33°C ; mean annual T is -13.3 . Annual precipitation does not exceed 200–240 mm (Reference Book on Climate of the USSR, 1966–1968).

2.2. Radiocarbon age of the sediment

Of about 70 ^{14}C AMS dates on macroscopic plant remains, insect and mammal fossils, obtained in the site area, almost 40 contribute to the chronology of IC in the MKh main section (Schirrmeister et al., 2002a); in addition, about 15 ^{14}C dates on bulk organic and more than 50 dates on collagen of mammal bones have been obtained by conventional dating, but only a few of them were used for the stratigraphy of the MKh section. Radiocarbon dating suggests that the sedimentation was mostly continuous from ca 48 to 12–12.5 ka (1000 years before present). The AMS dates on plant remains are quite consecutive in the upper part of the sequence, where they range from 12.5 to 28 ka (Fig. 2B), but much more variable in the older sediments. Minor inversions of dates are observed even within the same profiles (Fig. 2C). Extensive variation of dates older than 30 ka is in agreement with the complicated history of active carbon isotope production (Voelker et al., 1998). In the lower part of the section most finite dates are between 40 and 48 ka, with large statistical errors. Thus, the ages of particular layers below 20–25 m a.s.l. should be interpreted as approximate only. The following age intervals can be estimated for certain levels of the section: 48 (or more)–40 ka: 10–16 m a.s.l., 40–35 ka: 16–19 m, 35–29 ka: 19–22.5 m. In order to estimate the age of particular layers in the lower part, an attempt was made to calculate a regression for the age/height relationship, including all samples (Schirrmeister et al., 2002a). If we assume that the sedimentation rate was constant throughout the sequence, we can calculate the regression equation for the upper part of the section (which shows no inversions) and extrapolate it to the lower one. However, such extrapolation predicts younger ages for the lower part of the section than are observed there. Thus, we calculated a separate regression equation for the lower part, and the result suggests a somewhat slower sedimentation rate for it. Probably that is related to less stable sedimentation conditions in the lower part of the sequence, with more frequent local re-working of the sediment. In the end, we used two separate regressions to correlate the hypsometric position of samples with the radiocarbon time-scale, with an interpolated smooth transition between them in the

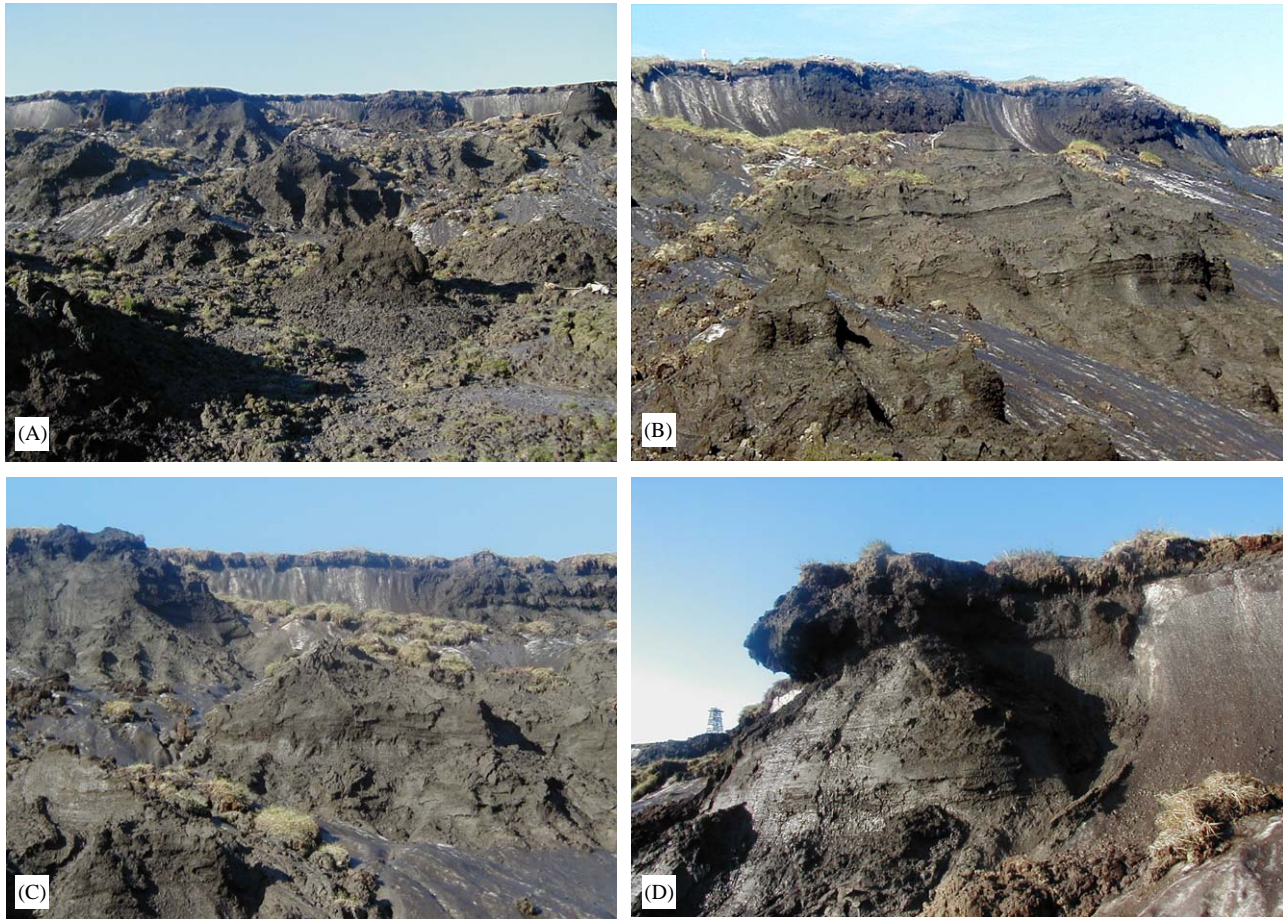


Fig. 3. Upper part of the MKh exposure. (A) General view of a series of baidzherakhs in SE area of the site; (B) the Pleistocene ice wedges and the insertions of Early Holocene “peat tussocks” in their upper part in the NW area of the site; horizontal “bedding” of partially cryogenic origin in baidzherakh “S” (28–36 m a.s.l.); (C) baidzherakhs and ice wedges in the upper-central area of the site; note the Early Holocene insertion at the top right; and (D) initial stage of formation of a baidzherakh of the top level (cf. also Sher et al., 2002b).

middle of the section, taking into account dated sampling points in that region.

2.3. Sampling for insect assemblages and their paleoenvironmental interpretation

About 70 samples of average weight 30–40 kg were screened for insect fossils (with 0.5 mm mesh) from the MKh main section. Altogether, they yielded nearly 11,000 insect fossils, belonging to a minimum of 5900 individuals and about 130 taxa, 93 of which were identified to species. For the analysis of the faunal change through the section we selected about 40 most representative samples (Table 1; Fig. 2). Paleoenvironmental interpretation of fossil insect assemblages is based on modern distribution and ecological preferences of species identified. All of them are extant, but do not necessarily live in the study area today. By their taxonomic composition, most Pleistocene insect assemblages are different from the modern tundra fauna of

this area. Although they all usually contain a large quantity of modern tundra inhabitants, the relative abundance of species, characterizing dry and wet tundra habitats, varies with time. Besides, most Pleistocene assemblages include species not currently known in the area, such as steppe insects, or species living in the forest zone or associated with trees. Finally, some species that are relatively rare in the area today, were the dominant species in some of the fossil assemblages. Changes of the ecological structure of insect assemblages with time provide sensitive paleoenvironmental and paleoclimatic reconstructions. A common practice to evaluate these changes is to classify the fossil species under several ecological groups, and to use the proportion of each group in the assemblage, based on minimum number of individuals in the sample, as a proxy measure of the corresponding habitat (Kiselyov, 1981; Kuzmina, 1989).

The following ecological groups of insects were recognized in our material (the names of the groups are informal and are designed to give general impression



Fig. 4. The studied profiles and details of the MKh exposure (cf. also Sher et al., 2002b). (A) Baidzherakh “O” of the top level (31–38 m a.s.l.); (B) baidzherakh “I” in the middle part of MKh01 profile (22–30 m a.s.l.); (C) lower part of baidzherakh “S” (cf. Fig. 3B); (D) horse tibia bone just thawed out of permafrost near the foot of baidzherakh “I” (24 m a.s.l.); (E) dense network of grass and willow roots in baidzherakh “W” (19–20 m a.s.l.); and (F) chopping frozen sediment for screening (after melting) in baidzherakh “O”.

Table 1
List of 39 insect samples selected for the present report

Sample number in Fig. 1C and D	Sample database number	Sample field number	Altitude, m above sea level.	Sum of fossils	Minimum number of individuals (MNI)	Sample number in Fig. 1C and D	Sample database number	Sample field number	Altitude, m above sea level.	Sum of fossils	Minimum number of individuals (MNI)
1	S21_74	Mkh-01-01	37.6	251	164	20	S21_57	Mkh-01-13	25.9	170	97
2	S21_73	Mkh-01-02	37.3	702	408	21	S21_21	MKh99-18aS	25.4	52	30
3	S21_72	Mkh-01-23	36.6	536	252	22	S21_56	Mkh-01-12	24.9	144	75
4	S21_71	Mkh-01-03	36.4	541	230	23	S21_55	Mkh-01-20	23.8	62	45
5	S21_70	Mkh-01-21	35.8	423	173	24	S21_54	Mkh-01-19	22.8	172	92
6	S21_69	Mkh-01-22	35.5	386	172	25	S21_20	MKh-B-17	22.5	157	88
7	S21_33 and 34	MKh99-5oS+5S	35.4	257	114	26	S21_53	Mkh-01-16	19.8	491	306
7a	S21_68	Mkh-01-05	35.3	156	88	27	S21_52	Mkh-01-17	18.8	313	154
8	S21_67	Mkh-01-04	35.2	234	121	28 (+28a)	S21_17 and 18	MKh-R-11+10	18.4	135	76
9	S21_31	MKh99-6S	34.3	109	56	29	S21_16	MKh-R-12	17.8	97	56
10	S21_66	Mkh-01-06	34.1	159	112	30	S21_51	Mkh-01-18	17.5	197	97
11	S21_65	Mkh-01-07	33.3	344	201	31	S21_12	MKh-R-5'	17.1	166	86
12	S21_63	Mkh-01-08	32.3	113	82	32	S21_15	MKh-R-5	16.6	358	183
13	S21_62	Mkh-01-09	31.3	155	91	33	S21_10	MKh-R-18	16.3	241	105
14	S21_29	MKh99-22aS	31.2	160	88	34	S21_09	MKh-R-15	15.7	83	53
15	S21_61	Mkh-01-10	29.4	115	70	35	S21_06	MKh-B-15	15.0	225	123
16	S21_26	MKh-B-18	28.5	96	53	36	S21_04	MKh-B-7	13.8	232	107
17	S21_60	Mkh-01-11	28.4	147	93	37	S21_03	MKh-R-8	12.5	191	97
18	S21_59	Mkh-01-15	27.8	172	105	38	S21_02	MKh-B-28	12.3	138	73
19	S21_58	Mkh-01-14	26.6	88	49	39	S21_01	Mkh-B-8	11.8	81	48
								Total		8849	4713

Some samples, closely positioned to each other and having similar ecological structure, were joined together for better statistical representation. About 30 samples were excluded mainly because of the small number of fossils, but some for their contamination or unclear stratigraphic position. The samples included contain 8849 insect fossils, representing a minimum of 4713 individuals. Sample numbers, accepted in this paper, are provided with the field numbers under which they were published in field reports (Siegert et al., 1999a, b; Sher et al., 2000, 2002a, b) and in Kuzmina, 2001.

of their content; as to the particular species, they were assigned to these groups depending on their prevalent modern distribution, but the names of the groups may not correspond to the accepted ecological definition of each particular species).

1. True, or “southern”, xerophiles, with four subgroups: 1a—steppe species; 1b—meadow-steppe species; 1c—broad xerophiles; and 1d—“sedge heath” species,
2. Dry tundra inhabitants, or “northern xerophiles”,
3. Arctic tundra species,
4. Mesic tundra inhabitants,
5. “Forest-tundra” insects, with three subgroups: 5a—taiga species; 5b—inhabitants of meadows in taiga; 5c—insects related to shrub plants (except dwarf shrubs of typical and arctic tundra),
6. Aquatic, including aquatic species proper (6a), and riparian insects (6b),
7. Varia, species with no clear ecological indications (including fossils resolved only to a genus that includes species with differing ecologies).

The complete list of insect taxa identified, with assignment to ecological groups, is given in Table 2.

The main modern ranges of true steppe insects, such as the weevils *Stephanocleonus eruditus*, *S. fossulatus*, the leaf beetles *Chrysolina perforata*, *Ch. purpurata*, *Ch. brunnicornis*, *Galeruca interrupta circumdata* are in the mountain steppe regions of southern Siberia (Altai, Sayany, Mongolia, Transbaikalia). Some of them occupy isolated areas in Central Yakutia, and the northernmost occurrences of some of these species are known on the relict steppe patches in the upper basins of the Yana and Indigirka rivers, where the mean July air temperature is 12–14 °C (i.e., at least 5–7° higher than on the Bykovsky Peninsula), and July soil temperature is 22–23 °C (Berman and Alfimov, 1993). The observations of the cited authors in the relict steppe areas show that the distribution of *S. eruditus*, for instance, is restricted by a certain threshold of heat received by the top soil layer during the summer, below which the beetles cannot complete their life cycle. Measured as sum of positive soil temperatures (SPST),¹ this threshold is 2200–2400°, while currently in the Lena Delta the SPST is hardly higher than 800°. This weevil also requires extremely dry soil (Berman and Alfimov, 1993). The presence of that and other steppe insects in fossil assemblages, even in small numbers, suggests highly continental climate with quite warm and dry summers.

The meadow-steppe subgroup includes species that have basically similar distributions to the true steppe ones, but their isolated northern occurrences extend to the Arctic. That probably means that they require less

summer warmth. Most of them are currently known in dry sandy or rocky habitats in the Siberian Arctic (e.g., the weevils *Coniocleonus cinerascens* and *C. astragali*). Some are represented in the North by subspecies or even species different from the south Siberian taxa (e.g., the ground beetle *Harpalus vittatus kiselevi*, and the leaf beetle *Chrysolina arctica*), but their close steppe affinities are evident. Under broad xerophiles we conventionally place the dung beetle *Aphodius* sp.; its fossils occur in our sequence only in the most xerophilic assemblages. This still undescribed species is not known in northern Siberia today, but is quite common in the Pleistocene; it probably fed on the dung of extinct mammalian grazers.

A pill beetle *Morychus viridis* is very common in the Pleistocene insect faunas of Northeast Siberia, quite often dominating fossil assemblages. Now it occupies isolated well-drained habitats in northeastern Siberia with sparse vegetation (mostly xerophilic sedges and moss), and with very dry continental climate (Berman, 1990). This kind of xeric environment, often with discontinuous or disturbed vegetation, is sometimes called “sedge steppe”, or hemicycrophitic steppe (Yurtsev, 1981; Berman et al., 2001); we label it “sedge heath”, and use the same name for the ecological subgroup of which *M. viridis* is the only member. The relative abundance of this species is usually in positive correlation with the presence of steppe insects and a high proportion of xerophiles among tundra species.

An alternative dominant species of Pleistocene assemblages is the weevil *Isochnus arcticus* that is now known from the arctic tundra of the Taimyr Peninsula to the Canadian Arctic, but is especially abundant on Wrangel Island (Khruleva and Korotyaev, 1999). Its larvae develop on prostrate willows, including *Salix arctica*. Abundance of this species, concurring with a high proportion of other tundra insects, indicates cold summer conditions. Its relation to moisture conditions is not evident. Together with a few other, but less abundant species, such as the leaf beetles *Chrysolina bungei* and *Ch. tolli*, *I. arcticus* is included in the arctic tundra group.

