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The late Pleistocene environment of the Eastern West Beringia based on the principal section at the Main River, Chukotka

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ABSTRACT

Chukotka is a key region for understanding both Quaternary environmental history and transcontinental migrations of flora and fauna during the Pleistocene as it lies at the far eastern edge of Asia bordering the Bering Sea. The now submerged land bridge is the least understood region of Beringia yet the most critical to understanding migrations between the Old and New Worlds. The insect fauna of the Main River Ledovy Obryv (Ice Bluff) section, which is late Pleistocene in age (MIS 3-2), is markedly different from coeval faunas of areas further to the west, as it is characterized by very few thermophilous steppe elements. From the fauna we reconstruct a steppe-tundra environment and relatively cold conditions; the reconstructed environment was moister than that of typical steppe-tundra described from further west. The data from this locality, if typical of the Chukotka Peninsula as a whole, may indicate that a barrier associated with the environments of the land bridge restricted trans-Beringian migrations, particularly the more thermophilous and xeric-adapted elements of the Beringian biota, supporting the hypothesis of a cool but moist land-bridge filter inferred from evidence from several other studies.

1. Introduction

For decades, ever since the Quaternary geological history of Beringia became broadly understood, there has been strong interest in the interconnected topics of species migration between the Old and New Worlds and the Pleistocene climate and environment of this largely unglaciated high-latitude region (see papers in Hopkins (1967); Hopkins et al., 1982, and *Quaternary Science Reviews* Volume 20 (2001), for example). The region is well studied, given its remoteness, as it contains a rich biological archive in the form of fossil floras and faunas, preserved in a range of depositional environments that were, in many cases, uninterrupted by glaciation. However, the land bridge itself remains poorly studied as most is presently submarine. Chukotka is the north-easternmost region of Asia (Fig. 1), and as such its history is important to our understanding of the land bridge.

The dominance of cold- and dry-adapted vegetation and a diverse mammalian fauna in Beringia in glacial stages is well documented (see references above; Colinvaux, 1964; Guthrie, 1968, 1982; Sher et al., 2005). It has been described by both Russian and American authors as a steppe-tundra ecosystem capable of supporting a high faunal biomass and it was compositionally and structurally quite unlike contemporary biomes, although a range of modern local Beringian communities have been invoked as possible small-scale analogues (Giterman et al., 1982; Yurtsev, 1982; Edwards and Armbruster, 1989; Zazula et al., 2006a,b). Closer inspection, however, reveals differences in both fossil and modern species across Beringia, particularly across the land bridge region. For example, the modern Chukotka biota most closely resembles that of neighbouring Siberia, but it also includes endemic species and species originating in North America, such as the common American weevil *Lepidophorus lineaticollis*, which has its only Asian foothold in Chukotka (Berman et al., 2002). Boreal plant taxa also differ between the two portions of Beringia (Swanson, 2003). Such

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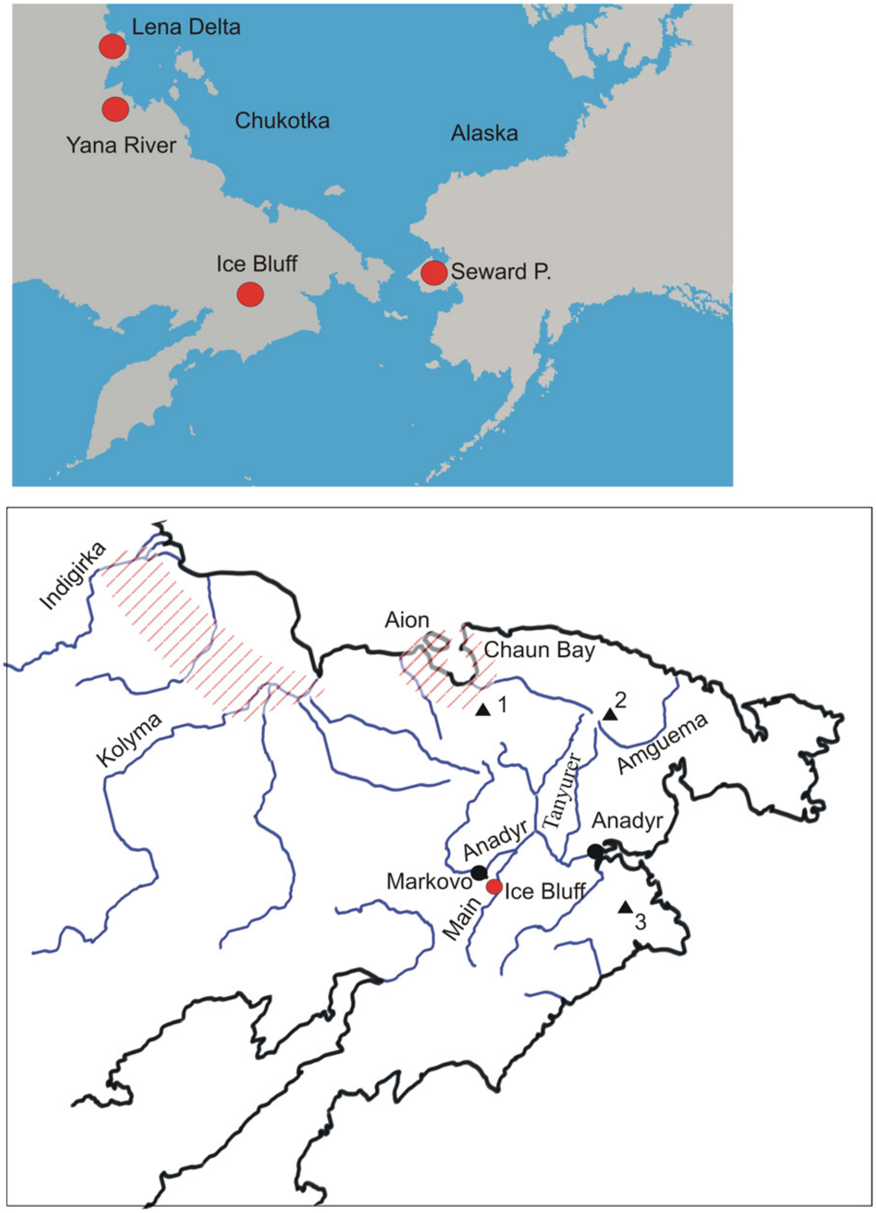

Fig. 1. Map of the studied area. Red circles – discussed fossil insect localities, red shading – areas of fossil insect research in Western Beringia, triangles – pollen record: 1 – "E" Lake (El'gygytgyn), 2 – Amguema exposure, 3 – Patricia and Gytgykai lakes.

patterns suggest that filters to species interchange were in place during the late Quaternary (Murray et al., 1983; Swanson, 2003; Elias and Crocker, 2008). In particular, several authors have argued that the land-bridge climate and/or land surface was cooler and/or moister than that of most of the region (Elias, 2007a; Elias et al., 1996, 1997; Guthrie, 2001; Elias and Crocker, 2008).

Chukotka is thus a key area for Beringian Quaternary studies, but it remains an under-studied part of Siberia. This is partly because if its remoteness, as it is situated far from Russia's main scientific centres. The geographic focus of previous studies has also been strongly determined by the presence of the skeletal remains of large mammals, which are more abundant in regions where ancient terrestrial deposits are widely distributed, such as the coastal lowlands of Yakutia. Furthermore, only the western Chukotkan areas of the Chaun lowlands and Aion Island and the Main River Ice Bluff in south-central Chukotka (Fig. 1) have widespread and significant Quaternary outcrops of loess-like sediment that provide the opportunity for multi-proxy reconstructions of past environments. In this paper we present the results of a palaeoentomological study of the Main River deposits. A further paper will detail reconstructions based on ancient DNA retrieved from the frozen sediments.

Fossil insects are an important tool for palaeoenvironmental reconstructions. The method itself, its advantages and disadvantages, and applications for different regions are described in a range of books and articles, for example, Elias (1994), Encyclopedia articles (Elias, 2007b), special issues of journals: Quaternary Proceedings (Volume 5 1997) and Quaternary Science Reviews (Volume 25, 2006).

The main advantages of fossil beetle studies are high sensitivity to environmental changes, the presence of mostly local fauna in the fossil records, and a low possibility of reworking. However, fossil beetle analysis is not a routine method in Quaternary studies; the approach presents challenges from adequate field sampling to identification of the fossil remains (beetles are the largest taxonomic group); thus it is demanding of both time and expertise. Andrei Sher understood the importance of insects as palaeoenvironmental indicators, and he provided considerable support to two Russian Quaternary entomologists: S. Kiselev and S. Kuzmina.

This Chukotkan study forms part of a larger research question being addressed by Andrei Sher's group: understanding the palaeoenvironments of different parts of Beringia during the Last Glacial Maximum (LGM) with a focus on fossil insects. This work was begun in 1998 following the first expedition to the Lena Delta region under a German–Russian project "The Laptev Sea System 2000". A multidisciplinary investigation at Mamontovy Khayata, Bykovsky peninsula, east Lena Delta, showed that sedimentation was mostly continuous from 48 to 12°ka. The fossil insect assemblages appeared to clearly differentiate environments through time (Schirrmeister et al., 2002). The section was studied in more detail from 1999 to 2001 (Hubberten et al., 2004; Sher et al., 2005) and taxa were assigned to bioclimatic groups; this method underscored the dominance of cold-resistant insects during the LGM and identified a short but well developed phase dominated by steppe insects at the end of the Weichselian. The site was unique in Beringia in having such a continuous and detailed insect record. In other areas there were only fragmentary fossil insect records, none of which covered the complete LGM. Thus there was an incentive to find other localities that could yield comparable results. In the summer of 2003 Andrei Sher led fieldwork to the Seward Peninsula, Alaska, where Kuzmina et al. (2008) studied LGM insects from a buried paleosol (Höfle et al., 2000); and in 2004 he led the Chukotka expedition. The participants of the summer 2004 fieldwork included both Andrei Sher and Anatoly Kotov, a geologist with a wide knowledge of Chukotka in general and the Main River site in particular. Sher developed the idea for this present article, which was to be the next one he submitted. Sadly, Kotov died during the winter of 2004, and thus this paper lacks the input of the two most experienced in Geology team members.

