ISSN 0031-0301, Paleontological Journal, 2015, Vol. 49, No. 7, pp. 679–867. © Pleiades Publishing, Ltd., 2015.

Quaternary Insects and Environment of Northeastern Asia

S. A. Kuzmina
Borissiak Paleontological Institute, Russian Academy of Sciences, Profsoyuznaya ul. 123, Moscow, 117997 Russia
e-mail: svkuz@yandex.ru

Received November 15, 2013

Abstract—Quaternary fossil insects from different sites of western Beringia (northeastern Asia) provide evidence of unique steppe–tundra environment. This was mostly treeless landscape occupied by mixture of steppe and tundra insect species. Insect assemblages reflect climate variations during the Pleistocene and Holocene. Classification of insect communities is helpful for comparison of records from different sections and regions. Comparison of insect faunas from northeastern Asia and northwestern North America shows that, despite climatic and environmental similarity on both sides of Beringia, migrations though the Bering Bridge were restricted, especially for xerophilous insects. The barrier was wider than the Bering Strait; it also included the eastern regions of the Chukotka Peninsula. The paper contains 35 figures, 6 insect photographs, 5 text tables, and 38 tables with insect lists from 17 Pleistocene and 9 Holocene sites from the Lena delta and Novosibirskie Islands in the west to east Chukotka Peninsula in the east of western Beringia.

Keywords: Quaternary insects, Beringia, steppe–tundra, environment reconstruction

DOI: 10.1134/S0031030115070011

CONTENTS

INTRODUCTION

Northeastern Asia is probably the most interesting land in the Arctic and Subarctic area. This land has never been covered by ice sheets in the Pleistocene and we have an uninterrupted fossil record of environmental changes for the last million years. A peculiar continental climate in the high latitudes gave rise to a unique long-lived ecosystem, mostly treeless grassy landscape, which was a habitat for tall herds of grazers and numerous small animals. Permafrost provides excellent preservation of fossils, so that, despite remoteness from the main research centers, northeastern Asia always attracts attention of paleontologists from Ivan Chersky to our contemporaries. Some relict plant and insect communities survived here until recently.

The stratigraphy of the Quaternary deposits in northeastern Asia is based on three main methods: evolutionary changes in large and small mammals, radioisotope method, and climate stratigraphy. Other methods, such as tephrachronology, thermoluminescence, paleomagnetic, and others could be useful for some parts of the region and geological units, but have a secondary importance. Each method has certain disadvantages. Thus, the evolutionary method does not work in Late Pleistocene deposits; the most popular radiocarbon method works only for the last 50 thousand years. Climate stratigraphy is widely used in Quaternary geology. Dramatic climate changes during the last two million years provides paleoclimatic markers, which are helpful in stratigraphy, but cyclicity of the process complicates the study on the larger scale.

The climatic methods work well in coordination with other methods of Quaternary stratigraphy. Traditionally, the main method of climatic reconstruction is based on pollen and spore studies (Godwin, 1934, Davis, 1963, Birks and Birks, 1980). Insects have been used as a climate-related stratigraphic tool in Quaternary since pioneering works of Coope in the United Kingdom (Coope, 1959, 1961). At present, the method is well developed and widely used in many countries (Elias, 1996, 2006; Kiselev, 1987), but it is still less popular than botanical studies.

Fossil insect studies play an important role in multidisciplinary research of this region and environmental reconstructions. In addition to climate stratigraphy, insects provide information on paleobiogeography, evolution, development of ecological crises, and many other fields.

Fossil insects have been studied from numerous sites of western Beringia (northeastern Asia) and eastern Beringia (northwestern North America) (Fig. 1) (Kuzmina and Matthews, 2012). This paper reports some results of a long-term study in northeastern Asia. The history of fossil insect research in the region has already been described by Kiselev (1981) and Kiselev and Nazarov (2009). The present study provides information about fossil insects from several new sites, figures of fossil insects, and some new discussion.