Dry tundra species usually occupy the best-heated sites in this zone, most commonly well drained, with diverse grasses and herbs. Most of them do not reach the arctic tundra today, but quite often enter the taiga zone along suitable biotopes. Some species, such as *Hypera ornata* and *Sitona borealis*, feeding on legumes, can be found today on relict steppe patches. The most common member of this group is a ground beetle *Curtonotus alpinus*. Some other dry tundra carabids, such as *Poecilus nearcticus*, were much more common in the Pleistocene than now. The species included in the mesic tundra group, are more often related to relatively wet and colder sites; at present, they are the most common and abundant species in the tundra zone. The ratio between the proportions of dry and mesic tundra insects

¹Annual sum of average daily temperatures above 0 °C—a common soil science parameter.

Table 2 (continued)

Sample no. in Fig.1C and D		1	2	3	4	5	6	7	7a	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39											
<i>Mesotrichapion wrangelianum</i> Kor.	dt	—	—	3.2	5.2	2.9	4.1	1.9	5.7	—	—	—	0.5	—	—	—	—	—	—	—	—	—	—	—	—	—	—	7.6	—	—	0.6	5.5	1.8	4.1	2.3	1.6	—	1.9	2.4	3.7	1.0	1.4	2.1									
<i>Hemitrichapion tschernovi</i> T.-M.	dt	—	0.2	21.8	12.2	4.0	1.2	6.7	—	—	1.8	—	—	—	1.1	1.1	—	—	—	—	—	—	1.0	6.7	4.0	—	—	5.7	6.9	—	—	—	—	1.0	1.2	0.6	—	—	2.4	1.9	—	4.1	8.3									
Family Curculionidae—weevil or snout beetles																																																				
<i>Phyllobius fumigatus</i> Boh.	me	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0.9	—	—	—					
<i>Phyllobius</i> sp.	me	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—				
<i>Sitona borealis</i> Kor.	dt	1.2	0.2	0.4	1.3	0.6	1.7	3.9	1.1	—	—	1.8	0.5	1.2	—	1.1	—	—	2.2	1.0	—	1.0	—	—	2.7	4.4	4.3	1.1	1.6	1.3	0.9	3.6	1.0	2.3	3.3	—	—	1.6	2.8	1.0	—	—	—	—	—	2.1	—	—				
<i>S. lineellus</i> Bonsd.	me	0.6	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1.3	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—				
<i>Coniocleonus cinerascens</i> Hochh.	ms	—	—	0.4	—	—	—	—	—	1.1	1.7	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—				
<i>C. ferrugineus</i> Fahr.	ms	—	—	—	—	—	—	3.0	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2.2	2.9	—	—	—	—	—	—	—	—	—					
<i>C. astragali</i> T.-M. et Kor.	ms	—	—	2.4	0.4	1.7	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—				
<i>Coniocleonus</i> sp.	ms	0.6	0.5	0.8	—	—	—	—	—	—	3.6	—	—	—	—	1.1	—	—	1.1	—	—	—	—	—	1.3	—	1.1	1.1	0.7	—	—	—	—	—	—	—	—	1.9	1.9	—	—	—	—	—	—	—	—	—				
<i>Stephanocleonus eruditus</i> Faust	st	0.6	—	0.8	2.6	1.7	1.7	1.8	—	2.5	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1.3	—	—	1.1	—	1.3	—	—	—	1.0	1.2	1.1	1.0	—	—	—	—	—	—	—	2.1	2.7	2.1	—	—			
<i>S. cf. eruditus</i> Faust	st	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—			
<i>S. fossulatus</i> F.-W.	st	0.6	—	—	—	1.2	—	—	—	1.1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—			
<i>S. paradoxus</i> Fahr.	st	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	
<i>Stephanocleonus</i> sp.	st	—	—	—	—	—	—	—	—	0.8	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—		
Cleoninae gen. indet.	ms	—	—	—	—	—	—	—	—	—	—	—	0.5	—	—	—	1.4	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	
<i>Lepyrus nordenskjoldi</i> Faust	sh	1.2	0.2	0.4	1.3	—	1.2	—	1.1	0.8	1.8	3.6	2.5	7.3	2.2	1.1	1.4	—	3.2	1.9	—	3.1	3.3	8.0	2.2	3.3	—	1.0	1.9	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	
<i>Lepyrus</i> sp.	sh	—	—	—	—	—	—	1.1	—	—	—	—	—	—	—	—	—	1.9	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	
<i>Lepyrus</i> spp.	sh	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>Hypera ornata</i> Cap.	dt	—	0.7	—	—	—	—	—	—	—	—	—	0.5	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—		
<i>H. diversipunctata</i> Schnk.	dt	1.2	0.2	1.6	1.7	—	1.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	
<i>Hypera</i> sp.	dt	—	—	—	—	—	—	—	—	1.1	—	—	—	—	1.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	
<i>Pissodes</i> sp.?	ta	—	—	—	—	—	—	—	0.9	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	
<i>Pelenomus</i> sp.	na	—	—	0.2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	
<i>Ceutorhynchus</i> sp.	oth	—	—	—	—	—	—	—	—	—	—	—	0.5	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	
<i>Dorytomus imbecillus</i> Fst.	sh	—	2.5	0.4	—	0.6	—	—	—	—	—	—	1.0	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—		
<i>Dorytomus</i> sp.?	sh	0.6	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	
<i>Notaris aethiops</i> F.	na	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>N. bimaculatus</i> F.	na	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
<i>N. ochoticus</i> Kor.	na	—	—	1.0	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	
<i>Isochnus arcticus</i> Kor.	tt	—	0.2	3.6	0.4	—	—	—	—	17.0	22.3	7.1	55.4	19.4	52.4	27.5	67.1	42.9	28.3	44.1	34.3	4.1	35.1	16.7	6.7	26.7	21.7	6.8	54.2	7.1	13.4	28.6	18.6	3.5	4.4	4.8	13.2	15.5	3.7	2.1	1.4	6.3	—	—	—	—	—	—	—	—		
<i>Isochnus flagellum</i> Erics.	sh	—	—																																																	

in fossil assemblages reflects not just a degree of humidity, but to some extent summer soil temperature as well. The ground beetles *Pterostichus* are most common in the mesic tundra group; several dominant species belong to a subgenus *Cryobius*, representing the most diverse and abundant group of all modern tundra beetles in Eastern Siberia. Besides that, the rove beetle *Tachinus arcticus* is quite common, inhabiting all tundra subzones up to the arctic tundra.

The “forest-tundra” group joins together the species, which in some or other way may indicate the presence of trees and more-or-less tall shrubs, thus indicating more southern vegetation type than is present on the Bykovsky Peninsula today. These species are rare in Pleistocene assemblages, but their number and diversity increases in the early Holocene. The *taiga* subgroup joins the species related to larch or shrub pine, such as the weevil genus *Pissodes*, or those currently distributed in the taiga zone only, such as ants, the carrion beetle *Phosphuga atrata* and some others. The same zonal distribution is typical for the next subgroup (*meadows in taiga*). Species considered under the *shrub* subgroup, such as the weevil *Lepyrus nordenskiöldi*, associated mostly with willows, can be found both in taiga and southern (shrub) tundra.

Most species comprising the “aquatic” group, joining the aquatic proper and riparian species, are widespread intrazonal insects, living in or near water. It has been noticed that their fossils can be especially abundant in the sediments of bogs or small water pools, so the usage of this group as an indicator of general landscape humidity can be misleading.

2.4. Other proxy records

More than a hundred pollen and sediment samples have been taken at the main MKh cliff and the adjacent exposures of much lower height to the NW (alass, or thermokarst kettle sections) and to the SE (erosional gully fillings). Most samples were originally collected from frozen sediment as general sediment samples, later subdivided into several subsamples for various analyses, including ^{14}C AMS dating. For the latter, small plant remains (twigs, microroots, etc.) were picked from the general samples. The exact position of the samples is given in the field reports cited above.

Sampling of adjacent exposures often yields conflicting dating results, as most of the organic remains there were re-deposited from the main IC succession, and mixed with Holocene material (Schirrmeister et al., 2002a). For that reason, in this report we only include the samples from the main cliff. Even among them, there were a few samples contaminated with Holocene organics (those taken near the boundary with the Holocene cover, or, occasionally, from re-frozen collu-

vium). After careful examination, such samples were also excluded.

Collecting the samples for plant macrofossils presented something of a problem. Earlier (e.g., Sher et al., 1979) we picked the seeds from the samples screened for insects with 0.5 mm mesh, or even from those screened for rodents (1 mm mesh), but the recent work of Frank Kienast on the Taimyr Peninsula (Kienast et al., 2001) has shown that many identifiable plant macrofossils are smaller, and were lost through those sieves. In other words, representative plant macrofossil sampling required a special sieving with a 0.1 mm mesh, or no field pre-sieving at all. This was not realized in 1998, when the whole section was studied in the most detail, so the only available samples for the carpological analysis were the general sediment samples (unscreened) of a very small volume. In 1999, we used a special method of screening through dense fabric bags, and those samples yielded many times the number of seeds, including those of the smallest size range. However, screening and picking of those voluminous samples is very time consuming, so only few were processed. The rest came as subsamples taken from the general sample of small volume (dried, but otherwise unprocessed). This makes the quantitative comparison of concentration of the plant remains very problematic. From the part of the MKh main section under consideration 15 samples have so far been studied. The number of plant macrofossils, identified in individual samples, varies from 100 to more than 3000. Our attempt to compare the plant macrofossil and insect records from the same horizons is also hampered by the fact that the sampling for those two kinds of fossils in 1998 was not properly coordinated. The next problem is that the ecological grouping of plants that was earlier suggested for vegetational reconstructions (Kienast, 2002) is hard to use for comparison with the beetle record. For that reason, we tried to modify the grouping of plant species (according to their modern habitat preferences and distribution) for maximum approximation to the ecological groups accepted for the insects.

2.5. Database of radiocarbon-dated mammal bones

About 900 fossil mammal bones were collected in the site area, nearly 160 of them within the main MKh cliff. Among almost 80 conventional ^{14}C dates on bone collagen obtained from this collection, only a few are essential for site dating. As usual in the IC bluffs, the finding of bones in genuine in situ position is very rare because of the high rate of their melting out of the sediment and subsequent sliding down with melted mud streams. The general characteristics of the MKh mammal collection and preliminary results of the ^{14}C dating have been reported (Kuzmina et al., 1999; Kuznetsova et al., 2001a). The detailed list of dated

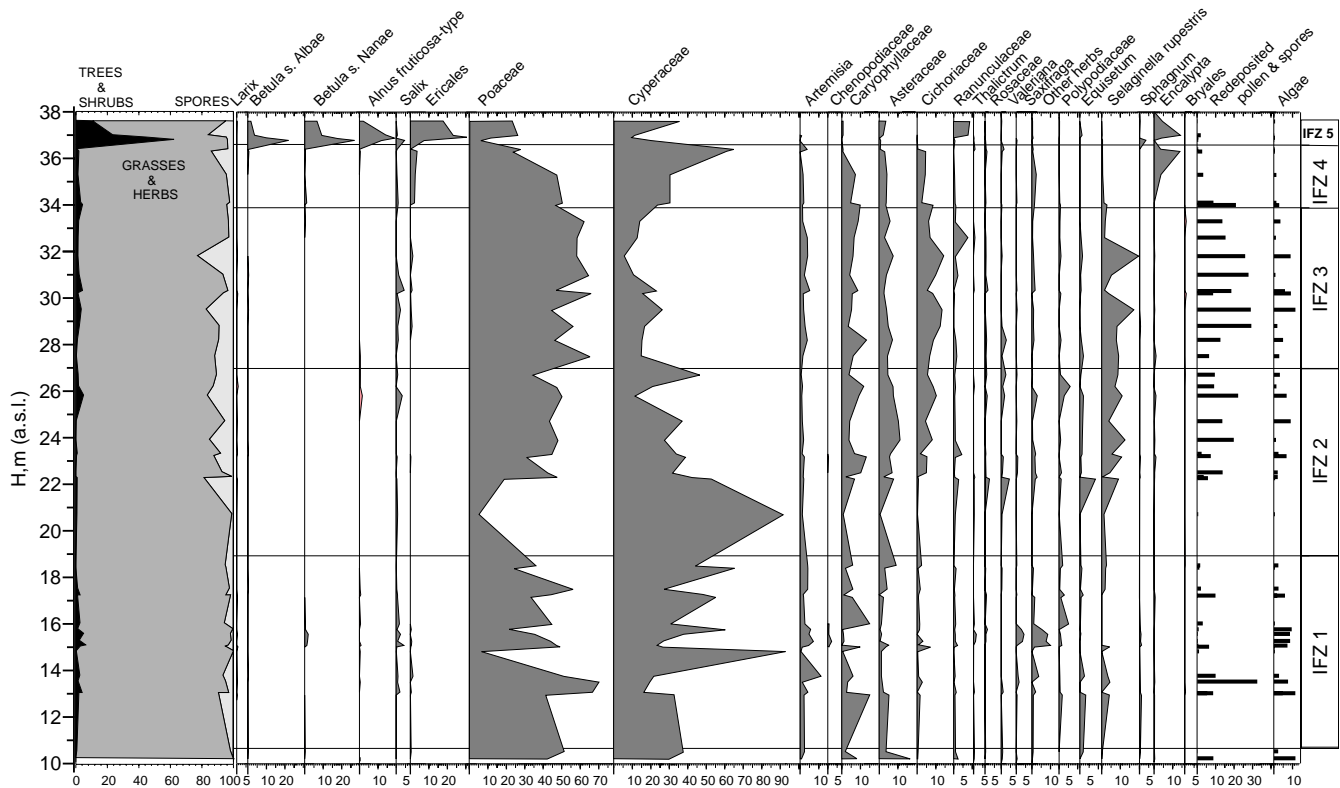


Fig. 5. Pollen diagram of the MKh main section. IFZ 1–5—Insect Faunal Zones. Pollen analysis by A. Andreev, compiled by A. Sher.

bones and their exact locations is given in the table in the online version of this paper. Having no exact position in the sediment succession, the vast majority of dated bones just represent the time of existence of certain mammalian species in the region. For that reason, and in accordance with the aims of this paper, we tried to operate with as large a number of mammal dates from the whole Laptev Sea area as possible. The database under analysis (see electronic Appendix Table A1) includes dated mammal records from the other Russian–German expeditions in the same region (Bol. Lyakhovsky Island and the Lena Delta), as well as all bone dates from this area published so far (ca 430 ^{14}C dates).

3. Results

3.1. The pollen sequence

The pollen record of the MKh IC shows surprisingly little variation in the general character of the vegetation through the studied time interval (Fig. 5; Andreev et al., 2002). All Pleistocene samples are dominated by grass and herb pollen. Maximum content of arboreal pollen (AP), mostly *Salix* and *Betula* sect. *Nanae*, is about 6%, often much less. Spores are also few (up to 20%); most commonly those of *Selaginella* dominate. Grass (Poa-

ceae) and sedge (Cyperaceae) together comprise 60–97% of all pollen grains; the grass pollen is more abundant than sedge in 70% of all samples; high abundance of sedge pollen is often, though not always, associated with peat layers or inclusions, i.e., is taphonomically biased. Significant amounts of pollen of Caryophyllaceae, Cichoriaceae, Asteraceae, as well as of *Artemisia*,² are quite common, though variable through the sequence. The very common presence of green algae (*Pediastrum* and *Botryococcus*), and their notable quantity, varying from 1% to 12% of all registered grains, indicate that water was the main depositional agent of the sediment. There is a high, though variable, amount of re-deposited pollen and spores, especially of pre-Quaternary Pinaceae (upto 30–35%). Possible source sediments for those alien pollen types are absent in the immediate vicinity of the site; however, poorly cemented terrestrial deposits of Early Eocene age with abundant Pinaceae pollen (Kengdey Suite) are widespread 30–50 km southwest, in the Kharaulakh Ridge, and 80–100 km northwest, in the Bykovsky Channel Depression (Grinenko et al., 1998). Thus, the presence of the re-deposited Pinaceae

²*Artemisia*, or sage-brush, is one of few genera of Asteraceae, or Compositae of earlier taxonomic system (Asteraceae + Cichoriaceae), easily recognized by palynologists; for this reason, but also because of xerophilic preferences of practically all species in the genus, it is separately distinguished in pollen diagrams.

pollen in the MKh sediments is one of the arguments for their fluvial origin, and the variable abundance of this type of pollen may indicate the relative activity of erosion and water runoff from the nearby mountains. Similar conclusions follow from the sedimentological data (Siegert et al., 2002). The early Holocene sediments on top of the IC show very different pollen spectra, with a dramatic increase of tree and shrub birch, shrub alder, and Ericales pollen.