2. Regional setting

The Quaternary deposits of the Chukotka Peninsula have multiple origins: marine and glacial-marine deposits in eastern coastal regions, glacial deposits in mountain and foothill regions, and in other areas, lacustrine, alluvial, or eolian deposits. The loess-like sediment of the Yedoma Suite is thought to have polygenetic origin (Svitoch, 1980; Kotov, 2002). The Main River area contains the best exposed and continuous Quaternary section among all interior Chukotka sites.

The Ice Bluff (Ledovy Obryv) site is situated on the Main River[2], not far upstream from Vaiegi village, a left tributary of Anadyr River in the central-southern part of Chukotka (64 06′ N, 171 11′ E; Fig. 1). The modern vegetation is larch forest; stone pine, birch and aspen also occur. Modern beetles (collected by S. Kuzmina and E. Yan) are riparian and forest species, and no tundra or steppe species were observed. This area is warm enough permit restricted agriculture; local people from the closest villages plant vegetables in open ground, which is unusual for Chukotka. The climate data from the nearest weather station at Markovo indicate a mean July temperature of 13.6 °C, mean January temperature −25.2 °C, mean annual temperature −8.9 °C, and annual precipitation 432 mm (Melnikova, 1965). Because the site is situated far from the sea, the climate is more continental than that of coastal regions of Chukotka. While mean annual temperature in this area is close to average for Chukotka, mean July temperature is the warmest of all Chukotka weather stations.

The first mention of alluvial Quaternary sediments and the first geological map of the Main River valley dates to the beginning of 20th century (Polevoy, 1915). The section's age and formation have been much disputed. Vtyurin (1964) and Tomirdiaro (1972) focused on lithology and on the permafrost features of the exposure. Tomirdiaro's interpretation of mid- and late-Pleistocene ice-rich sediments of aeolian origin was opposed by Svitoch (1980), who found resemblances with the Turkutsky Suite of the Middle Pleistocene (Svitoch, 1975; Kaplin, 1980). However, studies of rodent remains indicate that the age is Middle Pleistocene or younger (Kaplin, 1980). Kiselev (1980b, 1981) initially adopted the older chronology, but later acknowledged a younger age for the deposits (Kiselev, 1995). The late-Pleistocene age of much of the deposits at the three key exposures on the Main River (Ust'-Aldan (Aldan Mouth), Mamontovy Obryv (Mammoth Bluff) and Ledovy Obryv (Ice Bluff)) is now secure (Dort-Gol'ts, 1982; Kotov and Ryabchun, 1986; Kotov, 1988; Kotov et al., 1989; Lozhkin et al., 2000; Anderson and Lozhkin, 2002). At the Ice Bluff exposure a series of radiocarbon dates (conventional ages) ranges from 42,000 ± 1300 near the section base to 19,500 ± 500 near the top; the topmost material was dated to late-Holocene age (Anderson and Lozhkin, 2002).

Kiselev (1980a,b, 1981) reports insect faunas from Chaun Bay, Aion Island, and the Main River Ice Bluff. While insects from west Chukotka have been well-studied (Kiselev, 1980a, 1981; Sher et al. Database, 2006; Kiselev and Nazarov, in press), only nine samples with fossil insects have been reported from south-central Chukotka: one species-poor sample from the Mammoth Bluff site and eight from the Ice Bluff, of which only four assemblages are species-rich (Kiselev, 1980b, 1981; Sher et al. Database, 2006).

3. Materials and methods

3.1. The modern exposure: stratigraphy and dating

The Main River Ice Bluff exposure extends for about 1 km at an elevation of 30 m on the left bank of the Main River (Fig. 2). In the 1970s and 1980s the section was better exposed, particularly the southern part, which is currently covered by vegetation, as is the lower part of the entire bluff. Kotov et al. (1989) differentiated the exposure into northern and southern parts. The lowest three units (alluvial and flood-plain; thermokarst lake deposit; and peat that developed after lake drainage and dated to 42 ka) are now covered (Fig. 2). These are common to the whole section. The northern exposure is dominated upward by ice-rich deposits that are similar to widespread yedoma sediments on the coastal Yakutia lowlands. The southern portion of the exposure is dominated upward by a further sequence of superimposed thermokarst lake deposits. The overall setting of the exposure is shown in Figs. 2 and 3. The slumped lower material is evident, and the locations of the trenches in the upper part of the exposure are indicated.

In the summer of 2004 only the northern part of the exposure was accessible. It consists of an ice-rich silty and sandy outcrop with interbedded peat layers (Figs. 2 and 3). Grass roots and shrub remains are visible in the silty sediment, while plant and insect remains, although present in the sandy sediment, are only revealed after screening. Six trenches were cleaned at the exposure. Large bulk sediment samples were taken for insect analysis (for screening) and frozen samples were collected for DNA analysis (Figs. 2 and 4). DNA samples were taken in triplicate (Fig. 4), and they were kept frozen in a field freezer with power supplied by a portable generator. The duplicates were back-up samples as

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[2] The name "Main" has no English meaning; it is a direct transliteration of the local name; pronunciation is close to English word "mine".

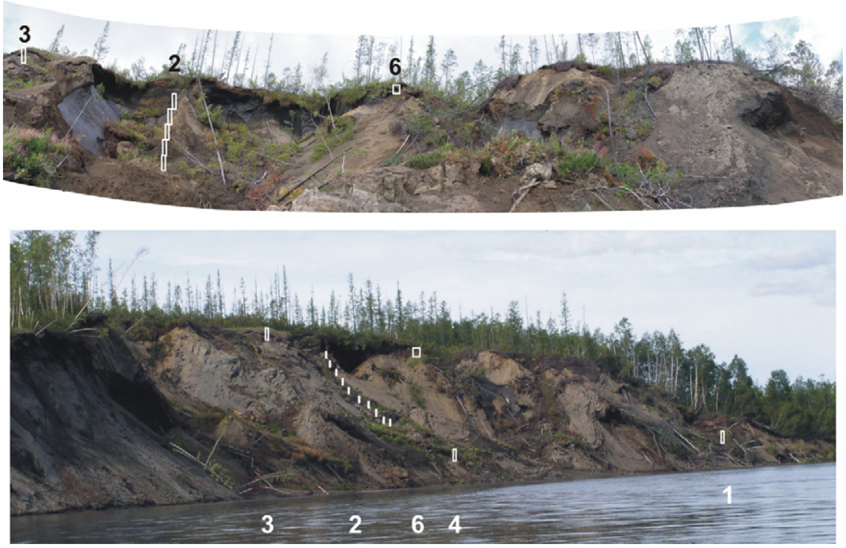

Fig. 2. Ice Bluff exposure. See details in Figs. 3 and 4.

returning samples to the lab successfully can be difficult due to the long distance that must be travelled. Fortunately, all frozen samples were returned in good condition; the extra volume allows other analyses, for example, radiocarbon dating and pollen studies. Radiocarbon dating was carried out at the radiocarbon facility in Oxford, UK (Fig. 4, Table 1).

The geological description, including permafrost features and section stratigraphy, was made by Andrei Sher and Anatoly Kotov; unfortunately, their detailed field notes are unavailable. Sher made the section scheme based on his field observations and this forms the basis of Figs. 2 and 4. Further geological and stratigraphic observations were made by SK. We have used these data and data reported earlier (see Anderson and Lozhkin, 2002) to provide a basic description of the locality.

3.2. *Insect sampling and analytical methods*

During the summer of 2004 insect sampling was one of the main tasks of the fieldwork. The lowest sample B9, comes from a sandy unit with small ice-wedge casts 3 m above river level. Based on its height above river level, this bed is tentatively assigned to the first, alluvial-flood-plain unit (Kotov and Ryabchun, 1986), but fossil insects from here are not in concordance with an aquatic environment, and furthermore, no overlying peat layer was observed; the stratigraphic relation of this unit to other described units is thus unclear. All other insect samples from 2004 field season were taken from the ice-rich upper part of the section.

In total, 48 bulk sediment samples were taken and screened for insect remains using a sieve with a 0.4 mm mesh. All sediment types were screened, not only organic-rich ones. The weight of screened sediment was about 50 kg, but in organic-poor beds we screened additional material. The dried detritus was processed in a laboratory, and fossil insects were picked up under a low-power stereo binocular microscope. Kerosene flotation (Elias, 1994) was not used to extract the insect remains as our experience shows that fossil insects from permafrost have such extremely good preservation that use of kerosene can actually cause missing of some heavy remains.

3.3. *Interpretation of fossil insect assemblages*

Terrestrial permafrost sediment is usually rich in subfossil insects with relative hard chitin exoskeletons: Coleoptera (beetles), some Hymenoptera – mostly ants and parasitic Hymenoptera, some Heteroptera (true bugs), and occasionally specimens of other insect orders. Most fossils retrieved here belong to terrestrial habitats; aquatic insects are uncommon. We use beetles, ants and true bugs for environmental reconstructions; other fossils are represented by single chitin sclerites but these are hard to identify. The interpretation of the fossil insect assemblages uses traditional approaches based on ecological/bioclimatic groups (see Sher et al., 2005; Kuzmina and Sher, 2006; Sher and Kuzmina, 2007). By screening a large sediment volume, we are able to retrieve numerous insect fossils, and this enables us to work not only with a list of species but with estimates of the relative abundances of different ecological groups of insects.

In this research we use the following ecological groups found in Pleistocene faunas from Siberia (Sher and Kuzmina, 2007; see Fig. 4):

St – thermophilous steppe insects that are never associated with modern tundra. This group is usually a quite diverse assemblage of exotic southern steppe species, although some of them survive in the steppe communities of Yakutia today.