CHAPTER 1. METHODS OF THE QUATERNARY INSECT RESEARCH

Quaternary insects are mostly represented by modern species, so that it is impossible to use them as traditional fossils (evolutionary stratigraphy), but gives an excellent opportunity for paleoenvironment reconstructions (Coope, 1994). Insects are preserved in various Quaternary deposits. The most common and best preserved group is beetles (Coleoptera) because of their abundance and hard chitin exoskeleton. Other insects are occasionally found in Quaternary deposits, but less important for environment reconstructions. We usually work with beetles, ants, and a few true bug species.

Quaternary fossil insects are rarely concentrated in deposits. Researchers apply different methods of field sampling and laboratory proceeding. In the field, we can take a bulk sample (more than usual size) or screen great volume of sediments. Screening is not necessary if the sediment is rich in insects. This rare case of accumulation may be caused by specific reasons and looking for bulk samples can provide a distortion in representativeness. For example, ice wedge casts usually accumulate organic matter, including insects. Units with ice wedge casts become better sampled; insects from the sections reflect only warm conditions of the time of permafrost melting.

Screening can give good results even for deposits poor in organics. This method allows detailed sampling of the whole section and creates a sequence of "cold" and "warm" insect assemblages. Screening in the field also reduces the weight of a sample which becomes incredibly important for transportation in remote areas.

Laboratory proceeding also varies. Some researchers prefer flotation in light liquids (see description in Elias, 1996; Bidashko, 1987), others pick up insects without flotation. We tried both methods. Flotation works well for tiny insect remains, but many large and heavy fragments may be missed. Insects from the permafrost are usually well preserved and many fragments are large and heavy; in an experiment, most of fragments were missed. Thus, it is impossible to apply flotation for samples from northeastern Asia.

1a. Analysis of Fossil Insect Assemblages, Ecological Groups

The species composition of fossil insect assemblages from the Pleistocene of northeastern Asia is rather monotonous. The assemblages differ from each other mostly in the relative abundance of specimens of certain taxa. That is why we, following Kiselev (Sher et al., 1979; Kiselev, 1981), use a quantitative approach to estimation of faunal and environmental changes through the time. We divide all species into a number of ecological groups according to their preferred modern habitats and count the total number of individuals belonging to all species in each group. This approach allows us to compare assemblages within a section rather than different sequences, recognize the major and minor fluctuations, correlate them, and trace environmental changes.

The following 13 main ecological groups are recognized:

1. Steppe (**st**). Members of this group presently inhabit the steppe zone; some occur in the mountain belt of southern Siberia and Mongolia. Some survived under special microclimatic conditions in the relict steppe patches in northeastern Asia. However, the presence of any of these species is evidence of a rather high summer temperature (Alfimov and Berman, 2001; Alfimov et al., 2003). The group includes the ground beetles *Harpalus pusillus* Motsch., *Cymindis arctica* Kryzh. et Em., the leaf beetles *Chrysolina perforata* Gebl., *Ch. brunnicornis bermani* Medv., *Galeruca interrupta circumdata* Duft., the weevils *Stephanocleonus eruditus* Faust, *S. fossulatus* F.-W., and *S. incertus* T.-M.

2. Meadow–steppe insects (**ms**). This group consists of species common in dry (steppe-like) meadows in various natural zones. They are more tolerant of cold than the previous group. At present, they survive even in the tundra zone, in the warmest spots. The group includes the ground beetle *Harpalus vittatus kiselevi* Kat. et Shil, the soft-winged beetle *Troglocollops arcticus* L. Medv., the leaf beetle *Chrysolina arctica* Medv., the weevils *Phyllobius kolymensis* Kor. et Egorov, *Coniocleonus cinerascens* Hochh., *C. ferrugineus* Fahr., and *C. astragali* T.-M. et Kor.

3. Insects of hemicryophytic steppe (**ss**). Hemicryophytic steppe (Yurtsev, 1981) is a cold steppe-like environment, dominated by a few species of xerophilous sedge and moss. It has extremely contrasting microclimatic conditions, very hot and dry in summer and snowless and very cold in winter. The hemicryophytic steppe occurs on the very dry snowless hill tops in the taiga zone or, rarely, in the tundra zone (Berman et al., 2001a). This environment, currently found in the Kolyma Highlands, Chukotka Peninsula, and Wrangel Island, is believed to have much in common with some variants of the Pleistocene tundra–steppe. This group includes only one species, the pill beetle *Morychus viridis* Kuzm. et Kor.