3.2. Plant macrofossil record

The plant macrofossil assemblages from the MKh samples contain an average of 25–30 taxa, representing a wide range of ecological groups (Kienast, 2002). The most remarkable feature of the majority of the Pleistocene samples is the high abundance of xerophilic plants; many of them are currently found in the relict tundra-steppe communities. On the other hand, mesophilic and water plants are also rather common. According to Kienast (2002), all the studied assemblages portray grass- and herb-dominated vegetation that represented a mosaic of habitats, which varied with degree of moisture supply. These habitats ranged from extremely dry ones, probably with a discontinuous plant cover, to those of wet tundra with small ponds. Assemblages with a high percentage of aquatic and riparian plants are rare; we believe that they are most probably taphonomically defined, i.e., are preserved in the sediment of the pond where they grew. Most samples are not so local: they contain plants growing in various habitats, and hence give a more integrated record of the past vegetation.

Among 15 plant macrofossil samples, which can be more or less precisely correlated with the insect samples, one is dominated by aquatic plants, one by willow fossils, and one by the inhabitants of wet tundra (the Early Holocene sample). The other 12 are dominated by plants currently occurring in dry tundra habitats. All samples contain a varying amount (0.5–24%) of xerophilic plant fossils, mostly occurring on dry steppic meadows, or in well-drained, poorly vegetated sites (pioneering plants of dry bare ground, ruderals). A few of the identified plant species are currently not known in the tundra zone (Kienast, 2002); several species, by analogy with the beetles of meadow-steppe group, have their main distribution in Southern and Central Siberia, and only isolated occurrences in the Arctic. We could not find any regularity in the occurrence of relatively more thermophilic plants through the section.

3.3. Fossil insect assemblages

Fossil insect assemblages (Fig. 6) show more impressive variation along the sequence than pollen. They vary widely in the composition of ecological groups; for

instance, the total of all xerophiles (both “southern” and “northern”) varies from 10% to 85%. However, these variations are not random, and certain intervals within the sequence show more-or-less similar structure of fossil insect assemblages. That is why we prefer to use the insect record as the primary one to trace environmental changes through the MKh section and to recognize certain periods in the development of the environment and climate. Analysing the graphic presentation of the succession of the MKh fossil insect assemblages (Fig. 6), we use the technique basically similar to the recognition of pollen zones. Accordingly, we call these periods “insect faunal zones (IFZ)”. Subsequently, we compare these zones with our interpretation of the paleobotanical record. This comparison reveals some interesting correlations between these independent sources of proxy evidence.

The most remarkable and statistically significant finding is the inverse correlation between the proportions of true (southern) xerophiles in the insect assemblages and the amount of *Selaginella rupestris* spores in the pollen spectra ($r = -0.488$, $p = 0.047$). Both are related to dry habitats, but their requirements of summer temperature are very different. Thus, it can be assumed that a relative abundance of one or another can be reliably interpreted as a signal of dry environment under a higher or lower summer temperature, respectively. Most peaks of the willow weevil *Isochnus arcticus*, correspond to maximum amounts of willow pollen in the spectra; however, because of poor production, the total amount of *Salix* pollen is very low (0–4%), and the sample-to-sample correlation is not significant. However, this correlation is evidently corroborated by the fact that the zone with dominance of *I. arcticus* (28–32 m.a.s.l.) provided the highest amount of willow macrofossils through the whole section (Kienast, 2002).

Some visible, but statistically insignificant (mostly because of insufficient number of samples) correlations between certain groups of insects can be observed. For instance, the pattern of the steppe insect curve has common features with the curve of the “sedge-heath” subgroup (*Morychus viridis*), though the percentage of the latter is commonly much higher. On the other hand, there is no correspondence in the chronological distribution of *M. viridis* with sedge pollen, although currently this pill beetle forms a very close association with a few xerophilic sedge species. Interestingly, the few occurrences of insects related to taiga forest are all marked with the presence of steppe species in the same sample.

3.4. Insect faunal zones and the reconstruction of the environmental history

Basing on the general composition of ecological groups in the fossil insect assemblages (Fig. 6), we

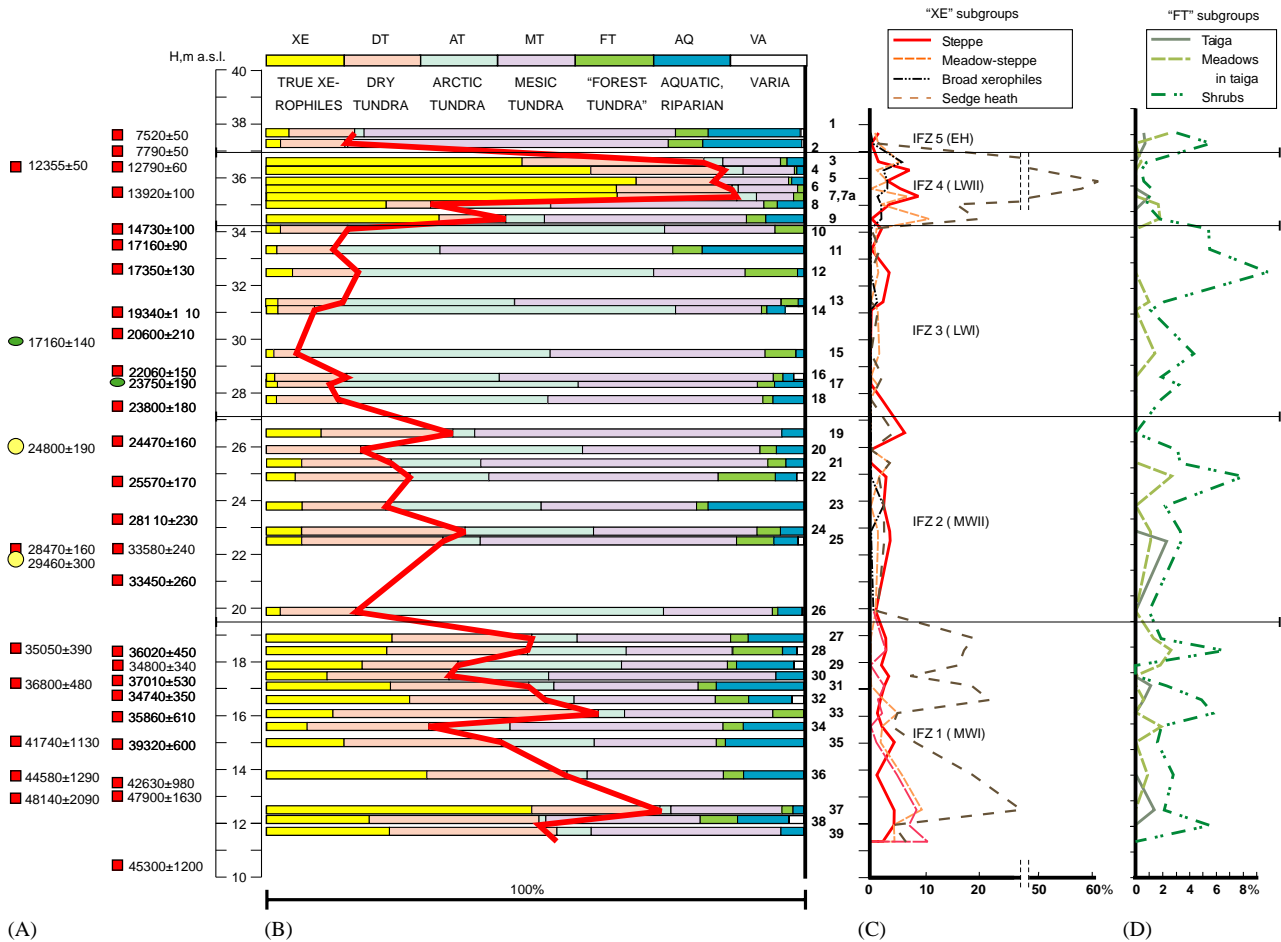


Fig. 6. Ecological structure of fossil insect assemblages, the distribution of radiocarbon dates and the IFZ in the MKh main section. (A) Radiocarbon dates: right column: exactly or closely corresponding to the insect samples (same profiles); left column—taken in other profiles and correlated with the insect samples by altitudinal position. AMS dates: on plant remains (red squares) and on insect fossils (green ovals); conventional dates on mammal bones (yellow circles). (B) Percentage of main ecological groups of insects in each sample represented by a single bar; minimum number of individuals in the sample equals 100%. Main ecological groups: XE—true (southern) xerophiles, DT—dry tundra inhabitants (“northern xerophiles”), AT—arctic tundra insects, MT—inhabitants of mesic sites in tundra, FT—“forest-tundra” species, AQ—aquatic and riparian insects, VA—species with uncertain ecology (see more details in text). Sample numbers to the right correspond to those in Figs. 2B and C. The thick red curve shows the total percentage of all xerophilic species (“southern” and tundra, XE plus DT). (C) Subgroups of true xerophiles; (D) subgroups of “forest-tundra” species; (note a different horizontal scale in (B–D), and the break of the axis in (C)). See original data on insect species distribution in Table 2.

recognized five IFZ in the MKh main section. They are characterized in Table 3, where the pollen spectra of these zones are also described. Let us consider now the main features of environment and inferred climate in the area during the periods, corresponding to these zones.

The most ancient in the studied section, IFZ 1 is approximately dated as >46 to 34 ka and corresponds to the early part of the Middle Weichselian—chronological equivalent of the early half of MIS 3. It is remarkable for the highly xeric character of both plant and insect communities. Generally, insect, pollen, and plant records suggest a complex mosaic of biotopes, reflecting local distribution of moisture and soil temperature. High diversity of xerophilic insects and herbaceous plants, both in the pollen spectra and plant macrofossil assemblages (Kienast, 2002) allow the

reconstruction of grassland vegetation on mostly dry substrate as the dominant habitat type. In particular, Caryophyllaceae and *Artemisia* pollen reach the highest levels throughout the section. Plant macrofossil spectra are dominated by xerophilic grasses and herbs, such as *Potentilla* cf. *stipularis*, *P. arenosa*, *Dryas punctata*, *Minuartia rubella*. Some plant species, represented by less abundant macrofossils, have close affinities with steppe and meadow-steppe communities (*Carex duriuscula*, *Linum perenne*); some of them are halophytes occurring in arid regions with varying moisture supply (*Hordeum brevisubulatum*, *Puccinellia distans*). Many others currently occupy the driest and warmest habitats in tundra. In general, dry tundra inhabitants strongly dominate all the plant macrofossil spectra in this zone. The permanent presence of the steppe weevils

Table 3

Insect faunal zones recognized in the main Bykovsky section (MKh), their pollen characteristic and inferred vegetation types.

Insect faunal zones	¹⁴ C age	The section interval, m a.s.l., and number of samples (insect/pollen).	Dominant insect ecological groups	Dominant pollen types	Inferred vegetation
IFZ 1—MW I (early MIS 3)	46 (or more)—34–35 ka	11–19 m 13/16	Dry tundra species (av. 28%), tundra mesophiles (av. 28%), true xerophiles (av. 22%). Steppe species consistently present (up to 4%). <i>Morychus viridis</i> forms three peaks: up to 28% at 12.5 m a.s.l., and successively lower at 16.6 and 18.4 m). <i>Isochnus arcticus</i> is usually below 8%, with two peaks up to 17% and 29% (at 15 and 17.8–18.4 m a.s.l. “Forest-tundra” insects almost always present (2–9%), mostly related to shrubs, but with taiga species encountered in 3 samples.	Poaceae (av. 41%), Cyperaceae (av. 39%, up to 92% in anomalous samples), Caryophyllaceae (up to 15%, av. 5%), <i>Artemisia</i> (up to 11%, av. 4%), Asteraceae (av. 2.5%), Cichoriaceae (up to 7%, av. 1.5%). Very few arboreal pollen (0–6%, av. 2.2%), mostly <i>Salix</i> (0–4%, av. 1%). Minor amounts of <i>Larix</i> pollen (0.3–0.8%) in almost half of samples. At 15–16 m a.s.l. in peat a minor peak of <i>Betula sec Nanae</i> (2%), <i>Salix</i> , Chenopodiaceae (2%), <i>Saxifraga</i> (4%).	Herb-rich, quite diverse, grass-sedge dominated vegetation with abundant <i>Artemisia</i> and some willow, probably a dwarf arctic form, and very few other shrubs. The main climate signal is dryness. Single trees or scattered groves of larch could exist at local sites with higher moisture. Complex mosaic of grass-dominated biotopes, reflecting local moisture and heat conditions. Minor alternation of mesic-xeric condition in time.
IFZ 2—MW II (late MIS 3)	34–24 ka	19–27 m 8/11	Mesic tundra species (av. 39%), dry tundra insects (av. 21%). Very few true xerophiles (av. 5.6%), but some steppe species fossils occur in most samples (av. 2.3%). <i>M. viridis</i> —normally 2–3% only. <i>I. arcticus</i> varies between 7% and 27%, but makes high peaks at 19.8 m (54%) and at 26 m (35%). “Forest-tundra” insects average 4% (mostly shrub subgroup), taiga species in one sample (containing steppe species as well).	“No-data” zone—19–22 m a.s.l. (one anomalous sample). In the second half of the zone: Poaceae (av. 39%), Cyperaceae (av. 37%), Asteraceae (up to 11%, av. 7%), Caryophyllaceae (up to 13%, av. 6.5%), <i>Selaginella rupestris</i> (up to 12%, av. 6.4), Cichoriaceae (up to 8%, av. 3.6%), <i>Artemisia</i> —1–2%. Almost no arboreal pollen (av. 1%), a few grains of <i>Salix</i> in 5 samples of 11 and single grains of <i>Larix</i> in 4 samples.	Herb-rich, grass-sedge dominated vegetation with more abundant Cichoriaceae and Asteraceae, but less <i>Artemisia</i> , than in zone 1. Open spaces covered with <i>Selaginella rupestris</i> . Almost no shrubs, but small groves of larch could hold out (a single ant fossil). No evident trend in pollen through the interval.
IFZ 3—LW I (early MIS 2)	24–15 ka	27–34 m 9/11	Arctic tundra insects (20–67%, av. 44%), mesic tundra species (av. 35%), dry tundra species (av. 10%). All true xerophiles are very low (av. 2.5%), steppe insects totally absent in the interval 28–31 m, build 2–4% in the other samples. <i>M. viridis</i> has the lowest values in the whole sequence (below 2% in 4 samples, absent in 5) while <i>I. arcticus</i> becomes a superdominant. “Forest-tundra” group averages 4%, mostly shrub-related,	Poaceae (av. 55%), Cyperaceae (av. 16%), Cichoriaceae (up to 15%, av. 9.2%), <i>Selaginella rupestris</i> (up to 20%, av. 7%), Caryophyllaceae (up to 13%, av. 7%), Asteraceae (up to 7%, av. 4.3%), <i>Artemisia</i> —up to 5%, av. 2.6%. A peak of Ranunculaceae at 32.6 m (up to 7.6%, av. for the zone 1.5%). Slight increase in arboreal pollen (av. 2.2%), <i>Salix</i> (up to 4%) is present more consistently (in 7 samples of 11), minor peak (1.5%)	Grass-sedge dominated vegetation, herb-rich, especially with Cichoriaceae, Asteraceae and Caryophyllaceae, with wide distribution of <i>Selaginella</i> communities. Clear advantage of grasses over herbs has no single interpretation. Almost constant presence of <i>Salix</i> (probably, a dwarf form) may suggest slightly more mesic local biotopes, possibly due to the snow patches. Existence of other shrubs or trees is unlikely, except