Ms – meadow-steppe species that are more tolerant to a cold environment than St species; these may live on steppe-like patches inside the tundra zone.

Ss – sedge steppe or cryoxeroplilous steppe insects. This group includes only one, but a very important species – the pill beetle *Morychus viridis*, which is extremely abundant in the most Pleistocene insect assemblages of West Beringia.

We attribute insects in these three groups to a steppe association, and their presence among common tundra species indicates a steppe-tundra environment; this can be represented by a range of assemblages and is considered a specific ecosystem that is different from modern tundra.

Ks – xerophilous insects with wide ecological preferences.

Dt – xerophilous tundra insects; the group includes various insects such as *Curtonotus alpinus*, which is common in modern tundra (in East Beringia represented by *Amara (Curtonotus) alpina*) on the one hand, to the Pleistocene relict species *Poecilus nearcticus*, which is rare today—the species was described only in 1966.

Tt – cold-resistant insects typical of arctic tundra.

Mt – insects of moist or wet tundra habitats.

These three groups belong to the tundra association.

Other groups usually do not play an important role in the Pleistocene fossil insect assemblages of West Beringia (although they may dominate in the Holocene). These are as follows: sh – shrub, me – meadow, fo – forest, ri – riparian, aq –aquatic, and oth – other insects.

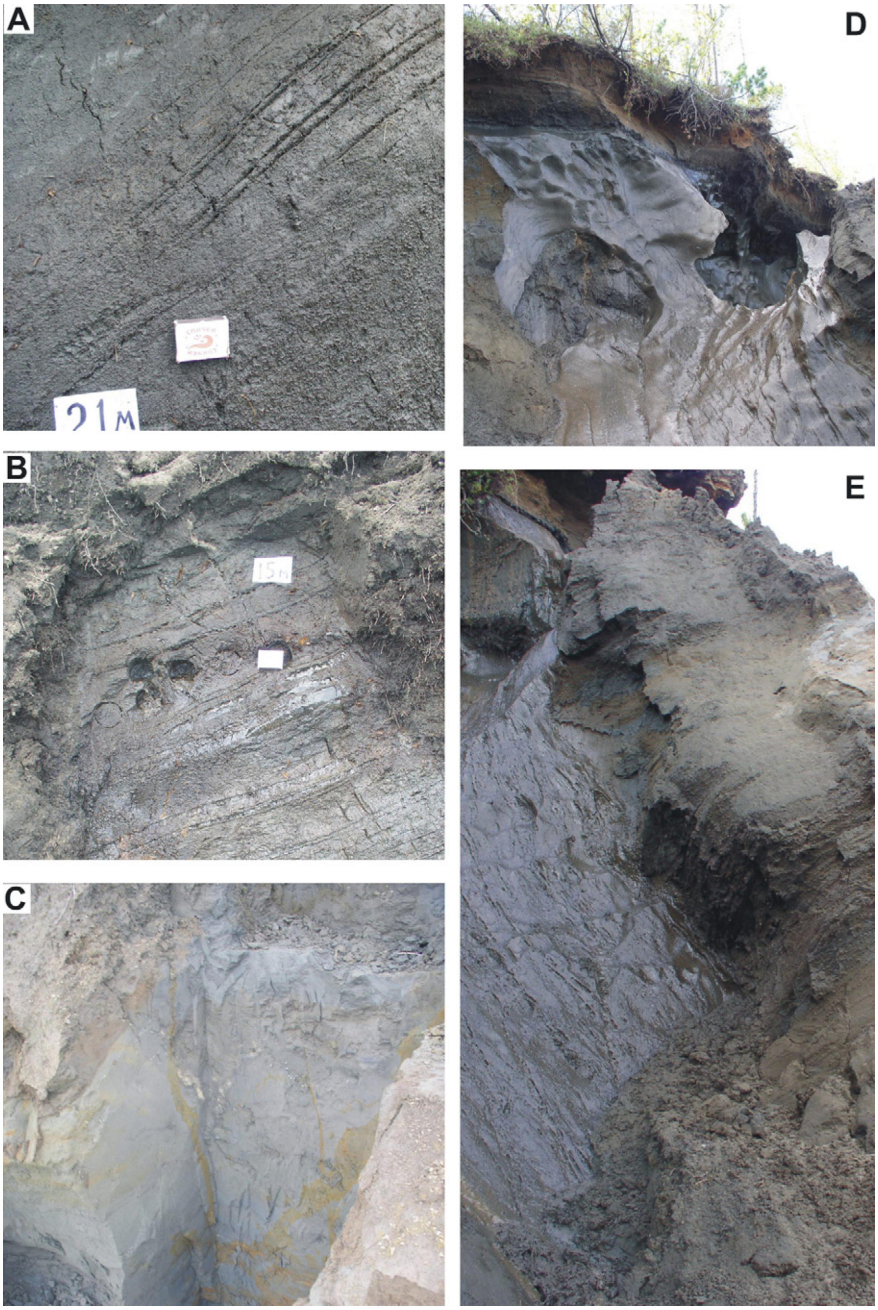

Fig. 3. Details of the Ice Bluff exposure. A – trench IB-2, alt. 21 m, sand with sparse plant remains; B –trench IB-2, alt.15 m fine sand with plant remains; C – trench IB-4b – sand the ice wedge cast marked by ironish layers; D – top of the section, ice wedge and grey fine sand; E – ice wedge and trench IB-2.

Each species is assigned a group, even when there may be ambiguity. For example, the tundra ground beetle *Pterostichus brevicornis* can be found in forest habitats or in dry places in the tundra. We placed this species to the mt group, however, because the main habitat of this species is wet tundra. This formalized system obviously has some limitations, but it has proved effective in clarifying the structure of ancient insect communities and allowing us to track environmental changes in time and space.

4. Results

4.1. Chronology

The radiocarbon data show that the studied deposits were formed approximately between 33 ka and 16 ka (see Table 1, Fig. 4). The dates are not reversed within trenches, but between trenches there are some discrepancies (Fig. 4). According to the radiocarbon chronology, if we assume that the rather even overall rate of deposition shown by the dates in the main trench, IB-2 (≈1 m per 800 yr), also applies to the side trenches near the top of the section, the sediment of left trench IB-3a would be older, but the sediment of right trench IB-6 is younger than sediments in IB-2 at the same level. The bedding in the upper part of the section appears to be oblique (Fig. 3 a,b,e, Fig. 4). We observed in trench IB-2 that the beds rise toward the face of the outcrop, and we can speculate that the reasons of such tilted bedding are related to the influence of a complicated system of large ice wedges (one of which can be traced almost across whole section from 1.5 m below the surface to 11 m above river level and probably continues deeper; Fig. 4, Fig. 3e) or possibly from neotectonic warping of the area, in

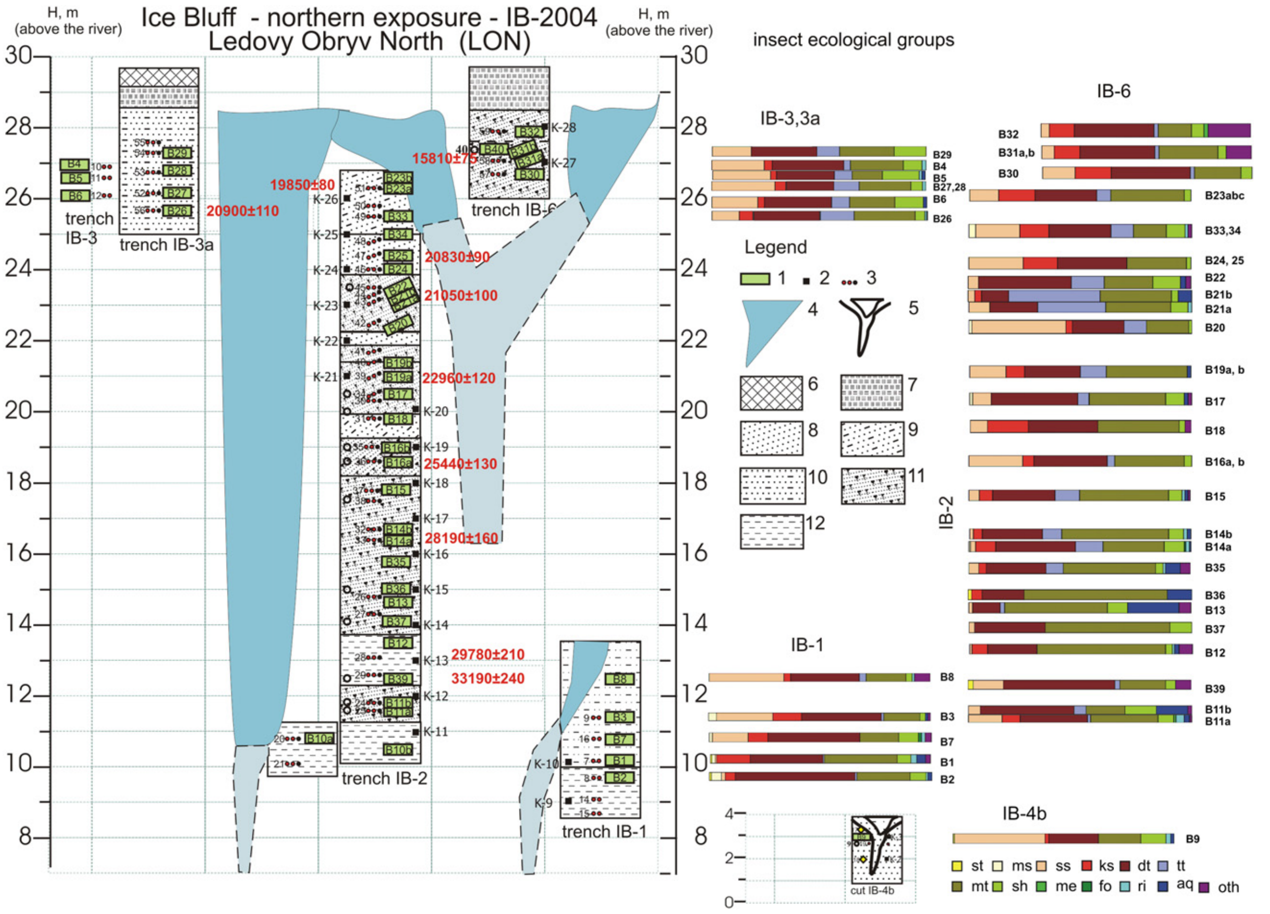

Fig. 4. Scheme of the Ice Bluff showing sampling points, radiocarbon ages and fossil insect assemblages. 1-3 sampling points: 1 insect, 2 bulk, 3 DNA; 4 – ice wedge; 5 – ice wedge cast; 6 – peat; 7 – silt and sand with peat lenses; 8 – sand; 9,10 – silty sand with different bedding: 9 oblique, 10 horizontal; 11 –fine sand with grass roots; 12 – silt. Ecological group of fossil insects: st – steppe, ms – meadow-steppe, ss – cryophyte steppe, ks –xerophilous insects; dt – tundra xerophilous; tt – insects of typical and arctic tundra; mt – tundra meso-hygrophilous; sh – shrub; me – meadow; fo – forest; ri – riparian; aq – aquatic; oth – others.

which case small unobserved faults may explain the dating differences.