4. Xerophilous insects of various habitats (**xe**). This group includes some widespread species of xerophilous habitats in tundra, taiga, and steppe, such as the ground beetle *Notiophilus aquaticus* L., the dung beetle *Aphodius sp*. (probably an extinct species), and others.

5. Insects of dry tundra habitats (**dt**). The insects of this group usually occupy the best-heated sites in the tundra zone, most commonly well drained, with diverse grasses and herbs. Most of these species do not reach the arctic tundra today, but quite often enter the taiga zone along suitable biotopes. Some species also occur today in relict steppe patches. The group includes the ground beetles *Bembidion dauricum* Motsch., *Poecilus* (*Derus*) *nearcticus* Lth., *Pterostichus* (*Petrophilus*) *abnormis* Sahlb., *P.* (*Tundraphilus*) *sublaevis* Sahlb., *Stereocerus haematopus* (Dej.), *Curtonotus alpinus* Payk., *Amara interstitialis* Dej., *A. glacialis* Mnnh., *Dicheirotrichus mannerheimi* Sahlb., the leaf beetle *Chrysolina marginata borealis* Medv., the weevils *Mesotrichapion wrangelianum* Kor., *Hemitrichapion tschernovi* T.-M., *Sitona borealis* Kor., *Hypera ornata* Cap., *H. diversipunctata* Schrank., *Lepidophorus thulius* (Kiss.), and others. Some species from the subgenus *Pterostichus* (*Cryobius*) apparently belong to this group, but species identification is often uncertain here and we have to include all species of the subgenus to the succeeding group.

6. Insects of typical and Arctic tundra (**tt**). This group includes the most cold-resistant species from different habitats in the Arctic, such as the leaf beetles *Chrysolina tolli* Jac., *Ch. subsulcata* Mnnh., *Ch. bungei* Jac., the weevil *Isochnus arcticus* Kor.

7. Insects of mesic tundra habitats (**mt**). The insects of this group are presently found in different, mostly wet and relatively cold habitats in tundra; some occur in boggy patches in forest–tundra. The group includes the ground beetles *Carabus truncaticollis* Esch., *Blethisa catenaria* Brown, *Diacheila polita* Fald., *Pterostichus* (*Cryobius*) *ventricosus* Esch., *P.* (*Cryobius*) *pinguedineus* Esch., *P.* (*Cryobius*) *brevicornis* (Kirby), *P.* (*Lenapterus*) *vermiculosus* Men., *P.* (*Lenapterus*) *costatus* Men., *P.* (*Lenapterus*) *agonus* Horn., small carrion beetle *Cholevinus sibiricus* (Jean.), the rove beetles *Olophrum consimile* Gyll., *Tachinus arcticus* Motsch., *T. brevipennis* Sahlb., and the leaf beetle *Chrysolina septentrionalis* Men. Some species of the subgenus *Pterostichus* (*Cryobius*) apparently should be added to the **dt** group, but species identification is often not clear and we have to include all species of this subgenus to the **mt** group.

8. Shrub inhabitants (**sh**). These beetles feed on shrubs, mostly willows, except for dwarf shrubs of typical and Arctic tundra. The group includes the leaf beetles *Chrysomela blaisdelli* Van Dyke, *Phratora polaris* Schn., *Ph. vulgatissima* L., the weevils *Lepyrus nordenskioeldi* Faust, *L. gemellus* Kirby, *Dorytomus rufulus amplipennis* Tourn., and *Isochnus flagellum* Erics.

9. Insects of meadows (**me**). Insects of this group live mostly in the forest zone, although some species occur in tundra meadows. The group includes the pill beetles *Byrrhus fasciatus* Forst., *Cytilus sericeus* Forst., the click beetle *Berninelsonius hyperboreus* Gyll., the leaf beetles *Bromius obscurus* L., *Phaedon concinnus* Steph., *Ph. armoraciae* L., the weevils *Phyllobius virideaeris* Laich., and *Sitona lineellus* Bonsd.