Table 3 (continued)

Insect faunal zones	¹⁴ C age	The section interval, m a.s.l., and number of samples (insect/pollen).	Dominant insect ecological groups	Dominant pollen types	Inferred vegetation
			no taiga species encountered.	of <i>Alnus fruticosa</i> (+ <i>Salix</i>) at 26 m, single grains of <i>Larix</i> in 2 samples.	some shrub alder in the lower part of the zone.
IFZ 4—LW II (MIS 2 termination)	15–12.5 ka	34–36.6 m 8/4	True xerophiles reach the highest values in the whole sequence and dominate most insect assemblages (up to 69%, av. 48%). The highest peak of steppe insect species (up to 9%). Dry tundra inhabitants (8–34%) on the average (20%) are as abundant as tundra mesophiles. <i>M. viridis</i> also reaches the highest values (up to 60%), while <i>I. arcticus</i> drops (av. 7%). “Forest-tundra” group is low (0.5–4%), but some taiga insects are found in one sample.	Cyperaceae (av. 46%), Poaceae (av. 37%), Caryophyllaceae up to 7%, av. 3.2%), Cichoriaceae (up to 5%, av. 2.9%), Asteraceae (av. 2.6%), <i>Artemisia</i> (up to 4%, av. 1.8%), Ericales (av. 2%). A peak of <i>Encalypta</i> spores at 36.3 m (up to 14%, av. 5.2%). Few <i>Salix</i> and <i>Betula</i> pollen, <i>Larix</i> pollen absent.	Grass-sedge dominated vegetation with abundant various herbs (Caryophyllaceae, Cichoriaceae, Asteraceae, <i>Artemisia</i>). Almost no shrubs (very few dwarf birch and willow). Increase in sedge pollen and appearance of Ericales towards the upper border, as well as sharp decrease in <i>Selaginella</i> spores may signal a trend to increasing humidity at the end of the interval, accompanied by soil disturbances (<i>Encalypta</i>).
IFZ 5—EH (early MIS 1)	8–7 ka	37–38 m 2/4	Mesic tundra species 60%, “aquatics” 18%, dry tundra 12%, “forest-tundra” 6% (mostly shrub-related), other groups show very low amount (less than 1–2%).	First time in the sequence arboreal pollen rises up to 60% (av. 35%). <i>Betula</i> sec. <i>Nanae</i> , <i>B.</i> sec. <i>Albae</i> , Ericales, <i>Alnus fruticosa</i> (= <i>Alnaster</i>) are dominant. Sedge and grass pollen dominate in non-arboreals. The percentage of all herb families (except Ranunculaceae) decreases. <i>Encalypta</i> spores are still high (up to 14%, av. 5.6%), <i>Selaginella</i> is very low. Unlike lower in the sequence, <i>Sphagnum</i> spores are present in all samples (av. 1%).	Radical change in vegetation—forest-tundra with tree birch, shrub tundra (birch-shrub alder), abundant Ericales, locally <i>Sphagnum</i> bogs, wet disturbed soils.

Stephanocleonus (mostly *S. eruditus*, sometimes *S. fossulatus*, rarely *S. paradoxus*) and steppe leaf beetles (such as *Galeruca interrupta circumdata*, *Chrysolina* cf. *purpurata* and *Ch. brunnicornis bermani*) indicates a high input of heat to the soil surface in summer. Some vegetation patches in the mosaic were probably too arid to support more-or-less rich herb communities; they probably had disturbed soil, discontinuous plant cover, and hosted xerophilic sedges, some ruderal plants, and open-ground insects (sedge heath, or hemicryophytic steppe). On the other hand, local depressions on the

floodplains (oxbows and high-water channels) probably held water, or at least remained wet through the summer. These small water bodies could serve as habitat for aquatic plants and aquatic and riparian beetles; these insects were relatively abundant during MW I. The water bodies were well heated in summer, which is evidenced by the presence of such thermophilic species among the water plants, as *Callitriche hermaphroditica* and *Potamogeton vaginatus* (Kienast, 2002). Interestingly, the insects of the “forest-tundra” group, including even some taiga species, are almost continuously

present, though in rather small numbers. The pollen data suggest that single trees or small groves of larch could probably have been present at local sites with higher moisture. This further emphasizes the complex, mosaic character of the landscape.

The most evident example of this complexity is provided by an autochthonous moss peat layer about 1 m thick, which is traced in several baidzherakhs (thermo-erosional mounds) in the middle part of the Zone 1 interval, at 15–16 m a.s.l. The peat was sampled in great detail for pollen (Andreev et al., 2002). This interval is marked by minor peaks of *Betula* sec. *Nanae*, *Salix*, *Saxifraga*, *Thalictrum*. On the other hand, it shows high values of *Artemisia* and the only record of Chenopodiaceae pollen through the whole section. The plant macrofossil assemblage from the peat has a notable amount of mesophilic plants, including sedges and cotton grass, common in wet tundra. At the same time, the macrofossil spectrum is highly dominated by *Dryas punctata* and includes such steppe and meadow-steppe plants as *Carex argunensis*, *Silene repens*, and various plants typical of dry tundra. It can be assumed that the peat accumulated in a local depression. Shrub birch and willow grew around it, but within a narrow mesic belt, which was surrounded by very dry biotopes. Thus, both pollen and plant assemblages are taphonomically affected by the local environment of a small tundra peat bog, and the general climatic signal is distorted. This can explain the previous controversial climatic interpretation of the paleobotany of the peat layer. In fact, the fossil record does not allow us to assume more favourable (warmer) or, alternatively, colder climate, or a general increase in humidity, suggested by different authors in Schirrmeister et al. (2002b). For taphonomic reasons, there were practically no insect fossils in the peat itself. The fossil insect assemblages from the same level are also of a complex character: they have a high percentage of both mesic and xeric tundra insects, but also include steppe species and other “southern” xerophiles. At the same time, the percentage of xerophilic insects, and especially of *Morychus viridis*, is lower than below and above the “peat interval”, which may mean some general increase of moisture in the environment as a whole. It should be noted, however, that no taiga insects were found in the “peat interval”, and only one pollen sample from it contained a few grains of larch pollen.

While retaining the described general features, the environmental signal from Zone 1 shows some variations (cf. Fig. 6). There are three peaks of xeric insects, each of 2–3 samples, at about 13, 16.5 and 19 m a.s.l. (subzones 1a, 1c, and 1e), separated by samples having a higher percentage of mesic tundra and arctic species: at 15–16 m (the “peat interval”, subzone 1b) and at 17–18 m (1d). The earliest peak is the highest, the others

are successively lower, suggesting a more general trend to lesser aridity.

Based on the insect record, only some of these subzones are reflected in the vegetation records. For instance, the “dry” peaks of subzones 1a and 1e more-or-less correspond to the peaks of xerophilic plants in macrofossil record, and the higher values of Caryophyllaceae pollen, while the “peat interval” (1b) is marked by lower values of xeric insects, plants and of the named pollen group. At the same time, the amount of *Artemisia* pollen does not exactly follow that pattern of variation.

Due to a large variation in ^{14}C ages from this zone, the chronology of the subzones can only be provisionally estimated. The xeric subzone 1a is definitely older than 40 ka and may be as old as 48 ka (or more). The next xeric period (1c) seems to be no younger than 35 ka, but its lower age limit depends on the dating of the intermediate peat layer, which is rather controversial (Andreev et al., 2002). A cautious estimate would be to assume that the peat was formed between about 43 and 39 ka, and the xeric peak of subzone 1c could have occurred about 2000 years later. The latest xeric subzone (1e) can be dated around 36–34 ka. According to our calibration of ^{14}C dates, the ages of the three xeric peaks are about 45, 39 and 35 ka, respectively.

It is possible that the recognized subzones represent real changes in the degree of aridity of the environment, and, likely, in summer temperature. However, the case of the “peat interval”, examined above in detail, shows how difficult it is to separate general climatic phenomena from the local, mostly taphonomic, ones. For that reason, we refrain from assigning regional status to the oscillations observed within Zone 1. However, the combination of the curves of insect and plant xerophiles allows us to assume that the general trend during the corresponding time period (MW I) was not so much an increase in humidity, as a decrease in summer temperature.

IFZ 2 (about 34–24 ka, Middle Weichselian II) corresponds to the later part of MIS 3. It is marked by a sharp decrease in true xerophilic insects from 20–30% to 5–7%, replaced by various tundra species. In fact, this change is mostly due to the dramatic reduction of *M. viridis* fossils. The ratio between the percentages of dry tundra and wet tundra inhabitants is variable, but the general trend through the interval is a slight decrease of the former and increase of the latter, i.e., the trend to a little more humid environment. In contrast to that, the role of aquatic and riparian insect species, also very variable, decreases. The percentage of arctic tundra insects (mainly *Isochnus arcticus*), though extremely variable, is on average much higher than in the Zone 1. In the pollen record, the lower half of the corresponding interval was virtually unsampled. The upper half of the Zone 2 interval shows rather homogeneous spectra, essentially similar to those of Zone 1. *Artemisia* becomes

less abundant, while Cichoriaceae and Asteraceae show higher values. Caryophyllaceae retain their importance. The most remarkable feature of the pollen record of Zone 2 is a prominent increase in *Selaginella rupestris* spores (up to 12% in some samples). Two samples of plant macrofossils are quite similar in the dominance of species of dry and relatively warm tundra habitats. True (southern) xerophiles have low percentages, but are present in both samples. Herbs preferring dry habitats, such as *Minuartia rubella*, *Papaver sect. Scapiflora*, various species of *Potentilla*, and many others, are found together with xerophilic (tundra-steppe) sedges, such as *Carex argunensis*, *C. duriuscula*, *C. nardina*. The upper sample, dated about 25 ka, shows much higher diversity in all ecological groups of plants than the lower one (28.1 ka); the latter does not include any aquatic or riparian plants at all. That can be explained by the very different size of the two samples—more than 4000 plant macrofossils in the upper and only 70 in the lower, as the first sample was a specially processed plant macrofossil sample, while the second — a subsample of the general sample of much smaller volume (cf. Section 2.4). Thus, we do not think that the plant assemblage of the lower sample can be interpreted as indicating a polar desert environment (cf. Kienast, 2002).

At first glance, the paleoecological evidence from Zone 2 is a little contradictory. The insect data indicate a sharp reduction in true xerophiles (although a few steppe species survived) and decrease of dry tundra inhabitants. Plant macrofossils, on the contrary, show extremely high percentage of tundra xerophiles and even some thermophilic xerophiles. It seems that the key features of Zone 2 are the increase of *S. rupestris* spores and the growth in the percentage of arctic insects. Both imply the presence of relatively cold biotopes, while the abundance of club moss indicates that those biotopes were dry. We suppose that while aridity remained the main signal from all the records in Zone 2, there was some general decrease in summer temperature. The best-heated sites could still support steppe-like insect and plant communities, but the proportion of these sites in the landscape was decreasing. Accordingly, the areas occupied by cold steppe communities were expanding. Local depressions were not as well heated as during the Zone 1 time, and could host mesic tundra communities. As demonstrated below, in general the environment and climate of Zone 2 were transitional between those of Zones 1 and 3.

IFZ 3 (from 24 to about 15 ka) comprises most of the Late Weichselian except its latest part and corresponds to LW1, or most of MIS 2. The trends outlined for Zone 2 reach their peaks here. All insect samples are marked by the lowest values of true xerophiles (less than 5%), very low percentage of steppe species (totally absent in the interval 28.0–31.2 m), and the dominance of arctic tundra insects (up to 67%). The mesic tundra inhabi-

tants compete for dominance with the arctic species, and are always more abundant than tundra xerophiles, which show the lowest values in the whole sequence; no taiga species were encountered. The pollen spectra retain high diversity of various grasses and herbs, but also show the highest contents of *S. rupestris* spores. Plant macrofossil assemblages are marked by very abundant willow remains, which is in agreement with the dominance of the willow weevil *Isochnus arcticus* and with a rise in *Salix* pollen. For the rest, the plant macrofossil spectra remain basically similar to those of Zone 2: dry tundra plants dominate, and thermophilic xerophiles are present (Kienast, 2002).

Thus, we have the same problem between insect and plant record here as in Zone 2, but it is even more pronounced. The only possible solution seems the same: a further decrease in summer heat influx, with persistent aridity, expelled most thermophilic insects (“southern” xerophiles), while affecting much less the plants of dry and relatively warm habitats. Insects seem to be more sensitive to the amount of summer heat than many thermoxerophilic plants, sometimes even their host plants. For instance, some steppe weevils and leaf beetles live on *Artemisia*, but they do not reach the northern limits of distribution of this plant. According to the insect record, the trend to cooler summers can be traced through Zones 1–3, reaching its peak between 19 and 22 ka, which corresponds well to the global minimum of temperature during the LGM (MIS 2).

IFZ 4 is dated from around 15 ka to about 12.5 ka; hence, it corresponds to the second part of the Late Weichselian (LW II), or the late MIS 2. In the insect record, this zone demonstrates the highest values of true xerophiles in general and steppe species in particular. Dry tundra insects are also more abundant, than mesic tundra inhabitants. Finally, the “forest-tundra” group also rises. The character of the insect spectra of Zone 4 is in good agreement with both the pollen record (disappearance of *Selaginella* spores) and with the plant macrofossil assemblages. In particular, no mesophilic sedges were found here, only xerophilic ones, and the percentage of *C. duriuscula*, for instance, is higher than anywhere else in the section.

This short but remarkable period (LW II) requires a much more detailed chronology than is available at the moment. The section interval of 32.6–33.3 m a.s.l., dated from $17,350 \pm 130$ to $17,160 \pm 90$ BP, yielded insect assemblages similar to the previous zone, LW I. There is one more undated insect sample of similar kind, a little higher in the section. The first rise of true xerophiles among the insects is documented in the sample from about 34.1 m a.s.l. and directly dated to $14,730 \pm 100$ BP (cf. Figs. 1C and 3). That means that the beginning of LW II took place shortly before 15 ka. The peak of xerophiles is dated $13,920 \pm 100$ BP; insect

samples with a high proportion of true xerophiles were found up to the contact with the early Holocene sediment (up to ca 37 m.a.s.l.). The latest Pleistocene date in this area of the section is $12,790 \pm 60$ BP (36,3 m.a.s.l.); hence, LW II terminated not earlier than 12.5 ka BP. The dates from the lower part of the Holocene sediment cover are around 8 ka, and the supposed gap in the record is about 4000 years. The existence of this gap in the main Bykovsky section does not allow us to reconstruct the very important transitional period between the Pleistocene and Holocene.

IFZ 5 (Early Holocene, EH) corresponds to the thin cover of Holocene deposits overlying the IC on the top of the Mamontovyy Khayata main section and dated from 8.2 to 7.5 ka. All records—insect, pollen, and plant—show that the environment was dramatically different not only from Zone 4, but also from the whole section of the IC. The diversity of herbs is sharply reduced, birch (shrub and tree), shrub alder and Ericales dominate the pollen spectra, and wet tundra species are the leading group both in insect and plant macrofossils. A sharp increase in humidity is evident, but the insect spectra also suggest some increase in summer temperature (a few taiga insects, such as ants). Interestingly, for the first time since around 50 ka, the increase of heat coincided with an increase in moisture, and, combined with the essential change of vegetation, the result was insect assemblages having no analogues in the Pleistocene, but still different from modern ones. For instance, a practically new ecological group appeared in the early Holocene faunas: insects living in leaf litter (especially, the rove beetles, Staphylinidae, other than *Tachinus*, very common both in the Pleistocene and Holocene). Various inhabitants of leaf litter live now in southern tundra and taiga; they were much less common in the Pleistocene.