4.2. Stratigraphy

We developed a series of trenches into the exposure at different but overlapping elevations and at different lateral locations that enabled an almost continuous upward examination of the sediments. Lateral shifts were determined by the presence of ice wedges and the accessibility of the cliff (see Figs. 2 and 4). In the following description the river level is the 0-m datum.

4.3. 1–4 m

The lowest visible material was in cut IB-4b (Fig. 4). The unit is sandy; it has a small ice-wedge cast and is overlain by a peat (probably reworked) layer (Fig. 3-c). It lies below the sample dated at 29,780 ± 210 ^{14}C yr B.P. Above this unit the section was inaccessible for several meters.

4.4. ~8.5–28.5 m

The majority of the section height is exposed in cut IB-1 and cut IB-2 (see Fig. 4). The radiocarbon dates indicate it covers the

Table 1
Radiocarbon from the Ice Bluff sections.

Laboratory no	Sample ID	Trench	Height above river (m)	Corresponding faunal sample	Delta C13	Uncalibrated age	Material dated
OxA-15347	29C	IB-2	12.6	n/a	d13C = −26.1	33190 ± 240	Plant remains, rootlets
OxA-14928	28C	IB-2	13.1	n/a	d13C = −25.9	29780 ± 210	Plant remains
OxA-15349	33C	IB-2	16.4	ChM-B14a	d13C = −26.6	28190 ± 160	Plant remains, rootlets
OxA-14957	36C	IB-2	18.6	ChM-B16a	d13C = −26.2	25440 ± 130	Plant remains
OxA-15348	39C	IB-2	21.0	ChM-B19a	d13C = −26.9	22960 ± 120	Plant remains, rootlets
OxA-14929	44C	IB-2	23.3	ChM-B21b	d13C = −25.9	21050 ± 100	Plant remains
OxA-15667	47C	IB-2	24.4	ChM-B25	d13C = −26.7	20830 ± 90	Plant remains, rootlets
OxA-14958	56	1B-3A	26.0	ChM-B26	d13C = −25.1	20900 ± 110	Plant remains
OxA-15668	51	IB-2	26.3	ChM-B23a	d13C = −27.1	19850 ± 80	Plant remains, rootlets
OxA-14930	58	IB-6	27.4	ChM-B31b	d13C = −26.1	15810 ± 75	Plant remains

interval from >30 to <20 ka. Based on the observed stratigraphy (Fig. 4) and the previous descriptions of Kotov et al. (1989) and Anderson and Lozhkin (2002) we have not divided the major portion of the exposure into smaller units. The material is ice-rich grey silt grading upwards to sandy silt with numerous plant remains: shrub roots, grasses, and leaves (Fig. 3-b). It becomes less organic near the top of the section. The upper part of trench IB-2 consists of fine sand with numerous grass roots. Close to top, coarse yellow-grey sand becomes prevalent and plant remains are sparse (Fig. 3c).

The uppermost part of the exposure was studied in the cuts IB-3, IB-3a, and IB-6 (Fig. 4). These sediments are grey fine sand and silty-sand; in cut IB-6 they are obliquely bedded with grass roots while in cuts IB-3 and IB-3a they are horizontal and contain fewer plant remains. Dates of 15,810 ± 75 and 20,900 ± 110 ^{14}C yr B.P. within these short sections indicate that sediments in IB-6 and IB-3/3a are not coeval (Table 1; Fig. 4), and this is supported by differences observed in the respective insect faunas (see below).

The Holocene is likely represented by an abrupt shift to peat or silt and sand with peaty layers in the uppermost 1–2 m of the section in cuts IB-6 and IB-3a, but we did not obtain dates from this level. Anderson and Lozhkin (2002) list a date of 2300 ± 100 on woody fragments and peat from 1.0 to 0.5 m below the top of the exposure.

4.5. *Fossil insect results*

The first fossil insect samples from this locality come from the Svitoch expedition of 1975. No entomologists participated in this expedition, and only organic-rich plant horizons, where geologists expected to see insect remains without screening, were sampled. By using the description of the sequence by Kiselev (1980b), we have correlated our new samples to those taken previously. The richest previously collected insect samples (Kiselev's LO.2 and 3) were collected from the lower, now inaccessible part of the exposure represented by shallow-water lake sediment, and these contained a high number of aquatic species (Kiselev, 1980b, 1981). The next assemblage, from sample LO.4, reflects a dry environment and is likely to come from the base of the fourth unit (ice-rich deposit or Yedoma). Sample LO.5 comes from the southern part of the exposure and again contains significant numbers of aquatic insects; here, lake sediments are correlated with subaerial loess-like sediments at the same level in the northern part of the exposure. The last of Kiselev's (1980b) samples, LO.6 and LO.7, were taken from Yedoma in the upper part of the exposure and correlate with samples taken in 2004 from an elevation 24–26 m above river level.

Insect faunas recovered from old (Kiselev, 1981) and our new samples are similar, with the exception of aquatic species, which are known only from previous studies. Other observations such as a near absence of thermophilous steppe insects and abundance of dung beetles *Aphodius* sp., were noted both in the previously collected and in the new samples and illustrate the peculiarity of the local entomofauna. The species list is presented in Table 2 and the images of fossil insects are shown in Fig. 5. The samples in Table 2 are placed first by trenches, and second within trenches by elevation, from older to younger. The sample numbers were given in the field and reflect the order of sampling. Thus, the reader should follow the height designations rather than the sample numbers for orientation.

The assemblages are described upward, beginning with the lowermost unit. The oldest and lowest sample from 2004 was taken from trench IB-4b (Fig. 4). The insect samples were taken from grey sand; there was no visual organic matter, but plant and insect remains were recovered after screening. The sample is rich in fossil insects that are typical of a Pleistocene steppe-tundra fauna, as described previously by Kiselev (1981) and Kuzmina (1989, 2003); the cryophyte-steppe pill beetle *M. viridis*, dominates the remains (more than one third of all insects), the ground beetle *Harpalus vittatus alaskensis* is common and there are xerophilous species such as the ground beetles *Notiophilus aquaticus*, *C. alpinus*, *Amara glacialis*, and weevils *Mesotrichapion wrangelianum* and *Sitona borealis*. Mesic tundra species are present but less abundant. They are represented by the ground beetles *Pterostichus* subgenus *Cryobius* and the rove beetle *Tachinus brevipennis*. One interesting find is the leaf beetle *Chrysomela blaisdelli*, which feeds on willow and is rarely found to north of the southern shrub tundra zone.

The following five samples were taken from trench IB-1. The lowest sample (B-2) from this trench was taken at 10 m above river level and the upper one (B-8) from 12.5 m above river level. All samples are fairly rich in insect remains. The steppe association increases in dominance upwards. The two lowermost samples, while containing a relatively low percentage of steppe insects, contain a single individual of the true steppe ground beetle *Cymindis arctica* and a few remains of the meadow-steppe weevil *Coniocleonus* sp., but both beetles are otherwise rare at the Ice Bluff site. Relative proportions of the pill beetle *M. viridis* increase upwards. There are also single occurrences of the arctic weevil *Isochnus arcticus* and the arctic leaf beetle *Chrysolina tolli*. There are no radiocarbon dates associated with this sequence of samples.

The majority of samples (29 in all) were taken in the main cut, IB-2b, between ~11 and 26 m above the river (see Table 2 and Fig. 4). It should be noted that the lower samples (B-11a,b and B-39) overlap with the upper samples of cut IB-1 in elevation, but they are represented by different fossil insect assemblages – the assemblages B-11a,b and B-39 have a less pronounced steppe element. The sediments also differ, suggesting that either one or other section contains displaced material, or that the sections are not coeval. In trench IB-2b, we focus on samples above the radiocarbon date of 29,780 ± 210.

The assemblages in samples B-12 to B-15, from ~12 to ~18 m above datum, and, according to the radiocarbon dates, representing a period from ~30 to ~25 ^{14}C yr B.P., show a gradual decrease of steppe insects and all xerophilous groups, while mesophilous tundra insects increase in dominance and shrub insects become more significant. One of the assemblages (B-13, 14,8 m) contains abundant remains of aquatic insects (the water scavenger beetles *Hydroporus acutangulus*, *Hydroporus lapponum*, *Agabus moestus*). These features of this sequence, the high content of tundra mesophilous and shrub group, the less important role of xerophilous species, unstable variation of steppe group insects, which is poor in species diversity, and permanent presence of the arctic group, are typical for the MIS3 interval and this faunal sequence in agreement with what was observed in the Bykovsky Peninsula fossil insect fauna (Sher et al., 2005).