10. Plant litter inhabitants (**pl**). The group includes insects of intrazonal habitats, such as plant litter, or

fungi. These species could be an indirect indicator of tall shrub, forest–tundra, and forest environments. There are beetles mostly from the families Leodidae (*Cyrtoplastus irregularis*) Rtt., Lathridiidae (*Corticaria* sp.), and Staphylinidae (*Eucnecosum* sp., *Lathrobium* sp., *Quedius* sp.).

11. Forest insects (**fo**). The group includes tree-associated insects and insects restricted to the taiga zone in their distribution, such as the ground beetle *Pterostichus* (*Petrophilus*) *magus* Man., the click beetle *Denticollis varians* Germ., the weevils *Hylobius piceus* DeG., *Pissodes insignatus* Boh., *P. irroratus* Reitt., the bark beetles *Ips cembrae* Heer, *Polygraphus* sp., the ants *Leptothorax acervorum* Fabr., *Formica gagatoides* Ruzs., and *Camponotus herculeanus* L.

12. Riparian insects (**ri**). These insects live near water in several zones, but most of them are restricted to the taiga zone. The group includes the ground beetles *Pelophila borealis* Payk., *Nebria frigida* Sahlb., *Elaphrus lapponicus* Gyll., *E. riparius* L., *Dyschiriodes melancholicus* Motsch., *Bembidion umiatense* Lindrt., *Agonum quinquepunctatum* Motsch., the rove beetles *Stenus spp*., the ladybird *Hippodamia arctica* Schneid., the leaf beetles *Donacia* sp., *Hydrothassa hannoverana* F., the weevils *Phytobius leucogaster* Marsh., *Notaris bimaculatus* F., and true bugs of the family Saldidae.

13. Aquatic forms (**aq**). These insects live in various tundra and taiga water bodies, mostly in small ponds. The group includes all species of predaceous diving beetles and whirligig beetle families, the aquatic scavenger beetles *Helophorus splendidus* Sahlb., *Hydrobius fuscipes* F., and the aquatic bug *Sigara* sp.

14. Others (**oth**). The group includes fossils impossible to identify to species (of genera comprising ecologically different members) or ecologically neutral species, such as some ladybirds or carrion beetles.

Calculation. In the burial, the beetle body is frequently divided into the head, pronotum, two elytra, and, sometimes, abdomen sclerites. This division may result in overestimation of the number of individuals, especially for abundant and common species. To avoid this, we calculate the *minimum number of individuals* (MNI), i.e., the number of beetles which can provide these remains (Elias, 1994). One head, one pronotum, left and right elytra should belong to one beetle if their color and size are similar. Otherwise (for example, left elytron is 3 mm, but right elytron is 3.1 mm), we take them for different beetles. The tables show MNI; the number of fossil specimens is usually greater. All insects (MNI) from one ecological group are summed up; the final graph shows the percent of each group. This is a very simple method, but it works well for our purposes.

The next step is comparison of different insect assemblages, revelation of zoogeographical and stratigraphical patterns. Fossil insect assemblages in the area under study are very monotonous. We deal with about 200 common species (Kuzmina and Matthews, 2012); the species are mostly long–lived, at least from the Early Pleistocene to Recent and most of the studied assemblages are similar in species composition (Kiselev, 1981). It is impossible to recognize cold and warm stages by key species, which is usual practice in Europe (Clark and Edwards, 2004; Coope, 1990; Whitehouse, 2006) and southern part of Canada (Morgan, 1972; Morgan et al., 1986). In the arctic and subarctic regions of North America and Asia, the situation is significantly different. The group of the core species is more or less the same, but insect assemblages differ in the proportion of ecological groups. This method of comparison of the ecological group proportions was proposed by Matthews (1983) for Alaska and Yukon faunas and developed by Kiselev. For example, a fauna from a cold stage is dominated by tundra species, but additionally includes steppe and sometimes single forest species. A fauna from a warm stage is dominated by forest insects, but includes tundra and single steppe species. We can recognize these two stages using the proportions of ecological groups instead of the presence or absence of the key species.