To summarize, the five environmental stages recognized from the insect assemblages, are mostly in agreement with other types of proxy record. The remaining inconsistencies are not very serious, and can be explained by various secondary phenomena, such as differing ecological responses of various groups of organisms, changes in taphonomy, or greatly varying sample sizes and the imprecise correlation of the samples for various fossils. The recognized stages form a regular trend through the last ca 50 ka, which is itself further evidence of their real significance.

The most general inference from the sequence is that all of it is marked by very arid environments. That is the main signal from almost all the studied biological groups, which suggests that the climate remained very strongly continental from ca 50 to 12.5 ka. The main changes in the composition of these groups can be interpreted as the result of variation in the summer heat input.

3.5. Dated fossil mammal record in the Laptev Sea area

About 3000 fossil mammal bones were collected in the south-eastern part of the Laptev Sea coast and New Siberian Islands by Russian–German expeditions (1998–2002) under the “Laptev Sea System 2000” project. The registration of all identifiable fossils found within the cliffs and on the shore allowed a statistically reliable reconstruction of the structure of the Pleistocene mammal fauna. The taxonomic composition of such bulk collections can be strongly biased by the local geological situation, by taphonomic conditions, and other random factors, so they may give a distorted picture of the relative abundance of species in the past. However, repeated estimates allow some generalized inferences. *Mammuthus primigenius* (woolly mammoth) bones dominate all our collections from the Laptev Sea coast (25–35%), followed by *Equus caballus*, horse (20–25%), *Bison priscus*, bison (15–20%) and *Rangifer tarandus*, reindeer (14–18%). Other large mammals, such as musk ox (*Ovibos pallantis*) and woolly rhino (*Coelodonta antiquitatis*), usually compose only 1–2%, although the former is more common in the Bol. Lyakhovsky collection (about 7%). The occurrence of fossils of saiga antelope (*Saiga* sp.) on that island is very important, as this animal is a reliable indicator of dry and firm soil surface in summer and very thin snow cover in winter. Large carnivores, such as the big Pleistocene panther (*Panthera spelaea*), and wolf (*Canis lupus*), are very rare as usual. Fossils of hare (*Lepus tanaiticus*) are very common in the IC (usually found in situ or close position).

Even total registration of all encountered bones does not, unfortunately, allow us to make any quantitative estimates of past animal numbers; earlier attempts of that kind (Budyko, 1967) involved too many unconstrained assumptions. However, the general regularities of taphonomy (Efremov, 1950) suggest that organic remains, successfully preserved as fossils, represent only a minor fraction of formerly existing animals. Even in a permafrost environment, very favourable for organic conservation, the bodies of dead animals and their parts, prior to their burial, pass through numerous “taphonomic grids”, or destructive filters: animal consumption, physical weathering, chemical alteration, abrasion by running water, etc. Thus, a single bone found represents not only the hundreds of missing bones of the same animal, but perhaps thousands of unpreserved bones of many other individuals. That means that even if only single bones are common in the sediment, as in the case of the IC, they must evidence relatively abundant individuals.³ The second argument for a relative

³Special cases of secondary accumulation, such as “mammoth cemeteries”, tar pits, or traps, such as the Mammoth Site of Hot Springs in South Dakota, are not considered here.

abundance of animals in the past is a biological one: mammoth, horse, bison, reindeer are all herd species, they never browse alone for a long distance. For example, a few bones of a 1.5–2 year old baby mammoth, found in the MKh section (33.5 m a.s.l.) and dated to 14.3 ka, were not accompanied by adult mammoth bones, but must nevertheless represent at least 5–6 individuals of its family unit, and very likely at least several other units (cf. Redmann, 1982, for social organization in the elephants). For both of these reasons, the large amounts of bones of these species, scattered through each sequence of the IC deposits, definitely indicate relatively high numbers of these grazers in the past, and allow us to assume the existence of the appropriate pastures and tolerable climate.

Our extensive programme of ^{14}C bone collagen conventional dating (ca 140 dates), and a few AMS dates, together with published dates on mammal bones from the Laptev Sea area, provide unique evidence on the history of large mammals on the Laptev shelf land. The list of all the dates (ca 440 dates, including 60 infinite ones), is given in Appendix Table A1 in the online version of this paper; it also represents the first official publication of bone dating results from the Russian–German collaboration, performed at the Geological Institute of the Russian Academy of Sciences, Moscow (conventional) and Leibniz Labor (AMS). Altogether, in the surroundings of the Laptev Sea area, from the Taimyr Peninsula to the coast of the Dmitry Laptev Strait and the islands of Severnaya Zemlya and New Siberian archipelagos, we were able to analyse 268 dates on mammoth (236 of them finite). The other species received fewer dates (about 70 for horse and 40 for bison) and do not provide statistically reliable series.

The distribution of finite dates on these three species in time and by the region is presented in Fig. 7.

Only the mammoth date collection can be considered as representative. But even this series shows some strange patterns in the distribution of dates over the regions. For instance, it is hard to explain the lack of mammoth dates between 41 and 36 ka in the eastern sector of the Laptev Sea coast (the Lower Lena–Dm. Laptev Strait), as there is a sufficient amount of such dates on the adjacent territory both to the west and to the north, on the New Siberian Islands (Fig. 7). Other “gaps”, such as in the Khatanga–Olenyok record, can be more easily explained by a relatively low total number of dated samples from that area. For these reasons, to reveal the most general pattern from the largest number of dates, we analysed the whole collection of mammoth dates from the Laptev Sea surroundings together (Fig. 8C).

The low number of finite dates on mammoth bones older than 42–40 ka (average 2.8 dates per 1000 years) can be explained for technical reasons, as this period has many infinite dates, which are not included here. After that time, the number of dated mammoth bones is more or less steadily high (av. 7.6 per 1000 years) from about 40 until about 25 ka. Then it starts to decrease progressively through about 10,000 years, with a minimum at 17–16 ka (only one date in that millennium). After 15 ka, the number of mammoth dates jumps sharply up and stays at high levels (av. 7.4 per 1000 years) until 12,500 and 10,000 y BP in the Taimyr area. Thus, the analysis of the whole collection of mammoth dates from the Laptev Sea area suggests only one remarkable feature: the notably low number of dates between 20 and 15 ka. It should be noted that this

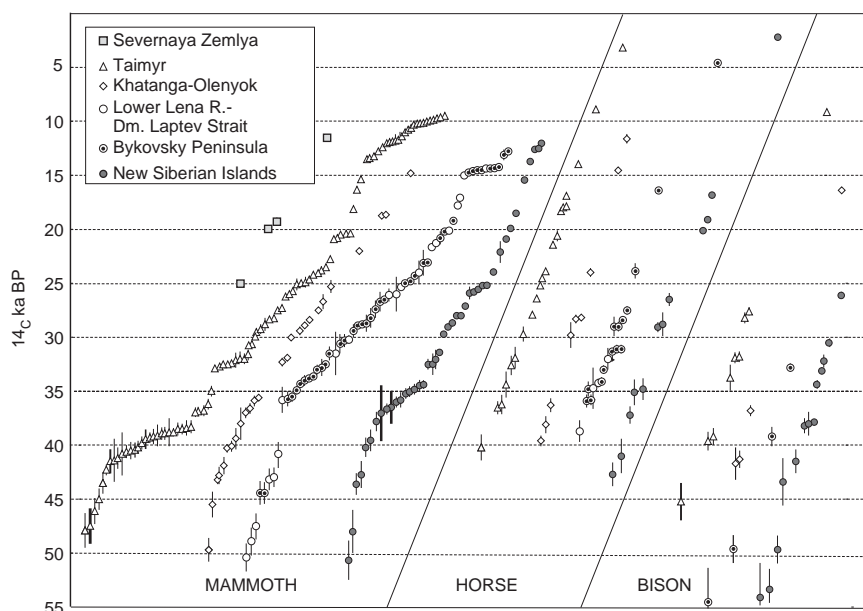


Fig. 7. Distribution of ^{14}C dates on mammoth, horse and bison bones by the regions around the Laptev Sea (cf. Fig 1A).

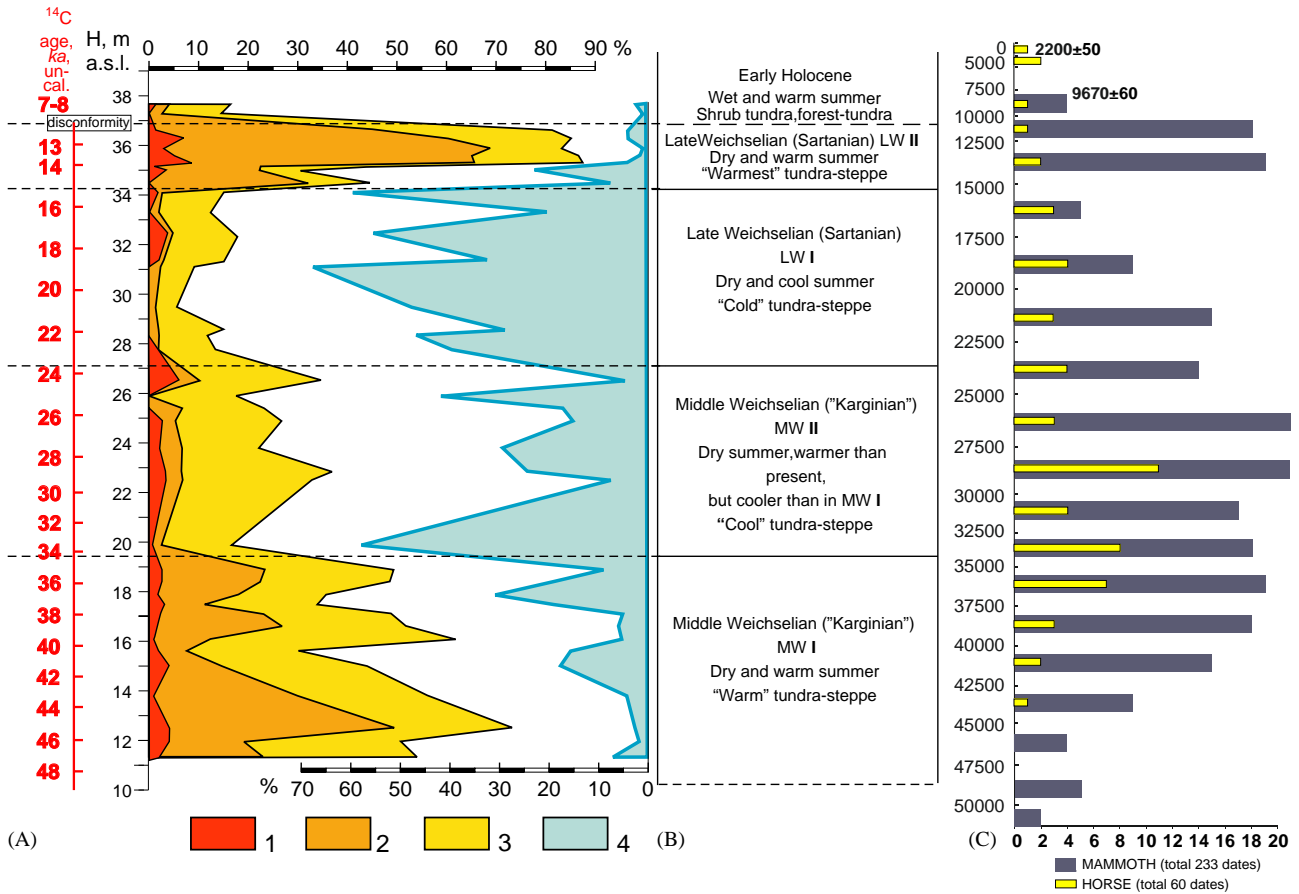


Fig. 8. Inferred summer climate changes and dated record of mammals in the Laptev Sea area. Uncalibrated ¹⁴C ages in the left column are calculated from two separate regression equations after about 40 AMS dates. (A) Fossil insect record in the MKh section, Bykovsky Peninsula. Percentage of selected ecological groups of insects: *True, or "southern", xerophiles* (XE on Fig. 6): 1—steppe species; 2—other xerophilous insects (except tundra ones); *Insects, currently common in tundra*: 3—dry tundra inhabitants, DT (prefer warmer sites); 4—Arctic tundra insects, AT (plotted from the right axis). (B) Climatic and environmental interpretation of the insect assemblages from the MKh section. (C) Radiocarbon dates of mammal bones from the Laptev Sea area (number of dates in 2,500-year intervals). The latest available dates for mammoth and horse are indicated at the top.

“low” is preceded by a gradual decrease of the number of dates after 25 ka, and is followed by a very sharp recovery after ca 15 ka.

Can we believe that the revealed pattern in the distribution of mammoth dates broadly reflects former abundance of animals? Chronological variation in the numbers of radiocarbon dates is subject to many factors, such as collecting biases, occurrence of sediments of a certain age in a particular region, changes in taphonomic conditions, etc. Attempting to estimate the dynamics of abundance of a species in the past from the ¹⁴C databank, only large samples from a vast territory can be used, but even those data should be treated with caution. In our case, we believe that the observed pattern is reliable for the following reasons:

1. Looking at the history of accumulation of mammoth ¹⁴C dates, we can see that the first reviews (Sher and Sulerzhitzky, 1991; Lavrov and Sulerzhitzky, 1992;

Sulerzhitsky, 1995) operated with about 120–130 mammoth dates for the whole Siberian Arctic. The published histograms showed 5–6 intervals, each from 1000 to 3000 years long, where the number of dates was less than two per 1000 years, including four intervals of 1000 years without any dates. The increase in the number of dates up to 170 (Sulerzhitsky and Romanenko, 1997), then to 200 (the Taimyr dates by MacPhee et al., 2002), and currently to almost 350 (268 dates for the Laptev Sea area alone) resulted in the gradual obliteration of most of those “lows” and “gaps”, except the one between about 15 and 20 ka, and one at the limit of dating.

2. Detailed study of continuous successions covering the whole range of radiocarbon dating, such as Bykovsky, shows no major changes in the taphonomic conditions that might be responsible for different degree of bone preservation at 40–25, 25–15, and 15–12 ka. The sedimentary environment remained

basically very similar through these periods, the growth of syngenetic ice wedges was continuous, and a slightly lower rate of sedimentation in the lower part of the sequence (Section 2.2) does not explain the local pattern of date distribution.

3. In four large areas around the Laptev Sea, with different number of dates, the pattern of date distribution is similar in its most general features. Analysing the percentage of dates for each 5 ka interval for these regions, we find only two intervals where it is much lower than the average in all four regions (12.5 dates per 5 ka): 50–45 and 20–15 ka (Fig. 7). No other intervals show such coincidence across all the regions.
4. A huge area of northeastern Asia to the east of the Laptev Sea region (the Indigirka and Kolyma basins, Chukotka, including Wrangel Island, and Kamchatka) has so far yielded few dates on mammoth bones (about 40, excluding special series, such as Berelyokh Mammoth Cemetery and the Holocene Wrangel Island population). However, the general pattern of distribution of those dates is the same: the lowest number of dates is more than 45 ka and between 20 and 15 ka; the highest, between 15 and 10 ka. No dates between 21 and 16 ka are known in this series.
5. Very similar general regularity can be seen in the large series of mammoth dates from Alaska and Yukon (Guthrie, 2003). The average number of dates per 1000 years between 24 and 16 ka is 2.5 times lower

than between 15 and 12 ka; in our series for the same time span the ratio is about the same (2.0).