In the next upward portion of the section (samples B-16 to B-20, ~18–22 m) radiocarbon dates of 25,440 ± 130 (~18 m) and 21,050 ± 100 (~23 m) bracket the sequence. Xerophilous taxa again dominate, with steppe taxa gradually increasing until the steppe group is once again as significant as it was in sample B-9. All samples contain the arctic weevil *I. arcticus*.

The next three higher samples, B-21a, b and B-22, are close to each other and characterized by an increase in arctic species – up to 41% in the assemblage B-21b. This set of samples, which are closely spaced, are dated to ~21ka. The uppermost insect assemblages from trench IB-2 (samples B-24 – B-23) are similar to those below samples B-21 and B22.

As described above, the upper part of the section is represented by trenches IB-3 and IB-3a, which are situated just to left of the main trench, and trench IB-6, which lies to the right (Figs. 2 and 4).

Table 2
Fossil insect data from the Ice Bluff sections, reported in minimum number of individuals per sample. Samples are reported in stratigraphic order rather than sampling order, beginning with the lowest elevation.

section cut (IB)	EcoCode	4b	1					5	2																												3			3a				6				
sample ChM-B		9	2	1	7	3	8	38	10b	11a	11b	39	12	37	13	36	35	14a	14b	15	16a	16b	18	17	19a	19b	20	21a	21b	22	24	25	34	33	23a	23b	23c	6	5	4	26	27	28	29	30	31a	31b	40	32
Ord. Coleoptera																																																	
Fam. Carabidae																																																	
Carabus truncaticollis Esch.	mt	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	1	—	1	—	—	—	—	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	1	—
C. odoratus Motsch.	dt	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1?	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
C. shilenkovi O.Berlov	dt	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
C. arvensis Hbst.	fo	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Carabus sp.	oth	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Notiophilus aquaticus L.	ks	2	4	25	4	11	1	—	—	3	—	—	6	—	—	2	3	7	4	2	—	—	4	—	—	1	1	—	1	—	—	—	—	—	12	2	1	—	—	1	13	—	—	—	8	2	1	—	4
Notiophilus sp.	oth	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Diacheila polita Fald.	mt	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—
Elaphrus splendidus F.-W.	na	—	1	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
E. riparius L.	na	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—
Bembidion (Peryphanes) dauricum Motsch.	dt	—	—	—	—	—	1	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Bembidion (Peryphanes) sp.	na	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—
Bembidion (Plataphodes) sp.	oth	—	—	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Pterostichus (Cryobius) ventricosus Esch.	mt	1	—	5	—	—	1	—	—	2	—	1	3	1	2	3	2	1	—	—	2	1	—	—	1	2	—	—	—	—	—	—	—	—	—	—	—	—	—	1	1	—	—	—	—	—	—	1	—
P. (C.) pinguedineus Esch.	mt	—	—	9	1	1	—	—	—	—	—	—	—	1	—	3	2	—	—	3	—	—	—	—	—	2	2	—	—	—	1	—	—	—	2	—	—	—	—	—	2	—	—	1	1	—	—	—	—
P. (C.) brevicornis (Kirby)	mt	2	2	3	1	2	3	—	—	2	—	—	26	8	—	7	—	—	5	1	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	2	1	—	1	—	1	—	—	4	—	—	—
Pterostichus (Cryobius) spp.	mt	12	4	22	6	6	5	2	3	8	4	6	19	12	14	18	15	13	32	8	3	2	2	7	3	2	5	2	2	2	7	1	1	1	4	4	2	2	2	6	20	—	3	3	6	—	2	—	2
P.(Lenapterus) agonus Horn.	mt	—	—	2	—	1	—	—	—	—	1	—	—	—	—	2	1	—	1	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
P. (L.) costatus Men.	mt	—	—	—	—	—	—	—	—	—	—	—	1	—	3	2	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	1	—	—	—	—	—	—	—	—
P. (L.) vermiculosus Men.	mt	—	—	—	1	—	1	—	—	—	—	—	—	—	1	1	—	1	5	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	1	1	—	—	—	—	—	—	—
P. (Petrophilus) abnormis Sahlb.	dt	—	—	1	—	—	—	—	—	—	1	—	—	—	—	—	—	1	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	4	—	—	—	—	—	—	—	—
P. (P.) montanus (Motsch.)	dt	—	—	1	—	—	—	—	—	—	2	—	—	—	—	1	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
P. (P.) tundrae Tschitsch	dt	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—
P. (Tundraphilus) sublaevis Sahlb.	dt	—	1	1	1	1	—	—	—	1	—	1	2	—	—	—	1	—	—	—	—	—	—	1	1	—	—	—	1	—	—	—	—	—	—	—	—	—	—	1	1	—	1	—	—	—	1	—	—
Stereocerus haematopus (Dej.)	dt	2	4	12	4	1	7	—	2	2	—	2	5	6	2	3	2	6	9	3	4	1	—	6	—	1	3	—	—	2	1	1	—	1	3	2	2	1	1	2	5	1	1	1	3	1	4	1	2
Curtonotus alpinus Payk.	dt	19	18	20	10	9	10	3	1	11	10	14	9	5	3	4	8	13	8	7	3	4	3	7	4	2	9	6	5	4	5	1	1	6	4	5	6	8	10	11	51	—	6	8	4	4	3	1	5
C. bokori Csiki	dt	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	1	—	—	—	—	—	—	—	—	—	—	—
Amara glacialis Mnnh.	dt	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	1	1	1	1	—	1	—	1	1	—	1	1	—	1	1	—	—	—	1	1	1	6	1	—	1	1	2	—	—	1
A. interstitialis Dej.	dt	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Dicheirotrichus mannerheimi Sahlb.	dt	—	—	—	1	2	9	—	1	1	—	—	—	1	—	—	1	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Harpalus vittatus alaskensis Lth.	ms	1	1	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—
Cymindis arctica Kryzh. et Em.	st	—	1	1	—	—	—	—	—	—	—	1	1	—	—	1	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Fam. Dytiscidae																																																	
Hydroporus acutangulus ? Thoms.	aq	—	—	2	—	—	—	—	—	—	4	—	—	—	4	2	5	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—
H. lapponum (Gyll.)	aq	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Hydroporus sp.	aq	—	—	—	—	—	—	—	—	—	—	—	1	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Agabus moestus (Curt.)	aq	—	—	2	—	1	—	—	—	2	4	—	1	—	6	2	1	—	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
A. thomsoni (J.Sach.)	aq	—	2	3	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Agabus sp.	aq	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	1	—	—	—	—	—	—	—	—	2	1	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—
Fam. Hydrophilidae																																																	
Helophorus splendidus Sahlb.	aq	1	—	—	—	—	—	—	—	—	—	—	—	—	2	2	—	—	—	—	—	—	—	—	1	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—
Cercyon sp.	na	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Fam. Leiodidae		—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Cyrtoplastus irregularis Rtt.	oth	—	—	1	—	1	7	—	2	1	—	2	4	—	—	—	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Fam. Staphylinidae																																																	
Micralymma brevilingue Schiodte	mt	—	—	2	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Olophrum latum Maekl.	oth	—	2	2	2	2	2	2	2	2	2	2	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Lathrobium sp.	oth	—	—	—	—	—	—	—	—	—	—	—	—	—	3	—	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Stenus sp.	na	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Tachinus arcticus Motsch.	mt	—	2	—	—	—	—	—	—	—	4	—	—	—	—	—	—	—	—	—	—	—	3	6	2	4	—	3	9	1	—	—	—	1	15	6	2	—	—	1	46	—	—	9	3	4	—	—	1
T. brevipennis Sahlb.	mt	10	19	13	1	3	6	2	—	9	—	2	7	1	6	5	16	19	12	20	6	4	7	2	4	—	5	7	9	4	—	—	—	6	—	5	—	9	5	6	20	—	7	2	2	2	1	2	4
Tachyporus sp.	oth	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—

Table 2 (*continued*)

Fam. Scarabaeidae																																																	
Aphodius sp. nov.?	ks	—	1	2	2	—	2	1	—	4	—	—	1	—	—	1	—	5	1	3	2	1	3	—	4	—	1	—	1	6	—	1	5	3	3	1	1	2	2	1	9	3	—	—	2	3	—	—	2
Fam. Scirtidae																																																	
Cyphon sp.	na	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Fam. Byrrhidae		—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Curimopsis cyclolepidia Muenst.	dt	—	—	—	2	—	—	—	—	1	2	2	—	—	1	—	2	2	4	1	—	—	—	1	—	—	1	2	—	3	—	—	—	1	—	—	—	2	—	1	7	—	1	1	—	—	1	—	1
Morychus viridis Kuzm. et	ss	55	2	1	11	—	34	6	8	13	3	6	1	1	1	—	4	3	2	4	7	7	3	5	4	6	29	5	2	2	9	2	7	5	6	6	4	13	19	14	44	3	14	11	9	2	1	1	2
Simplocaria sp.	dt	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Fam. Coccinellidae																																																	
Hippodamia arctica Schneid.	na	—	—	1	1	2	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Coccinella fulgida Wat. ?	oth	—	—	1	—	22	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
C. transversoguttata Fald.?	oth	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2	4	8	10
Coccinella sp.	oth	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Fam. Anobiidae																																																	
Caenocara bovistae Hoffm.	fo	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Fam. Chrysomelidae																																																	
Plagiodera versicolora Laich.	sh	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
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Hemitrichapion tschernovi T.-M.	dt	—	1	1	—	—	—	—	—	—	1	1	—	1	—	—	—	3	2	2	—	—	—	1	—	—	—	—	—	—	1	—	—	1	—	—	—	2	1	—	5	—	—	—	2	—	—	—	—
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Fam. Pentatomidae																																																	
Aelia sp.	ms	—	1	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
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sum		134	113	178	68	86	100	15	20	86	57	44	99	41	56	64	89	131	118	82	35	23	38	60	35	25	69	52	66	41	39	6	19	42	59	38	25	61	70	57	351	10	48	62	58	32	18	21	50

Samples B-30, 31, 32 (from right trench, IB-6) are all similar; they contain low amounts of steppe taxa, although most of the insects are xerophilous. All three samples contain abundant ladybird beetles of the genus *Coccinella*, most likely *Coccinella transversoguttata*. The fossil ladybird preservation is not perfect because of their minimal chitin and rounded form; we extracted many separated pieces and calculated the Minimum Numbers of Individuals (see Elias, 1994) using the best preserved parts. The radiocarbon datum of this unit is 15,810 ± 75; this is the youngest date obtained. The lower sample (B-30) of trench IB-6 overlaps in height with the upper sample B-23b of trench IB-2, but we suspect that the age of the insect assemblage B-30 is younger than B-23b; as mentioned above, the levels dated at 19,850 ± 80 ^{14}C yr B.P.in IB-2 and 15810 ± 75 ^{14}C yr B.P. in IB-6 are separated by less than 1 m,


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which means either a sudden decrease in sedimentation rate or a displacement of material between the two trenches. The second possibility seems to be more likely for this section (see above).