All insect assemblages from the northeastern Asia display common features. This is primarily the presence of a number of rare species which played a much more important role in the Pleistocene. These are the ground beetle *Poecilus nearcticus,* the pill beetle *Morychus viridis*, the leaf beetle *Chrysolina arctica*, the weevil *Lepidophorus thulius,* and some others. We also see a number of species recently occurring in steppes and absent in tundra, such as the weevils *Stephanocleonus incertus, S. tricarinatus,* and others. Many species from the Pleistocene insect community were discovered in relict steppes of northeastern Asia (Berman, et al., 2001a, 2011): *Cymindis arctica, Stephanocleonus eruditus, S. fossulatus*, *Chrysolina brunnicornis,* and others. We can definite these steppe or steppe in origin species as steppe–tundra indicators. These species are usually present in our fossil assemblages, but absent is some samples.

At the same time, the Pleistocene insect fauna always includes typical tundra species, such as the ground beetles *Pterostichus* (*Cryobius*) spp., *Curtonotus alpinus,* the leaf beetle *Chrysolina septentrionalis*, the rove beetle *Tachinus arcticus,* and many others.

Most of insects in the assemblage usually belong to the main groups: **ss, dt,** and **mt**. A high percentage of **st, ms**, and **tt** groups have only been recorded in a part of assemblages. The groups **xe, me, sh,** and **oth** have never played an important role in Pleistocene faunas. The proportions of the groups **fo, ri**, and **aq** are usually low, becoming greater in interglacial faunas. Some forest insects are found in many Pleistocene assemblages, not only in the interglacial ones.

1b. Dominant Types of Pleistocene and Early Holocene Faunas

According to our observation, the proportions of different ecological groups in assemblages are more or less uniform. Several types of ancient insect faunas that are helpful in environment reconstructions are recognized.

These types are designated by four letters, the first two indicate mostly the tundra-like (**TU**) or steppe–tundra (**S-T**) types of community; the last two indicate subtypes. The most common types of Pleistocene and early Holocene faunas are as follows:

1. Tundra/tundra type (**TU/TU**). The assemblages of this type do not include steppe–tundra indicators.

2. Tundra/xerophilous type (**TU/XE**). Some species exotic for modern tundra are present here, such as the pill beetle *Morychus viridis,* and meadow–steppe species, but thermophilous steppe insects are absent. This type is dominated by tundra species; *M. viridis* and meadow–steppe insects play a secondary role.

3. Tundra/steppe–tundra type (**TU/S-T**). This type is close to the previous one, but the steppe group is present. The role of steppe–tundra indicators is not very high; the sum of the groups ss, ms, and st is less than 30%.

4. Steppe–tundra/steppe–tundra type (**S-T/S-T**). The sum of the groups ss, ms, and st is more than 30%.

5. Steppe–tundra/meadow–steppe type (**S-T/MS**). The group meadow–steppe makes up more than 30%. Other steppe–tundra indicators are also present.

6. Steppe–tundra/hemicryophytic steppe type (**S-T/SS**). This type is strongly dominated by *Morychus viridis,* more than 50%.

7. Steppe–tundra/steppe type (**S-T/ST**). Thermophilic steppe insects play a relatively high role in this type, comprising more than 20%.

This classification is based primarily on experience rather than on formal features. Different groups take part in insect faunas differently. For example, steppe insects have never dominated in the studied fossil assemblages; 20% of **st** is an appreciable share for this group. At the same time, the proportion of 20% of the **ss** group is a relatively low value; this group sometimes reaches 80% of individuals in particular assemblages. We do not consider forest faunas, because they are extremely rare in the samples studied, paying attention to the most frequent faunas of treeless landscapes, which were widespread in eastern Beringia during the Pleistocene. This classification is useful for some evident and various steppe–tundra insect assemblages, which were observed mostly in the Kolyma and Yana–Indigirka lowlands. The classification is less meaningful in the case of uniform tundra-like (with occasional steppe elements) communities in the marginal parts of the studied region, such as the Laptev Sea coast or eastern Chukotka Peninsula. We do not use the classification for Holocene faunas, where the influence of steppe–tundra environment has become weak. The main goal of the above classification is gaining an understanding of the dynamics of specific grassy community of steppe–tundra rather than all kinds of environments, which have ever existed in the area studied.