It is hard to imagine that a similar pattern, observed over a huge territory with varying geology and collecting history, could be explained by a random play of various local factors, such as local geology or taphonomy. We therefore believe that it is related to a general forcing, such as broad-scale environmental changes that affected northeastern Siberia and northwestern North America at about the same time. Thus, we conclude that the revealed pattern of distribution of mammoth dates in time broadly reflects the general dynamics of mammoth abundance in the Laptev Sea area and probably in the whole of northeastern Siberia and Alaska. Evidently, these animals inhabited the Laptev Sea shelf land from the limits of ^{14}C dating to about 12.5 ka (and even later in some places). At the beginning of LGM, their numbers started to decrease, and reached the lowest values by the end of the LGM (17–16 ka), but very quickly recovered after 15 ka. It should be emphasized that even during the LGM mammoths (and horses) still inhabited the whole area of the Laptev shelf land, including the present northernmost islands, which is evidenced by a few fossils from Kotelnii and Fadeevsky islands, Lena Delta, Taimyr, and Severnaya Zemlya, dated from 22 to 16 ka (Fig. 9). That means that the LGM environment was probably less favourable for grazers, but not intolerable. The late Sartanian (15–12 ka) was the last interval of relatively high abundance of mammoths on the shelf land.

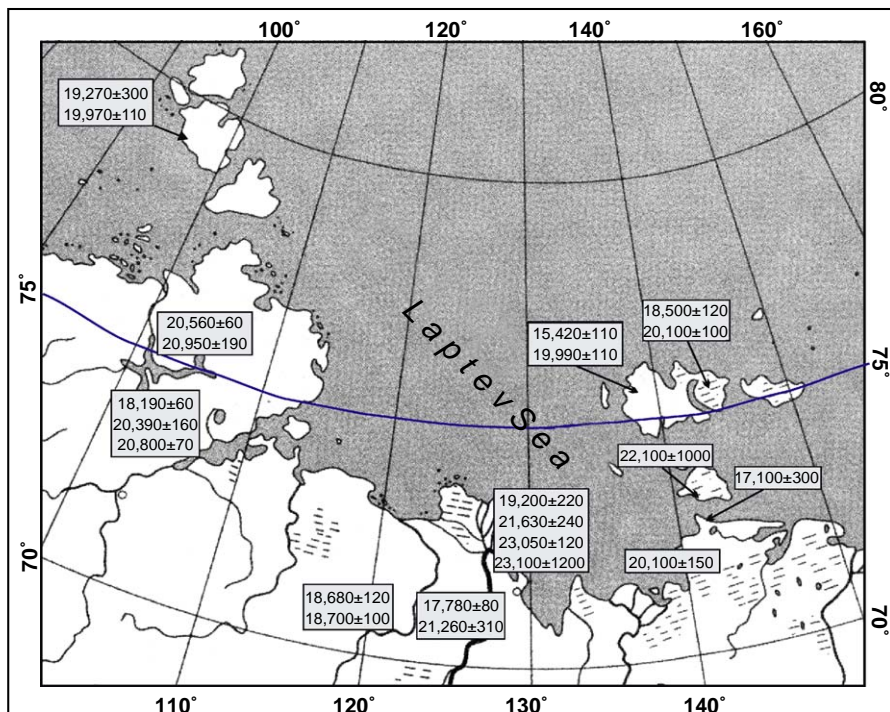


Fig. 9. Occurrence of dated mammoth fossils of the Last Glacial Maximum in the Laptev Sea area.

It seems unlikely that particular peaks and lows or even “gaps” in the distribution of mammoth dates in separate regions, e.g., on Bykovsky Peninsula or Bolshoy Lyakhovskiy Island (Kuznetsova et al., 2001b, 2003), other than those common for the whole Laptev Sea area, reflect actual fluctuations in animal numbers. Rather, they are caused by local taphonomic and other random factors, or are just related to insufficient number of dates. But at least one “regional” feature should be considered significant. The lack of dates younger than 12 ka in all regions east of the Taimyr Peninsula and their abundance on the peninsula itself (16 dates between 12,000 and 9600 yr BP) clearly indicates the beginning of an ecological crisis in most regions. It may also suggest total elimination of mammoth populations on the Laptev Sea coast east of Taimyr and on the New Siberian Islands around 12 ka. This is hard to prove, as that time was marked by a significant change of sedimentary environment and taphonomic conditions. Probably around that time the continuous accumulation of the IC stopped and a sharp intensification of thermokarst changed the environment dramatically.

4. Discussion

This most complete and continuous record of the Late Quaternary terrestrial environment in the Siberian Arctic, examined in a broad multidisciplinary project, provides new insights on the biotic history and climate of this area (Fig. 8).

All kinds of proxy evidence indicate that the regional climate retained the features of high continentality between 50 and 12 ka, i.e., during the Middle and Late Weichselian (“Karginskian” and Sartanian). Compared to the present day, the climate remained very dry, if not arid: this aridity is the main signal from the insect and plant records through all of that time. The high latitude position of the area and the ubiquitous permafrost, conserving huge amounts of moisture, put a special imprint on the generally dry environment, so it is probably more correct to call it “cryoarid”. Dry grassland habitats were interspersed with mesic ones more similar to modern tundra. The proportions between more and less dry sites varied in the record, but no significant changes in humidity during that period are revealed in the Bykovsky section: most of the documented mesic sites were likely only of local importance.

With the background of persistent high continentality in this part of the Arctic, the main driver of environmental changes during the Middle and Late Weichselian was the variation in summer temperature. According to the insect record, this was relatively high 46–42 ka, and gradually decreased (probably with minor variations)

through the “Karginskian” and most of the Sartanian. It reached the lowest values at the end of the LGM (17–16 ka) and sharply rose to probably the highest values between 15 and 12 ka. Winter temperature during the interval from ca 50 to 12 ka was constantly much lower than present, as evidenced by continuous growth of thick ice wedges and the stable isotope composition of ice (Meyer et al., 2002). Even during pre-LGM time (Middle Weichselian), the reconstructed winter temperature was at least 7 °C lower than today (Meyer et al., in prep.). That means that January air temperature was below –40 °C.

4.1. The Middle Weichselian and the “Karginsky Interglacial” problem

The results obtained in the Middle Weichselian part of the Bykovsky section are rather unexpected, as they notably differ from the existing concept of the “Karginsky Interglacial” or “Interstade” paleoenvironment. That widely accepted concept implies a rather pronounced variation in climate and vegetation during the period, corresponding to MIS 3, with several stages of increasing temperature and moisture and the northern advance of arboreal vegetation, alternating with colder and drier stages. Nothing of that kind was found in the Bykovsky continuous sequence. To explain this contradiction, it seems relevant to explore the “Karginsky Interglacial” problem at greater length in order to understand how the existing concept emerged and how well it is corroborated by recent evidence from sequences other than Bykovsky. Since the original concept was born in an area as far west from the Lena as the Lower Yenisey, and to the east the regional type-section for the Middle Weichselian (Molotkovskiy Horizon) is in the Kolyma Lowland, we need to examine the problem in a broad spatial content. A recent detailed and comprehensive review of pollen and dating evidence for that period (Anderson and Lozhkin, 2001) clearly demonstrates the problems which still exist in the interpretation of the environment and climate.

The most popular paradigm follows the climatic subdivision of the Karginskian with three warmer and two colder intervals suggested by N. Kind (1974) for the Lower Yenisey region:

- 50–45 ka BP—early warm interval (unnamed),
- 45–43 ka BP—early cool interval (unnamed),
- 43–33 ka BP—Malokhetskii warm interval (climatic optimum),
- 33–30 ka BP—Konoshchelskiy cool interval,
- 30–22 ka BP—Lipovsko-Novosyolovskiy warm interval.

This scheme was born during the dawn of ¹⁴C dating, when belief in the dating method in the scientific community was very deep, so it was soon extrapolated

to almost the whole of Siberia. Moreover, in the succeeding 30 years, most researchers tried to tie up numerous local sections to that scheme. Visible plant remains, such as peat layers or wood, were sampled for conventional radiocarbon analysis, and most commonly the dates fell into the “Karginsky” interval. For instance, of 166 samples collected by various students in the Yana-Kolyma Lowland in order to date the IC (Yedomo Suite), about a half obtained infinite or minimum dates ($>26\text{--}55\text{ ka}$); of the remaining finite dates, 93% fell between 22 and 50 ka (Sher and Plakht, 1988). The concentrations of plant remains in the sediment usually had an increased amount of shrub and sometimes tree pollen. If the site was presently located in the taiga zone, the pollen evidence (or the presence of wood) was interpreted as vegetation similar to modern; if the site was now located in tundra, it was interpreted as the northern advance of forest-tundra or taiga. The sampled unit was assigned to an episode of climate similar to or warmer than present; depending on the radiocarbon date, it was referred to one of Kind’s warm intervals. Correspondingly, the undated underlying and overlying units, where grass/herb pollen dominated, were referred to the preceding and subsequent cold intervals. That was common practice, and the amount of data, which seemed to support the concept of 2–3 cycles of climate changes during the “Karginsky”, increased accordingly.

For example, on the NW coast of Kotelnii Island (76°N), Lozhkin (1977) found peat lenses in the lower part of the IC section, overlying a sandy unit in a coastal cliff. Both the sands and the IC silts contained mostly Miocene, Pliocene and even Cretaceous pollen, while the amount of pre-Quaternary pollen in the peat was much lower. The suggested “native” component of the peat pollen record contained 38% of AP, namely (in descending order) *Betula* sect. *Nanae*, *Pinus pumila*, *Alnaster*, *Salix* and *Picea*; it remained unclear which part of that pollen was re-deposited or air-transported from a distance. Nevertheless, along with one tentatively identified species of sedge among the macrofossils, the site was interpreted as documenting a “warmer” climate interval. The ^{14}C dates of $29,750 \pm 1100$ and $28,220 \pm 1000$ y BP allowed the interval to be referred to the second half of the “Karginskian”. Later Kaplina and Lozhkin (1984) recognized the “Kuranakh-Sala warming” (30–24 ka) as a local equivalent of the last “Karginskian” warming of Kind’s scheme. The name was based on a poorly described section at the Kuranakh-Sala Creek, 150 km SE of Tiksi, where Timashev (1972) obtained a single date of $25,900 \pm 150$ y BP on a piece of wood from ice-rich silts beneath the IC; the section contained remains of tree birch, larch and alder, but tundra-type pollen spectra. The Kotelnii Island record mentioned above, along with a few other scattered sites with similar radiocarbon

dates, was referred to the same “warm interval” with northern advance of the forest.

In the same area of Kotelnii Island, Alekseev (1997) studied a sandy unit in a marine (?) terrace, containing up to 11% of *Alnaster* pollen and up to 24% of *Betula* sect. *Nanae*. A single radiocarbon date of $36,400 \pm 500$ y BP on plant detritus allowed him to refer the unit to the Malokhetskii (optimal) interval of the “Karginskian”. On the southern coast of Bolshoy Lyakhovskiy Island (73.3°N) Igarashi (2003) interpreted the pollen spectra dated to the same interval (40–34 ka, “middle stage of Karginsky Interstadial”) as “open taiga” with *Larix*, *Picea*, and *Pinus*. At the same latitude as the Bykovskiy section (71.8°N), but a few hundred km to the east, in an IC section in the lower course of Volchya R., a pollen zone yielding 30–38% AP and a radiocarbon date of $37,220 \pm 1000$ y BP, was also referred to the Malokhetskii optimum (Ovander et al., 1987). This zone occupies about 5 m in the section and shows significant amounts of shrub pollen, such as *Alnaster*, *Betula* sect. *Nanae* and *P. pumila* (up to 20–30%, 15–20% and 10–20%, respectively). All these sites are currently situated in arctic or typical tundra, so the data are interpreted as evidence of significant northern advances of shrubs (and sometimes trees) and of a “warmer” climate of the “Karginsky” middle (optimum) and late stages. There are many other sites with similar records further south, usually with a few, or even single radiocarbon dates of similar age.

Anderson and Lozhkin (2001) note two main problems in the reconstruction of the Karginsky environment: first, the lack of continuous sections covering more than one of the suggested Karginsky “warm intervals”, and second, the unreliable chronologies. Within the huge Yana-Kolyma Lowland, they were able to select only one section supposedly covering the whole Karginskian and corresponding to Kind’s scheme—Molotkovskiy Kamen’ on the Malyy Anyuy River (Lower Kolyma). Four peat horizons with relatively high AP percentage alternated here with silts including ice-wedge casts and/or ice wedges and dominated by grass/herb pollen (Sher, 1971; Kaplina and Giterman, 1983). The lowermost (T-1) has yielded only infinite dates ($>40\text{--}50\text{ ka}$), the middle (T-2), two finite dates ($34,400 \pm 1000$ and $42,800 \pm 400$ BP). The upper peat unit (T-3) was confidently dated to $28,100\text{--}24,550$ y BP with four bulk samples from two peat facies; the dates were processed in two different labs (GIN and MAG), with very similar results, and their ages corresponded to the depth of sampling. The uppermost peat (T-4) was dated around 8000 y BP and referred to the Holocene Optimum (Kaplina and Giterman, 1983).

The site is currently in northern larch woodland (lat. 68.35°N); single tree birch can be found in the hills near its northern limit. Abundance of *Betula* sect. *Albae*

pollen in both T-2 and T-3, plus significant amounts of *Alnaster* and *Pinus pumila* in T-3 (the latter confirmed by macrofossils, as well as larch and tree birch) left no doubt about the relatively “warm” climate during the formation of both peat units. Thus, the site was approved by the USSR Stratigraphic Committee as the type section of the regional Molotkovsky Horizon, corresponding to the Middle Weichselian interstade. By that time, some older dates for the T-2 peat unit had appeared, such as $48,030 \pm 1190$, and $>47,090$ BP, which cast doubt on the 34.4 ka date, so the age of the “early warm phase” remained uncertain, and the whole Molotkovsky Horizon was put in the age frame of 50–48 to 24.5 ka (Shilo, 1987). Thus, the best-studied equivalent of the “Karginsky” in the Kolyma Lowland acquired a two-peak, instead of three-peak pattern.

Meanwhile, the reliability of conventional radiocarbon dates on bulk plant organic samples invoked more and more doubts. Sher and Plakht (1988) showed that 35% of 91 finite dates in the range 30–45 ka from the Yana-Kolyma Lowland had to be rejected in the course of later dating involving the re-sampling of the same exposures. The age of many well-known exposures in the Lowland based on those dates had to be revised towards an earlier date, including the famous Duvanny Yar in the Lower Kolyma (compare its dating in Sher et al., 1979 and Sher, 1991), the type section of the Yedomia Suite and of the “Duvanny Yar Interval”, suggested by D.M. Hopkins to label the Sartanian (Late Wisconsin) epoch in Beringia.

In 1992, W. Eisner, then at Ohio State University, and A. Sher designed a project to investigate the Pleistocene-Holocene transition in the Kolyma Lowland and selected the Molotkovsky Kamen' section which had the best dated unit referred to the Late “Karginsky” warm interval (28–24.5 ka, correlated to the Lipovsko-Novosyolovskiy stage of Kind's scheme). They intended to use that peat unit (T-3) as the basic stratum for their research, and during a pilot investigation re-sampled both facies of it—autochthonous moss peat and partly allochthonous plant detritus peat. The dates obtained were $40,600 \pm 1000$ (GIN-7305) and $41,000 \pm 1000$ (GIN-7306), confirming a single date of $43,660 \pm 1250$ BP (LU-1035) for the same peat, published in 1982 but ignored in view of a very convincing series of younger dates for T-3 (Sher and Plakht, 1988).