Samples from the trenches IB-3 and IB-3a can be combined because the trenches relate to the same section; IB-3 was made early in the field season, and IB-3a is a renovation of the old trench. The radiocarbon date on of 20,900 ± 110 ^{14}C yr B.P. lies ~1 m above the date of 20,830 ± 90 of IB-2 trench, probably reflecting local tectonic disruption of the deposit (see above). The fossil insect assemblages from IB-3 and 3a are well correlated with the sequence IB-2. The arctic weevil *I. arcticus* is present, but not very significant, and the indicator of cold steppe, *M. viridis,* is abundant. Also the most numerous assemblage B-26 (age 20,900 ± 110) contains single remains of two meadow-steppe species: the weevil *Coniocleonus cinerascens* and the leaf beetle *Chrysolina arctica*.

5. Discussion

5.1. General features of the fossil insect faunas

The terrestrial insect faunas recovered from Kiselev's (1981) samples and our 2004 samples are similar, except that aquatic species are far more abundant in Kiselev's samples whereas only one 2004 sample (B-13) has a high count of aquatic taxa. This probably relates to differences in sampling technique and strategy. Kiselev did not see the site and relied upon samples collected by the Svitoch expedition; sampling was not done using appropriate protocols (see above) and samples were largely of poor quality. Only assemblages that came from the low-level lake sediment, now inaccessible, had numerous fossils, including abundant water beetles. Thus there is a bias towards the aquatic-dominated lake-sediment units in Kiselev's faunas.

The most important insect groups in the Main River Ice Bluff assemblages are the mesc and hygrophilous tundra group and the dry-tundra group. Taiga insects are virtually absent from the record; one generalist tree species with a habitat is restricted to the forest zone, the wood-boring beetle *Caenocara bovistaeis*, is present in one sample. Steppe elements of the steppe-tundra group are present, but the faunas diverge taxonomically from those of other western Beringian areas. They are similar to the other faunas in that the cryophyte-steppe pill beetle, *M. viridis,* is important, but otherwise there is a near absence of thermophilous steppe insects. For example, the weevil, *Stephanocleonus eruditus,* is one of the most tolerant and common thermophilous steppe insects across sites in western Beringia, except at Ice Bluff, where it is not recorded. In contrast, the thermophilous steppe ground beetle *C. arctica,* which is presently known only from relict steppe patches of Central Yakutia (Kryzhanovsky and Emets, 1979) is generally uncommon as a fossil and occurs occasionally in Pleistocene steppe-tundra communities across western Beringia; however, at the Ice Bluff site *C. arctica* is recorded from six samples from the lower part of the exposure. Furthermore, the abundance of dung beetles (*Aphodius*) is unusual for north-east Asian records, further underlines the unusual nature of the steppe-tundra faunal group at this locality.

5.2. Steppe-tundra at Ice Bluff?

The term "steppe-tundra" is widely used by western Beringia palaeoenvironmental researchers. While the landscape and ecosystem that it represents has no modern analogue (Sher, 1990, 1997), it was, according to the fossil record, a dominant feature of much of the Pleistocene during stadial periods that were characterized by cold, dry, continental climates. Consistent assemblages of insects are associated with deposits formed under these conditions; they include insects that feed upon plants associated with steppe environments and also species associated with dry tundra (S. Elias, pers. comm. Oct. 2009). Do Pleistocene fossil insect faunas at Main River represent steppe-tundra? Sher would certainly have argued "yes". The assemblages have a key indicator of steppe-tundra – a significant presence in almost all samples of the pill beetle *M. viridis*. *Morychus* is a stenobiotic taxon that is apparently limited to cold, dry and virtually snowless steppe-like patches that are dominated by xerophilous sedges, for example, today they are found on low mountain tops in the Upper Kolyma region within the boreal forest zone (Berman, 1990; Berman et al., 2001). While this beetle is currently found inside tundra zone (the middle fork of the Amguema River and Chaun Bay, Chukotka; and Wrangel Island; Berman, 1986, 1990), it is not found in true tundra habitats. Its habitats correspond to the cryoxerophilous steppe characterized by Yurtsev (1982). Thus, a high percentage of *M. viridis* in a fossil insect assemblage presumably indicates that the past landscape mosaic included areas of cryoxerophilous steppe or a close equivalent.

Kuzmina (2003) attempted a classification of steppe-tundra fossil insect assemblages, concluding that there were at least five different variants. The Main River assemblages appear to be a sixth: one with few insects with steppe affinities but a strong mesic tundra component, but still dominated by *M. viridis*. We therefore infer that throughout the period investigated, the Ice Bluff area, and perhaps central-southern Chukotka in general, was characterized by moist vegetation, closer to modern tundra than the drier steppe-tundra reconstructed for sites further west, but yet with a mosaic that included cryophytic steppe and perhaps occasional warmer steppe habitats. The actual term used to describe this unusual Chukotka paleoenvironment is not the key issue here (the identity of steppe-tundra is still contested), but we can state the palaeoenvironment was different from typical modern environments.

5.3. Palaeoenvironmental reconstruction

The detailed insect record gives insight into environmental changes that occurred during MIS3-MIS2. We can recognize two faunal units (Table 2, Fig. 6). The first, or lower, unit corresponds to the end of the Middle Weichselian time from older than 33 ka (the lower sample was taken 2 m below the layer with radiocarbon age 33,190 ± 240) to 24 ka, thus representing late MIS stage 3. The

Fig. 5. Fossil insects from the Ice Bluff site. 1 – *Carabus truncaticollis*, elytron, sample ChM-B17; 2,3 – *Curtonotus alpinus*, pronotum and elytron, sample ChM-B26; 4,5 – *Pterostichus (Cryobius) ventricosus*, pronotum and elytron, sample ChM-B19a; 6,7 – *Pterostichus. (Cryobius)* sp., pronotum and elytron, samples ChM-B29, ChM-B31b; 8 – *P. abnormis*, pronotum, sample ChM-B26; 9 – *P. tundrae*, pronotum, sample ChM-B29; 10 – *Stereocerus haematopus*, elytron, sample, ChM-B26; 11,12,13 – *Notiophilus aquaticus,* head, pronotum and elytron, sample ChM-B26; 14,15 – *Amara glacialis,* pronotum and elytron, sample ChM-B26; 16,17,18 – *Tachinus brevipennis*, head, pronotum and elytron, sample ChM-B26; 19 – *T. arcticus*?, elytron, sample ChM-B26; 20, 21, 22 – *T. arcticus – brevipennis* group., terminal abdominal sclerites (female tergitus and sternitus, male tergitus), sample ChM-B26; 23,24 – *Aphodius* sp., pronotum and elytron, sample ChM-B27; 25,26 – *Morychus viridis,* pronotum and elytron, sample ChM-B32; 27,28 – *Curimopsis cyclolepidia*, pronotum and elytron, sample ChM-B26; 29,30,31 –*Coccinella transversoguttata*, pronotum, metathorax and elytron, sample ChM-B32; 32 –*Hemitrichapion tschernovi*, connected elytra, sample ChM-B26; 33 –*Mesotrichapion wrangelianum*, connected elytra, sample ChM-B26; 34 –*Isochnus arcticus*, connected elytra, sample ChM-B26; 35 – *Coniocleonus* sp. elytron, sample ChM-B26; 36 – *Lepyrus volgensis*, elytron, sample ChM-B1; 37,38,39 – *L. nordenskioeldi*, head, pronotum and connected elytrons, sample ChM-B26; 40 – *L. gemellus,* elytron, sample ChM-B26; 41,42 – *Hypera diversipunctata*, head with pronotum and elytron, sample ChM-B26; 43 – *H. ornata*, elytron, sample ChM-B26; 44,45 – *Sitona borealis*, head and pronotum, sample ChM-B26. The scale bar is 1 mm.