Evidently, all the “Late Karginsky” dates (28–24.5 ka) had to be rejected. In fact, the T-3 peat with its excellent evidence of larch-birch taiga turned out to be older than 40 ka, and possibly even beyond the ^{14}C time range. Sulerzhitsky (1998) described that case in his review of examples of contamination of older plant material with younger carbon. We include here this remarkable story in detail because, first, its stratigraphic consequences have not so far been published and realized, and second, because it is quite relevant to the discussion of our new

data on the “Karginsky” environment. Strictly speaking, the Molotkovsky Horizon in the sense of the Stratigraphic Committee does not exist any more, as its age is uncertain. Moreover, this case strengthens the serious doubts on numerous conventional radiocarbon dates (single or short series) on plant remains (older than 30 ka (or even 25 ka) which were used in 1970s–80s to prove the “Karginsky” (or MIS 3) age of northern advances of taiga in Northeastern Siberia, or even the existence of modern-type forest close to its present limits. That means that the “Karginsky paradigm” of Kind should be re-considered in Arctic East Siberia. Likewise, the whole concept of the Karginsky Interstadial has been revised on its native territory, in the Lower Yenisey area, where the recent geological work has shown that the most important “finite Karginsky” dates came in fact from the Eemian, i.e., are the result of contamination by younger carbon (Astakhov, 2001).

With the revision of the type section of the Molotkovsky Horizon, not very much convincing evidence remains in the northern lowlands of “warm intervals” of the Middle Weichselian and northern advances of the forest limit at that time. The evidence, obtained in the Bykovsky section, seems more powerful than in many other scattered and fragmentary outcrops. The advantage of Bykovsky is its long and continuous record, extremely well provided with the AMS ^{14}C dating. These dates do not show any inversions down to 28 ka, and even if some of the earlier dates can be questioned, their whole sequence does not lead us to suspect any long gaps in sedimentation since about 50 ka. Neither pollen, nor plant, nor insect records through MIS 3 allow us to infer the presence of northern taiga forest within a reasonable distance of the Bykovsky Peninsula. Currently, the site is ca 70 km from the forest limit to the W and SW (the Lena valley) and to the south the forest is at a distance of about 150 km. The pollen rain in the Lena Delta at such distances today contains about 30% AP (Savelieva et al., 2000). A very low amount of AP in the Bykovsky spectra (except in the Holocene) clearly indicates that the forest, if it existed at all, was much farther south than today. For this reason, no particular “warm” interval in the sense of the “Karginsky” paradigm can be recognized in the Bykovsky sequence during the Middle Weichselian. We cannot agree with Andreev et al. (2002), who refer the interval dated from 42.5 to 33.5 ka in the Bykovsky section to the “Malokhetskii optimum” of the “Karginsky Interstadial”. This interval has very little AP (the mean AP content is less than 2%, maximum 4.9% (*Salix* 0–2.3%, *Betula* sect. *Nanae* 0–1.9%, *Alnaster* 0–0.6%). In our opinion, the occurrence of a few pollen grains (1–5) of these types in some samples can hardly be interpreted as a signal of “warmer” climate and the position of a forest line close

to the position of the modern one; more likely, it can be explained by deposition of exotic AP.

The basic problem is the methodology of the interpretation of former climate and vegetation. We believe, for instance, that terms such as “warmer climate interval” should be avoided (cf. Alfimov et al., 2003). The Bykovsky evidence shows that the MIS 3 climate was slightly warmer in summer, but much colder in winter. Thus, being “colder” in terms of mean annual temperature, that climate could be more favourable for some relatively thermophilic plants and insects, adapted to more continental climate and capable of withstanding very cold winters. Since a higher summer temperature was accompanied by very low humidity, this situation did not support the existence of northern taiga communities of modern type, but did not exclude the dispersal of some tree species, such as larch or even tree birch, to the north. The Bykovsky record allows us to suppose the presence of scattered small larch groves among the generally grass/herb-dominated communities, presumably at the sites with higher moisture. Thus, the interpretation of larch as evidence of taiga forest advance, even if confirmed by fossil wood, can be misleading.

According to the Bykovsky record, grass/herb vegetation dominated the region during the whole documented time of the Middle Weichselian, or MIS 3. The earlier half of the Middle Weichselian (ca 46–34 ka) was marked by relatively high abundance of insects living in warm and dry habitats, including steppe species, and a low share of high Arctic species. A rather high input of heat to the soil is confirmed by plant macrofossil and soil rhizopod evidence (Schirmermeister et al., 2002b). In the mosaic of habitats, more mesic ones were at the same time less heated, and hosted plant and insect assemblages similar to those of modern tundra. In general, the environment of that time can be characterized as a relatively “warm” variant of tundra-steppe. We do not know to what degree second-order variation in the insect assemblages during that time reflect the regional climatic situation, but the general trend seems evident (Fig. 8A), and is interpreted as a decrease in summer temperature. The later half of the Middle Weichselian (ca 34–24 ka) was marked by a notably lower level of “southern” xerophiles, while the role of dry tundra inhabitants remained important, and by a concomitant increase in relative abundance of arctic tundra species (Fig. 8). That indicates cooler summers than before, although the temperature remained high enough for local survival of steppe species. That is in agreement with the plant macrofossil evidence, suggesting dry and relatively warm summer conditions until at least 25 ka BP, although vegetation cover was probably getting sparser (Schirmermeister et al., 2002b). Consequently, we can label this period as a relatively “cool” tundra-steppe.

Thus, the most continuous record of Middle Weichselian times in Arctic Siberia does not support the idea of major fluctuations in vegetation and climate (Anderson and Lozhkin, 2001). Instead, it portrays a more or less uni-directional trend from warmer to cooler summers, and may suggest a division of the Middle Weichselian into two substages (Fig. 8B). The Bykovsky record also sheds some light on the unsolved problem of the supposed “Karginskian marine transgression”. Some researchers believe that the sea level in the Laptev shelf area in the Middle Weichselian was much higher than in the Early and Late Weichselian, and actually was close to the modern level, or even slightly higher than today (Alekseev, 1997; Fedorov and Bolshiyarov, 2002). While some evidence in support of the “Karginskian transgression” does exist in the North Siberian Lowland (SW of Taimyr) (Andreeva et al., 1982), for the Laptev Sea area such evidence is very vague. The persistence of a highly continental environment during most of the Middle Weichselian at the present shoreline location of Bykovsky suggests that the sea was far away at that time. Thus, our data better fit with the minimum estimates of the global sea-level rise during MIS 3, such as up to –75 m (Shackleton, 1987), than with those assuming its position was close to the modern level (cf. Anderson and Lozhkin, 2001).

4.2. The late Weichselian: LGM and the late glacial event (LGE)

The Middle Weichselian trend in the beetle faunal composition reached its culmination in the Late Weichselian (Sartanian). Most of this stage, from about 24–23 to 15 ka, corresponding to the Last Glacial Maximum, was characterized by the lowest contents of xerophilic insects, virtual disappearance of steppe species, and dominance of Arctic tundra inhabitants (Fig. 8A). The general character of vegetation did not change much, especially if compared with the later half of the Middle Weichselian, when *Selaginella*-covered patches became widespread. Willow, presumably in the prostrate arctic form, was an important member of the grass/herb-dominated communities. The floristic composition of these communities retained high diversity, but plant cover probably became more discontinuous (Andreev et al., 2002). The environment remained very dry, which is evidenced by various proxy data (Schirmermeister et al., 2002b). It can be assumed that the decrease in xerophilic insects was caused not by increasing humidity, but by the lower summer warmth, not sufficient to support their life cycles. However, there is some proxy evidence that the summer temperature could still have been higher than today. Some relatively thermophilic plant species survived (Kienast, 2002). The same is inferred from a preliminary attempt to estimate the LGM summer temperature at Bykovsky by the

MCR method on fossil insects (Sher et al., 2002a; cf. also Alfimov et al., 2003). This is an important conclusion, since most of the reconstructions and models predicted a summer temperature decrease for the LGM (Avenarius et al., 1978; Velichko, 1984; Ganopolski et al., 1998; Edwards et al., 2000). The second major point is that during the LGM, mammoths were still able to live not only in the Bykovsky area (72 °N), but much farther north, up to at least 75 °N on Taimyr and the New Siberian Islands, or even to 79 °N on Severnaya Zemlya, and presumably all over the shelf land. Horses, most probably, had a similar distribution. This fact, by itself, suggests that the animals could find sufficient grazing resources in high latitudes during the LGM. The assumption that they represented “rare individuals or populations wandering far from optimum habitats” occasionally (Colinvaux, 1996) is not realistic, as such grazers mostly do not travel far alone and cannot wander for hundreds of miles without food, or towards increasingly poorer pastures, and modern arctic tundra or polar desert could hardly have provided sufficient resource for a herd of mammoths or horses. This general consideration is supported by the proxy evidence from the Bykovsky sequence: despite the abundance of arctic plants and insects, the environment was still different from modern arctic tundra, and we classify it also as tundra-steppe, although it was probably the “coldest” type, with minimum heat supply.

One of the most remarkable and quite new features shown by the Bykovsky record, is the sharp peak of xeric and steppe elements at the end of the Late Weichselian (ca 15–12.5 ka). Very quickly, probably in just a few hundred years, the steppe components of the insect communities not only recovered from near-zero values, but reached their highest proportion during the whole studied history. In the pollen sequence, this period still belongs to the long and continuous Weichselian “herb zone”, but is marked by a sharp decrease of *Selaginella* spores. The re-appearance of steppe insects clearly indicates a rise in summer temperature. Although the chronology of this short Late Glacial Event (LGE) is far from detailed, it is clear that it pre-dated the interval of climate warming recorded further west as the Bølling-Allerød interstadial (ca 13–11 ¹⁴C ka BP). The end-Weichselian increase in summer temperature could have triggered initial thermokarst processes on the Shelf Land (Tumskoy, 2002). But it was not until 12.5 ka BP, or even slightly later, when the climate became more humid, that a general degradation of permafrost started, accompanied by a dramatic change in the environment.

The correlation in the pattern of mammoth dates with the record of xerophilic insects in the Late Weichselian is impressive. The supposed lowest numbers of mammoths during the LGM emphasizes their sharp peak after 15 ka. As shown above, the Late Glacial rise of

mammoth numbers seems to be a general phenomenon for the whole Beringian Arctic, but Bykovsky is so far the only site where this event is synchronous with another independent line of evidence (insects), and both can be explained by the same environmental change. Interestingly, a similar pattern can be observed in the distribution of ¹⁴C dates on bison bones in the Beringian Arctic (the sample in the Laptev Sea area by itself is too small for any conclusions). For the North Slope of Alaska (Matheus et al., 2003), the lowest frequency of bison dates is between 20 and 15 ka, then it shows a peak around 13–11 ka. The same pattern is shown for Central Alaska and Yukon (Stephenson et al., 2001). Finally, a new large series of dates on bison bones from Beringia (including Siberia) indicates their very low numbers between 19 and 14 ka, and a peak at 13–12 ka (Shapiro et al., 2004). The horse dates in the Laptev Sea area indicate generally low numbers after 27 ka, and do not show even a slight rise during the LGE. At that time a very small rise in horse date numbers may occur in northern (Matheus et al., 2003) and central (Guthrie, 2003) Alaska, but it was much less pronounced than for mammoth in the latter region, and for bison in both regions.

The chronological distribution of dates on saiga antelope over Beringia is very remarkable (Guthrie et al., 2001). Although their total number is limited (18), about a half of all dates are concentrated between 15 and 12 ka (with the peak at 14–12), and no dates are known at all between 25.5 and 15.5 ka.

To conclude, mammoth, horse, and bison survived the LGM in the Arctic; it was probably the worst time for saiga, but we have insufficient evidence to say more. At least three of these grazers (mammoth, bison and saiga) benefitted in the LGE from the recovery of steppe elements, which we interpret as due to an increase in summer temperature with persistent aridity. It seems that the bison rise was delayed for a couple of thousand years compared to the mammoth one; that could be explained by some difference in forage requirements, but it is premature to speculate. The fact that horses did not rise during the LGE remains enigmatic, unless we accept Guthrie's (2003) idea that the most cold/arid versions of tundra-steppe environment were the most optimal for horses, and they had the highest numbers in the LGM. So far, Siberia does not provide enough evidence to accept or reject that hypothesis.

4.3. Mammoth in tundra-steppe: the “productivity paradox”

It is evident from the foregoing that the LGM environment could still support large mammalian grazers, but since the proposed number of mammoths was then the lowest, we can assume the least favourable environmental conditions prevailed during that period.

That leads us to consider how our new evidence can contribute to the long-debated “productivity paradox” (cf. Introduction). In fact, this problem arose as a critical reaction (mostly by North-American palynologists, e.g., by Ritchie and Cwynar, 1982; Colinvaux, 1996) to the generalized idea of tundra-steppe (or Arctic-steppe) as a homogeneous highly productive grassland that supported large populations of grazers. By the 1980s, several major developments of the tundra-steppe concept had essentially narrowed the basis of this critique. These were (1) the extensive studies of relict steppe communities in north-eastern Siberia, thermophytic in the extremely continental areas of the upper Kolyma and Indigirka basins and cryophytic on Chukotka and Wrangel Island (Yurtsev, 1974, 1976; Berman and Mordkovitch, 1979; Berman, 1986); (2) the recognition of the complex mosaic character of vegetation in the Pleistocene, with alternation of steppic, tundra, meadow, marshy and other communities, very different in their productivity for grazers, each type representing a certain combination of heat and moisture supply depending on local topography (Giterman, 1976, 1985; Yurtsev, 1981); (3) the studies of fossil insect assemblages and the modern distribution and ecology of the most significant Pleistocene species of insects (Kiselyov, 1981; Berman, 1990). The “productivity debate” actually turned into a conflict of disciplines (e.g., palynology vs paleozoology), each with the restrictions and traditional approaches of its own.

The elaborated model of the tundra-steppe mosaic was developed by Yurtsev (1981) based on the detailed study of relict steppe-like plant communities, existing today under various levels of heat supply—from the upstream regions of the Indigirka (ca 63 °N) to Chukotka and Wrangel Island (ca 70 °N). This model allowed him to reconstruct the past mosaic as a succession of plant communities classified along a gradient of moisture and heat supply. Yurtsev believed that aridity was one of the main drivers of the tundra-steppe ecosystem, so that communities at the “arid end” of the sequence had many similarities with zonal dry steppe. As we discussed above, in the Arctic the driest (best drained) habitats are also the best heated in summer. They had the deepest summer thaw and the best soil aeration, similar to the arid or steppe type. The sites at the other end of the succession were less well-drained and less heated, more appropriate for typical tundra communities, but the variety of habitats between these two extremes included different types of grass-dominated communities, such as relatively dry steppe-like meadows, more mesic meadows, now common in taiga and southern tundra, and dry or wet arctic meadows. Some of these varieties are supposed to be of rather high forage resource value. Yurtsev’s model of a tundra-steppe mosaic is now corroborated by fossil evidence, including the Bykovsky succession, and it is

interesting to see how the details of this evidence support the predictions of that model.

According to Yurtsev, the grass/herb cover in tundra-steppe sites with minimum moisture supply was relatively low and sparse, as in normal steppe. This was in part related to the necessity to develop an extensive and dense root system—a typical plant strategy in arid ecosystems. In modern relict steppe communities in the Siberian Arctic the spaces between grass/herb plants and groups are filled by club moss, *Selaginella sibirica*, and xerophilic lichens; however, even beneath these spaces, the soil, as in steppe, is rather deeply penetrated by a dense system of thin grass roots. In the main Bykovsky Pleistocene sequence, it is hard to find a spot where silt is not penetrated by grass roots. In certain layers (including some within the LGM zone) the roots are especially abundant, and form long furcating systems, really permeating the silt with a kind of a dense network (Sher et al., 2002b). At the same time, the pollen spectra of LW I (LGM) contain up to 20% *Selaginella* spores (av. 7%), which is much higher than in modern arctic communities. The average percentage of these spores in recent surface pollen samples from various northeast Siberian tundra areas between the Lena River and Chukotka (Edwards et al., 2000) is 0.7%; local concentrations of *Selaginella* spores (4–11%) are recorded in less than 5% of all samples. According to Lozhkin (2002), *S. rupestris* spores comprise no more than 1% of modern spectra in arctic Beringia.