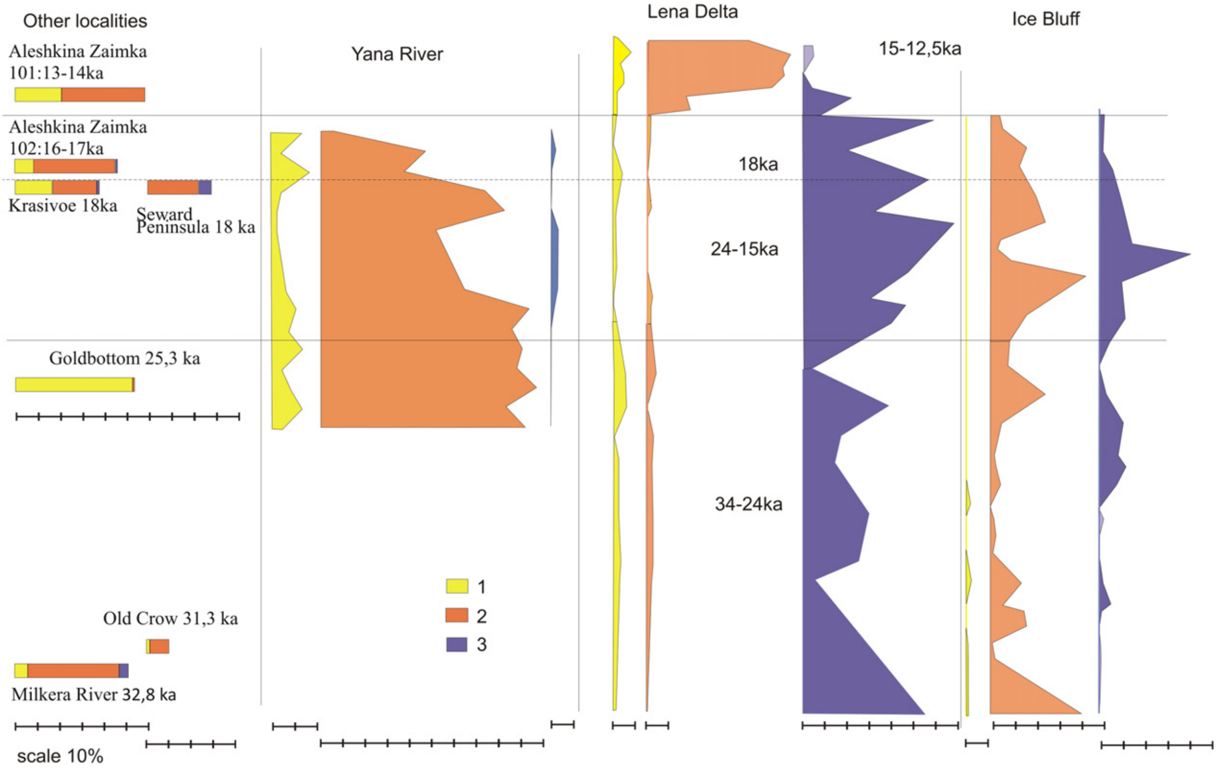

Fig. 6. Proportion of the steppe and arctic insects from different localities of Beringia. 1 – steppe; 2 – cryophyte-steppe; 3 – arctic insect groups.

second dates between ~24 ka and 15 ka, representing the glacial maximum and early late-glacial period.

The lower unit assemblages are variable in composition; overall the insect affinities are steppe-tundra, with a significant presence of the typical Pleistocene steppe-tundra pill beetle *M. viridis*, but with only *C. arctica* (see above) representing thermophilous steppe. The contribution of the steppe association (cold steppe, meadow steppe and thermophilous steppe together) during the first stage (Figs. 4 and 6) varies from 24% to zero, and the relative contribution of the arctic group varies from zero to 12%. The moist tundra group is an important component of most samples in this unit. Also, *Aphodius* species (dung beetles) is tightly linked to the presence of Pleistocene mammals, but mammalian remains themselves are less abundant here than at the well-studied sites on the Yakutian lowlands. It is possible that if the Pleistocene climate was moister than in neighbouring more continental areas that mammal dung (and also part of bones) would be more easily decomposed here, leaving dung beetles as the only evidence. It is also of interest that a stacked series of thermokarst lake deposits characterizes the southern exposure (not studied here, but see Anderson and Lozhkin, 2002). Dates suggest they formed during the period 34–14 ka (as well as earlier and later). The lakes presumably were tapped and drained by the Main River, but that they continued to form suggests enough moisture on the landscape to support their development. Thaw-lakes of full-glacial age were uncommon in most of Beringia (Walter et al., 2007).

The upper faunal unit (dated from approximately 24 ka to 15 ka) covers the LGM. Although arctic insects are present in most of the assemblages, there is a brief peak of the arctic group in these faunas suggesting particularly cold conditions at about 21 ka (Fig. 4). After the LGM, the insect faunas once again reflect a cool but moist environment, and the arctic group plays a restricted role; there is consistent presence of insects in the shrub tundra group in the samples representing this period.

The youngest samples are characterized by the presence of ladybirds, especially *Coccinella*. In general, ladybirds are extremely rare in the Pleistocene of Beringia. They feed on aphids and only occasionally invade high latitudes where aphids are uncommon (Korotyaev et al., 2004). According to fossil records (Matthews and Telka, 1997; Kiselev, 1981; Sher et al., 2006) ladybirds also avoid the steppe-tundra environment. Their presence in these fossil assemblages indicates difference of the local environment from common steppe-tundra.

5.4. *Comparison with pollen records*

Insect-based reconstructions can be compared with the few late-Pleistocene pollen records from the study area and surround regions. Two come from the Ice Bluff section itself. As reported by Anderson and Lozhkin (2002), the pollen spectra of the northern exposure corresponding to the approximate time span of the 2004 sections are dominated by herbaceous taxa (Poaceae, Cyperaceae, *Artemisia*) and spores of *Selaginella rupestris* and Bryales, though there is a low and variable contribution of pollen of woody taxa, mainly *Betula* and *Salix*. The record is coarsely resolved temporally; it shows little change between dated horizons of 31,400 ± 500 and 19,000 ± 500. The pollen record from zone LOS-4 of the southern exposure, which spans ~34–14 kyr BP (Anderson and Lozhkin, 2002) is characterized by an increasing proportion of shrub pollen, and *Pinus* and *Alnus* are also represented (though possibly are not locally derived). The zone is interpreted as a herb–shrub (*Salix, Betula*) tundra under conditions cooler than present.

It appears that both the insect faunas and the pollen assemblages differ between the northern and southern exposures at Ice Bluff, suggesting that there was a mosaic landscape of herbaceous and shrub tundra throughout much of the late Pleistocene. The intermittent development of thermokarst lakes in the area may have enriched the spatial and temporal mosaic of habitats in the local area.

The pollen record for the LGM from Lake "E" (Lozhkin et al., 2007), which lies in northern Chukotka at relatively high elevation, indicates cold, dry conditions and discontinuous tundra vegetation. Pollen records also exist for sites in south-central Chukotka, including studies from Patricia and Gytgykai lakes and the records from exposures in the Amguema River basin (Anderson and Lozhkin, 2002). The core from Patricia Lake shows a major vegetation change in the interval between 15,810 ± 110 and 12,140 ± 50 yr B.P., with increasing dominance of shrub birch. Prior to this change, the record is dominated by spores of *S. rupestris* and pollen of Cyperaceae, with Poaceae and *Artemisia*, but this part of the record is undated. A similar picture, but with lower values of *S. rupestris* and higher values of Poaceae, is recorded at Gytgykai Lake. Reversed radiocarbon dates (18,990 ± 100 and 24,030 ± 470) limit the chronological resolution, but this portion of the record likely represents the LGM. The Amguema exposure has a radiocarbon date of 20,640 ± 540, and two associated assemblages are dominated by *S. rupestris,* with Poceae, *Artemisia* and Cyperaceae. Notable are the high values of *S. rupestris*, which is typical of LGM assemblages and is associated with cold, dry environments.

The regional pollen signal indicates a typical (for Beringia) cold and dry environment during Marine Isotope stages 3 and 2. The local pollen records at Ice Bluff indicate more shrubs on the landscape than is typical, but they also show a clear signal of taxa indicating cool, dry conditions (e.g. *S. rupestris*). No pollen records in Chukotka indicate a short-lived LGM cold event, but they are generally poorly resolved temporally. Both pollen and insects indicate cool, moist conditions through much of the record, the insects alone indicate a short-lived cold event centred on 21 ka. Both pollen and insects from the lateglacial interval indicate an increasing importance of shrubs and the disappearance of the steppe-tundra communities.

5.5. Comparison of MIS 3-2 faunas with those from other regions of Beringia

A comparison of the late Pleistocene insect faunas of the different regions of Beringia is shown in Table 3 and Fig. 6. As eastern Beringian records in particular tend to be discontinuous, the table does not provide complete coverage of all regions for all periods. There are, however, evident geographic patterns in the data, especially across western Beringia, and these may reflect climatic patterns that are differently distributed from those of today. The Lena Delta localities reflect colder conditions during the LGM than the eastern regions (modern Yana-Indigirka and Kolyma Lowlands, Western Chukotka). Main River (Central-southern Chukotka) is likewise different from the other regions, but shows more similarity to the Lena Delta than to Western Chukotka.

Pre-LGM cooling is evident on the Lena delta, and less evident in Central-southern Chukotka, given the variable proportions of arctic insects at Main River, whereas the records from the Yana-Indigirka lowland (Pitul'ko et al., 2007) and Aleshkina Zaimka in the Kolyma lowland (Kiselev, 1981) reflect a typical steppe-tundra environment with no evidence of change. East Beringian records are poor for this time period. Unfortunately, J. Matthews, who pioneered the study of fossil insects in eastern Beringia, tended not to record the numerical abundance of fossils in his samples (further study of his collections would prove useful). Single insect assemblages (Matthews and Telka, 1997) suggest that cooling was not pronounced. The species lists from Rock River (∼25 ka B P) and Mayo Indian Village (26.9 ka B P) show an absence of arctic insects. Moreover, the Rock River assemblage contains three species of bark beetles—clear forest indicators.

A representative insect fauna from Goldbottom Creek, Klondike area, Yukon, (dated 25.3 ka BP) studied by SK (Zazula et al., 2006a) reflects a steppe-tundra environment with sharp domination, of steppe insects. This fauna has one of the highest steppe content (up to 52% of the fauna) of all insect assemblages in Beringia (Fig. 6).

A cooling associated with the LGM (here defined as the period centred on 21 ^{14}C ka) is observed in the insect fossil record from the Lena Delta (two localities: Bykovsky Peninsula (Sher et al., 2005) and Kurungakh Island (Wetterich et al., 2008)). The insect fauna dated to ∼18 ^{14}C ka from Seward Peninsula (Kuzmina et al., 2008), has a "cold" character compared with the regional record (Matthews, 1974; Matthews and Telka, 1997). We also observe a brief cooling in Central-southern Chukotka at the Main River. However, the record from Aleshkina Zaimka, Kolyma lowland (Kiselev, 1981) shows no traces of cooling.

The cold spike in the Main River assemblages is less pronounced and "the cold" interval is shorter (as it is defined primarily by one fossil sample) compared with the Lena delta curve (Fig. 6). At Bykovsky Peninsula (Sher et al., 2005), the dating is slightly different, with the coldest fauna dated to 19–17 ka, whereas at Ice Bluff it is at 21 ka. There are also other differences. Cold-resistant insects are less abundant in Chukotka, with the arctic group represented here mostly by the weevil *I. arcticus*, while cold-resistant insects are more diverse at Bykovsky. On the other hand, the species diversity in groups other than the arctic groups is greater in Chukotka. This could indicate a less severe environment during LGM in central-southern Chukotka compared with Lena Delta region, which would not be surprising, given the Lena Delta is situated much further north (Fig. 1). It is likely that climate factors other than latitude may influence this pattern, however, as Aleshkina Zaimka and Yana River are also much further north (Fig. 1), but their fossil insect assemblages do not display the dominance of arctic elements that characterize the Lena Delta assemblages, including in the pre-LGM samples (Fig. 6). It may be that the westward location of the Lena Delta, being that much closer to the influence of Scandinavian Ice Sheet, meant the region experienced more intensely cold conditions with less summer warming than regions further from the ice.

5.5.1. Implications for late Quaternary trans-Beringian migrations

It has been suggested that a mesic environment characterized the Bering Land Bridge, forming a moisture-controlled filter, or even a barrier, to migration of the steppe-adapted species during the late Pleistocene, particularly the LGM (Guthrie, 2001; Elias and Crocker, 2008). Study of submarine sediments has led to reconstruction of both shrub tundra (Elias et al., 1996) and dry tundra (Ager and Phillips, 2008); these differences may reflect both differential sampling of a spatial mosaic and the reliability of dating. Nevertheless, palaeoclimate models tend to simulate more moisture on the land bridge due to its (relative) proximity to the North Pacific (Braconnot et al., 2007). The reconstruction of a steppe-tundra environment strongly influenced by cool but mesic tundra elements in the landscape mosaic at Main River, if representative of the regional pattern, would indicate that moist environments extended into southern Chukotka, as part of a larger central region that may have been cooler and moister than the more continental extremes of Beringia.

We did not find any North American species in the Pleistocene fossil record at Main River that are unknown from other parts of West Beringia, whereas the modern insect fauna contains some American migrants. For example, the American weevil *L. lineaticollis* Kby, which is common in the Pleistocene of eastern Beringia, is found on Chukotka (Berman et al., 2002), but it was not found in the Pleistocene Chukotkan faunas. Perhaps this beetle reached Chukotka only during the Holocene or has been introduced

Table 3

Comparison of the Middle-late Weichselian environment in different regions based on fossil insect assemblages.

Age (th yr BP)	Western Beringia					Bering Land Bridge	Eastern Beringia				
	Lena Delta 71°–72°N 126°–129°E	Yana River 71°N–135°E	Kolyma River basin 64°–68°N 158°–162°E	West Chukotka 69°N–167°E	Ice Bluff 64°N–171°E		Seward Peninsula 66°N–164°W PB	West-central Alaska CC 63°N–156°W	North Slope of Alaska 70°N–155°W	Northern Yukon 67°–68°N–137°–140°W	Central Yukon 64°N–136°–139°W
15–12.5	Steppe-tundra 2+++; 1+; 5±	No record	AZ 101: 13–14 ka (64°N–58°E) Warm steppe-tundra 2+++; 1+++; 5–	No record	No record		No record		No record	P-hh75-9: 13.5 ka (67°N–137°W) Steppe-tundra with forest elements	No record
24–15	Cold steppe-tundra 5 +++; 1,2±	Steppe-tundra 2+++; 1+; 5±	AZ 102: 16–17 ka Steppe-tundra 2+++; 1+; 5± K: 18 ka (68°N–162°E) steppe-tundra 2++; 1++; 5±	No record	Cold steppe-tundra 5+++; 2+; 1–	20–14 ka Mesic tundra 3–; 4–; 5–	18 ka Steppe-tundra 4+++; 5+; 3–	16 ka steppe-tundra and mesic tundra 4+; 3–; 5–	No record	B-1: 20 k (67°N–139°W) Steppe-tundra 4; 3–; 5–	No record
34–24	Cold steppe-tundra with unstable arctic component 5+++; 2+; 1+	Steppe-tundra 2+++; 1+; 5–	No record	M: 32.8 ka Steppe-tundra 2+++; 1+; 5+	Steppe-tundra with unstable steppe component 2++; 5 ±; 1–		No record		T: 30–31 ka steppe-tundra 3,4; 5–	BB: 25.4 ka (67°N–137°W) Steppe-tundra with 4 and forest elements CRH32: 31,3 ka (68°N–140°W) steppe-tundra 4++; 3±; 5–	GB: 25.3 ka (64°N–39°W) Steppe-tundra 3+++; 4±; 5– MI:26.9 ka (64°N–36°W) Steppe-tundra 3,4; 5–

AZ – Aleshkina Zaimka; K – Krasivoe; M – Milkera River; T – Titaluk River; P-Upper Porcupine Basin; B – Bluefish River Basin; BB-Bell River Basin; CRH – Old Crow River; M I – Mayo Indian Village, GB – Goldbottom Creek, CC – Colorado Creek.

1 Stephanocleonus spp.; 2 Morychus viridis; 3 Connatichela artemisiae; 4 Morychus sp; 5 arctic group.

+++ dominant; ++ important; + significant; ± rare; – absent.

Fossil insect assemblages are from: Lena Delta (Sher et al., 2005; Wetterich et al., 2008); Yana River (Pitul'ko et al., 2007); Kolyma River Basin and West Chukotka (Kiselev, 1981; Kiselev and Nazarov, 2009); Ice Bluff current research; Bering Bridge and West-central Alaska (Elias and Crocker, 2008); Seward Peninsula (Kuzmina et al., 2008); North Slope of Alaska, Northern and Central Yukon (Matthews, 1983; Matthews et al., 1990; Matthews and Telka, 1997; Zazula et al., 2006a).

recently. Curiously, then, the relative proximity to North America in the Pleistocene appears not to have influenced the Chukotkan insect fauna during the late Pleistocene.

There are several true steppe insects in western Beringian faunas but only one in eastern Beringian faunas (the weevil *Connatichela artemisiae)*. A lower contribution of formal steppe species is typical also for East Beringian steppe-tundra assemblages; this feature can be explained biogeographically, in that the Laurentide and Cordilleran ice sheets restricted migration from the south. The steppe niche was probably occupied here by other xerophilous species that are not specific to steppe – the general xerophilous component in the east Beringian insect faunas is higher than those of Chukotka. Xerophilous taxa from eastern Beringia are not apparent at Main River; this therefore suggests that eastern Beringian taxa were precluded from reaching Chukotka across the land bridge.

There are of course multiple factors that influence transcontinental migrations, including, probably, chance. Despite the land bridge, the insect fauna of the Old and New Worlds show different patterns and migration was apparently limited. While the arctic weevil *I. arcticus* is recorded from both parts of Beringia (Matthews and Telka, 1997; S. Kuzmina, unpublished data), the most abundant component of the insect communities at Main River, *M. viridis*, is represented in East Beringian fossil insect faunas by its close relative, a different, undescribed, and probably extinct species of *Morychus* (for example, the Anadyr site (close to the mouth of Anadyr River not far from Anadyr Town) contains *M. viridis*, while the fauna of Seward Peninsula, western Alaska contains the American *Morychus* sp.; Matthews, 1974; Kuzmina et al., 2008; Kuzmina, unpublished). The border between the ranges of these closely related species most likely lay right on the land bridge, and that the Siberian species did not cross eastwards (or visa versa) might argue for a lack of suitable habitats on the land bridge. These disparate patterns are explored further by Elias and Crocker (2008), who conclude that a moist land bridge was a 'leaky filter' at best for insects. See more discussions in Berman et al. this volume.

6. Conclusions

The Main River site provides diverse insect assemblages from MIS 3 and 2 in south-central Chukotka. These are markedly different in composition from those described from western localities in the more continental regions of western Beringia. In particular, dry-, mesic- and shrub-tundra taxa characterize the steppe-tundra mixture, rather xerophilous or steppe species, which are more typical of many records from this period in eastern and western Beringia, respectively. While the local records may partly reflect conditions in the Main River Valley and the influence of nearby thermokarst lakes, which may have been characterized by locally moister environments than the surrounding landscape (for example a greater than usual presence of shrub-tundra), the lack of many steppe or xerophilous taxa suggests a cooler, moister environment generally. This appears to support the notion of moist of conditions here and on the adjacent land bridge, influenced perhaps by proximity to the North Pacific.

The hypothesis that mesic tundra on the Land Bridge formed a barrier for migration of dry-adapted species is certainly not refuted by this record from the western limit of the land bridge. However, the past and present patterns of species distribution across Beringia are complex, and not all are explained by a moisture-related filter. In order to obtain a better understanding of both the environmental conditions and patterns of migration during the late Pleistocene and especially the LGM, it would be advantageous to retrieve more dated insect records, particularly in key regions, such as the Yana-Indigirka and Kolyma lowlands, western Chukotka, and the coastal region of East Chukotka and from the terrestrial sediments of the Bering Land Bridge itself, as these records provide a more detailed perspective on Beringian palaeoenvrionments than does, for example, pollen.

A particular feature of the Main River expedition was the collection of samples for ancient DNA analysis. New techniques (Sønstebø et al., in press) promise that a detailed floristic record can be obtained from yedoma sediments such as those at Main River; we will address this in a forthcoming paper that also reflects Andrei Sher's commitment, via new collaborations, to learn more about Beringia by adopting promising new techniques.

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