The impressive abundance of Cyperaceae (sedge) pollen in some LGM spectra is often interpreted as evidence of mesophytic vegetation. Yurtsev (1981) has shown that in northern relict steppe herbaceous communities are often dominated by such xerophilic and mesoxerophilic sedges as *Carex duriuscula* and *Kobresia myosuroides*; he suggested that these sedges were important elements in the diet of Pleistocene herbivores. The first species (with an admixture of *Artemisia*, grasses and herbs) dominates dry steppe pastures on gentle slopes and valley bottoms in Transbaikalia (zonal steppe) and upper Indigirka (relict steppe); in both regions these pastures are heavily used by domestic sheep and horses, respectively. The second sedge species forms so-called “*Kobresia*-heath” in Altai mountain steppe areas, but is also common on dry and relatively well-heated cryophytic steppe patches and dry tundra meadows in the Arctic today. Various species of *Kobresia* grow in alpine steppe and are important forage plants for ungulates; the fruits of *Kobresia* dominated the gut contents of the 39,000 year old Selerikan horse (upper Indigirka basin) (Egorova, 1977). The LGM interval of the Bykovsky section contains about 15–25% Cyperaceae pollen. *C. duriuscula* and *K. myosuroides* were the only sedge species found in the plant macrofossils of that interval; of about a dozen

mesophilic sedge species identified in the section (including the early Holocene layers), none has been encountered in the LGM zone (Kienast, 2002).

A low pollen concentration is often reported as an argument for very low overall productivity of the tundra-steppe ecosystem, comparable to polar desert. It is true that in the High Arctic today the local pollen signal is very weak, and strongly overprinted by far-transported and re-deposited pollen. For example, Lozhkin (2002) was not able to get a representative sample of modern pollen on Kotelnii Island. That is, however, definitely not the case in the Bykovsky record, including LGM time. No data on pollen influx are available for that record, but the average amount of re-deposited pollen and spores is low (10%), which is an indirect indication of relatively good representation of autochthonous pollen. Only in a few samples is re-deposited pollen around 30%. Andreev et al. (2002) use the percentage of re-deposited pollen as an indicator of relative plant cover density; this will be discussed further below. Yurtsev (1981) has also noted that the abundance of insect-pollinated dicotyledonous plants in the Arctic, such as Caryophyllaceae and Compositae, could in part explain low pollen influx in the sediment, and we found that the Bykovsky sequence offers very remarkable evidence in that respect. In the grass-dominated LGM pollen spectra the relative amount of various herbs, especially of Caryophyllaceae and Compositae (Asteraceae + Cichoriaceae), was much higher than in modern tundra. Among the 84 surface pollen samples from various northeast Siberian tundra areas between the Lena River and Chukotka (Edwards et al., 2000) the percentage of Caryophyllaceae and Compositae pollen is broadly variable (0–18% and 0–20%, respectively), which reflects the local vegetation and seemingly rather short-distance dispersion of these pollen types. But the most frequent values for both families are below 2%, and the means for the whole set are 2.2% and 2.3%. Meanwhile, presumably more balanced LGM spectra (Fig. 5) never show such low values, and on the average have 7% and 13.5% of these pollen types, respectively. This may indicate higher diversity of these families in the LGM. For Caryophyllaceae this is to some extent corroborated by the occurrence of at least 10 species of this family in the LGM macrofossil samples (Kienast, 2002). At least seven of them prefer dry habitats, and some are not known in arctic tundra.

Thus, the Bykovsky record is in good agreement with Yurtsev's model of a tundra-steppe mosaic in the LGM. The theoretical interpretation of the LGM ecosystem suggested by Yurtsev (1981) is thus applicable to the shelf land environment reconstructed from our fossil record. The most remarkable feature of that ecosystem was the combination of arid and polar life strategies. The adaptation of plants to a very short growing season, the ability to survive long periods of unfavourable

conditions, and the fast recovery of green biomass as soon as conditions improved, were the typical features of the arid strategy, secured by a huge quantity of subsurface biomass of grasses and herbs. Those features were complemented by adaptations to relatively low levels of heat supply. Similar strategies are known in some extremely continental areas of the High Arctic (e.g., in the Canadian Arctic Archipelago), but these areas have very low summer temperature (below 8 °C) and their vegetation is actually a variant of arctic tundra or polar desert. The tundra-steppe ecosystem, recorded at the Bykovsky LGM interval, was very different from the polar desert, because it existed under higher summer temperature. That resulted in a higher taxonomic diversity of plants and insects. Some of the plant and insect species, found as fossils in that interval, have different ecological requirements, especially for degree of moisture, and could hardly have existed in the same habitat. This is a good argument for assuming that mosaic of habitats did exist even on shelf plains with low and relatively smooth topography.

Almost 30 years ago, one of the main results of the great discussion of the tundra-steppe “productivity paradox” was the recognition that a mosaic of grazing habitats was more important in supporting the herbivores than the particular productivity of a single habitat type (Schweger et al., 1982). Our new evidence confirms that the LGM environment was rather diverse, both biotopically, and taxonomically. Being controlled (both spatially and phenologically) by minor local variations in moisture supply under generally arid conditions, this diversity was always able to provide forage for mammals. In this climatic type, with fast establishment of frost and snow cover in the fall, some part of these forage resources was preserved as green or “freeze-dried” into the cold season, and due to very low snow cover, was available through the winter time. This can be observed today in extremely continental areas of Siberia, such as Verkhoyansk region, where Yakutian domestic horses are kept free on winter pastures, easily getting good-quality forage from under shallow snow (Gabyshev, 1972).

The Bykovsky evidence gives full support to Yurtsev's statement (1981) that the modern vegetation of the Arctic coast or most of the shelf islands cannot be used as a model for the tundra-steppe of the shelf land. In other words, neither the modern lowland forest-tundra, nor any plain tundra subzone or polar desert can be considered as a complete analogue of the past ecosystem, which existed in high latitudes but under extremely continental climate. Even in the LGM this resulted in a higher temperature in the growing season than is observed today anywhere in the Siberian Arctic. At present, there is no analogue of such a vast land in the north of Asia with a similar degree of continentality, and the past biota of that land must be considered as a

non-analogue one, which is supported by our new evidence. And of course, the most notable feature of that biota was the presence of various herbivores. As in other grazing ecosystems of the arid type, they made their own contribution to the functioning of the tundra-steppe ecosystem, by cutting and trampling grasses and fertilizing the soil, thus helping to perpetuate the ecosystem (Owen-Smith, 1987; Zimov et al., 1995).

The last, but not the least insight on the “productivity paradox” provided by the Bykovsky succession, is that in earlier discussions of the problem it was always restricted to LGM times. Even Yurtsev (1981) did not seriously consider the tundra-steppe problems for the “Karginiyskiy Interstadial” time. Within the framework of the earlier paradigm of “warmer and wetter” MIS 3 in the Siberian Arctic, he believed that there was almost no continuity between the vegetation of the stadials and interstadials, since during the latter forest, shrub and bog vegetation was much more widespread. Now we know, from the Bykovsky evidence, that this was not true. Continuity was very important, as it was basically the same type of grass/herb-dominated environment with pronounced aridity (Sher et al., 2003). Within this new paradigm, the LGM environment was just an impoverished variant of the MIS 3 (or LGE) tundra-steppe. In this respect, if we have managed to show that the “productivity paradox” was actually not a serious problem for the LGM, even less significant was it for the “richer” tundra-steppe of the other periods. In the following last section of this chapter, we shall summarize the dynamics of the shelf land environment from the MIS 3 to the LGM and to the LGE and suggest our interpretation of the grazing community response to those trends.

4.4. Weichselian environmental trends and the population response of grazers

As follows from previous sections, it can be assumed that landscape productivity for grazers even during the LGM was sufficient for the survival of all or most of them, but we have no direct means of quantifying it. Instead, we can try to estimate the relative grazing capacity of the shelf land in the course of the environmental changes. Here we summarize the most significant features, indicating the environmental trends during the time interval from about 50 to 12.5 ka, deduced from the fossil record:

1. The percentage of relatively thermophilic (southern) xerophiles among the insects generally decreased through the Middle Weichselian (from ca 48 to 24 ka), remained at low levels until 15 ka (no true steppe species between 22 and 19 ka) and then sharply increased to maximum values (until 12.5 ka). The opposite trend is observed in arctic tundra

species. As a whole, these trends are interpreted as a decrease in summer temperature during the MIS 3.

2. The taxonomic diversity of herbs did not follow the xerophilic insects’ decrease, and in Caryophyllaceae and Compositae even increased from the Middle Weichselian (MW I–II) to the Early Late Weichselian (LW I, or LGM).
3. The amount of *Selaginella rupestris* spores became significant in the Late Middle Weichselian (around 30 ka), increased during the LGM, then sharply dropped in the latest Weichselian (LGE).
4. Neither the pollen, insect nor plant macrofossil records indicate a significant increase in humidity accompanying the suggested summer temperature decrease; some plant evidence may rather indicate an increase in aridity.

Within the same time period, the proposed numbers of four mammalian grazers, deduced from their ^{14}C dates, underwent important variation. Mammoth and bison (the latter in the whole of Beringia) were rather abundant both in MW I (assumed for the early part of the stage) and MW II. At the end of MW II they started to decrease their numbers (first bison, then mammoth), and both were at their lowest point in LW I (LGM), between 20–18 and 15 ka. Both species showed a sharp increase in numbers at 15 ka (LGE). Horse (many fewer dates available) showed a similar rise in MW I–II (the peak being at 30–28 ka), becoming fewer during LW I, but not so sharply as mammoth and bison; so far, there is no evidence for a rise of horse numbers during the LGE. Finally, throughout Beringia saiga was present in MW I, common in MW II, absent in LW I (LGM), and showed a sharp peak in LW II (LGE).

Thus, at least three species of grazers were affected by the LGM environment: mammoth, bison, and saiga. The decrease in their numbers correlates with the decrease in relatively thermophilic insects, but this is much less evident in the changes of the plant record. Since the vegetation retained its main features (grass/herb-dominated cover with the prevalence of arid habitats and corresponding plant communities), we assume that the reason for such a response from grazers was in the change of the carrying capacity of the ecosystem. Our hypothesis is that the total area of better-heated dry habitats was decreasing in the course of the lowering of summer temperature. It was gradually replaced by less heated, but still dry patches, more suitable for club-moss than for most grasses and herbs. Thus, although no plant or insect species were lost, and the quality of forage did not decrease, the general quantity of habitats available for the grazers was slowly going down. Evidently, the overall resource availability, although decreasing, still remained sufficient to support normal population sizes. It was not before the end of MW II, and long after the start of xerophilic insects’

decrease, that mammoth and probably bison populations started to respond to the change by reducing their numbers. The further summer cooling in LW I brought the insect xerophiles to a minimum and eliminated the true steppe species from the fossil record, but for the grazers (except probably saiga) that change was not critical, as for them it was more quantitative than qualitative, and they were still able to cope with the lower amount of grazing resources available, which can explain the time lag between the lowest points of insects and mammoths.

Proxy evidence for the decrease of grazing habitats from MW I through MW II to LW I can be seen in the increasing percentage of re-deposited pollen and spores. Andreev et al. (2002) use this percentage as an indicator of the relative plant cover density. That is not a very strong argument, as the amount of reworked pollen depends not only on the availability of open ground, but also on depositional factors such as sedimentation rate, and we assume that the latter was about 30% higher in the upper part of the Bykovsky sequence, including the LGM. However, in this case that argument probably should not be ignored, as the average percentage of re-deposited pollen and spore grains in MW II was almost twice as high as in MW I, and doubled once more in LW I (LGM).

We further assume that the relatively low numbers of mammoth, bison and horse during the LGM were still in balance with the available forage resources, which thus were not critical for their survival/extinction. Such an assumption helps to explain why at least two of these grazers restored much higher numbers so fast during the LGE rise of summer temperature, with its corresponding recovery of better grazing habitats. It also helps to understand how these grazers could survive previous cold stages in the Arctic (e.g., MIS 4), which probably were not more severe than MIS 2, but lasted longer.

All kinds of proxy evidence from the uppermost part of the Bykovsky section—both biological (insects, pollen, plant macrofossils, soil microfauna) and sedimentological—depict the Early Holocene environment as completely different from the Pleistocene one. It was much more similar to modern southern shrub tundra and forest-tundra than any of the episodes documented by the main (IC) Bykovsky succession. The chronology of this environmental revolution remains unclear. According to the record of the adjacent allass section, tall shrubs and trees grew in the area as early as 9.5 ka BP. It is supposed that the active denudation of the IC and the development of deep thermokarst kettles with lakes started around 12–11 ka (Kuznetsova et al., 1999). The regional turnover of relatively dry grassland into boggy tundra with a huge number of lakes sharply reduced the area of tundra-steppe habitats favourable for grazers, and resulted first in fragmentation of their

ranges, and ultimately, in the disappearance of their regional populations.

So far, we know that different groups of organisms responded in various ways to the Pleistocene/Holocene environmental re-structuring. As we can see from the database of radiocarbon dates on mammal bones (Appendix Table A1 in the online version of this paper), even among large mammals that process was not simple and simultaneous for different species. Unfortunately, the Bykovsky section itself does not provide new evidence for the transition period, and for that reason this extremely interesting subject is beyond the scope of this paper.

5. Conclusion

The unique record of the Middle and Late Weichselian environment in the Bykovsky section clearly demonstrates that it did not undergo major changes during that period. The vegetation remained within the same basic type of mosaic arctic grassland with dominance of xeric habitats: the tundra-steppe type. The existence of the tundra-steppe biome was supported by constantly very continental climate, with summers warmer or at least not colder, and winters much colder than in the present coastal environment.

Variations within the framework of that broad climate and environment were caused mainly by fluctuations in summer temperature, which were generally related to the global trend, but overprinted by the effect of continentality. No major changes in humidity were observed. The summer temperature trends that occurred during the Middle and Late Weichselian were presumably of a rather small amplitude, but they still affected the composition of plant and animal communities. So far, environmental changes during that time can best be observed in the composition of insect assemblages; they can be interpreted as variants, or subtypes, of the tundra-steppe environment (Kuzmina, 2003).

Nevertheless, all those subtypes represented slightly different kinds of pasture ecosystems, relatively favourable for the mammalian grazers, and the latter inhabited the shelf lowlands through all the studied period. At the same time, the subtypes of tundra-steppe are believed to have different levels of general plant productivity, and their changes affected population numbers of mammals. The most remarkable events in the history of large mammal populations, revealed in the Laptev Sea area, were their lowered numbers during the LGM, especially toward its end, and the short but impressive peak of flourishing in the latest Weichselian, just before the collapse of the tundra-steppe biome.

The inferred fluctuations in summer temperature did not change the generally extremely continental climatic

type that existed in the region throughout the period, corresponding to MIS 3 and MIS 2. The climate remained very favourable for the aggradation of permafrost. No events of regional permafrost degradation were observed in the continuous Bykovsky succession until the very end (termination) of the Pleistocene.

The destruction of the tundra-steppe biome at the Pleistocene/Holocene boundary in the Laptev Sea area was very rapid, but is expressed in complicated fashion in the history of certain animal and plant species, which responded individually even to that major change in the environment. The collapse of this biome needs further investigation, with much higher chronological resolution, than is currently available in the region.

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Appendix A. Supplementary material

For a Table of radiocarbon age on collagen from fossil mammal bones in the Laptev Sea area see the online version of this paper, doi:10.1016/j.quascirev.2004.09.007.

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