Like any classification in a certain field of paleoecology, this one is open for criticism. The only reason why we propose it here is pragmatism. We need some sort of classification for extensive material with a lack of clear standards and the main explanation is intuition of an expert. This is not the first attempt to create a classification of steppe–tundra insect communities (Kuzmina, 1989; Kuzmina and Ponomarenko, 2001) and, probably, not a last one. For this study, the above classification works are better than others.

CHAPTER 2. STRATIGRAPHY AND LOCALITIES

2a. Development of a Stratigraphic Scheme of the Northeastern Asia

Quaternary stratigraphy remains an open question. The lower boundary of the Quaternary changed during the last 30 years and its time mark is presently much older than was previously thought. This circumstance causes confusions in interpretation of the results of fossil insect studies. We have to pay attention to the year of publication and the contemporary Quaternary stratigraphic scale.

The lower border of the Quaternary was considered by different researchers as 2.5 Ma, 1.8 Ma, or 0.7–0.8 Ma. Russian scientists followed the resolution of the Interdepartmental Stratigraphic Committee of the USSR (ISC USSR) from 1964, which considers the base of the Quaternary at 0.7–0.75 Ma; this scheme was used in the stratigraphy of northeastern Asia (Arkhangelov, 1977; Sher, 1971, 1979, 1984, 1997a; Sher et al., 1979, 1987). Unified Regional Stratigraphic Scheme for the Yana–Kolyma Lowland and its mountainous surroundings (Sher et al., 1987) accepted the base of the Pleistocene at 0.7 Ma.

Later, in 1989, ISC USSR decided to increase the volume of the Quaternary up to 1.6 Ma. Problems of correlation of the Soviet stratigraphic scheme and the international one forced ISC USSR in 1994 to change the scheme as follows: 1. The Quaternary System is divided into two series, the Pleistocene (1.6–0.01 Ma) and the Holocene (from 0.01 Ma). 2. The Pleistocene is divided into two subseries, the Eopleistocene (1.6–0.8 Ma) and Neopleistocene (0.8–0.01 Ma). 3. The Eopleistocene is divided into two substages, upper and lower, the Neopleistocene consists of three substages, upper, middle, and lower. The most recent Russian stratigraphic scheme (approved by the Russian Quaternary Commission (MSK) in 2007, see Borisov, 2007) accepted the base of the Pleistocene at 1.806 Ma (Calabrian), but proposal of its correction according

Table 1. Correlation of the Quaternary stratigraphic scales

<table>
<tr><th rowspan="2">Age (Ma)</th><th colspan="9">Scales, used in USSR and Russian works</th><th rowspan="2">Formation, horizon Kolyma Lowland</th></tr>
<tr><th colspan="2">Modern</th><th colspan="3">1994–2007</th><th colspan="2">1989–1994</th><th colspan="2">1964–1989</th></tr>
<tr><td>–</td><td colspan="2">Holocene</td><td colspan="3">Holocene</td><td colspan="2">Holocene</td><td colspan="2">Holocene</td><td>Holocene</td></tr>
<tr><td>0.01</td><td rowspan="7">Pleistocene</td><td>Upper</td><td rowspan="6">Pleistocene</td><td rowspan="3">Neopleistocene</td><td>Upper</td><td rowspan="6">Pleistocene</td><td>Upper</td><td rowspan="3">Pleistocene</td><td>Upper</td><td>Aleshkina, Edoma formations, Kuobakh Beds</td></tr>
<tr><td>0.12</td><td rowspan="2">Middle</td><td>Middle</td><td>Middle</td><td>Middle</td><td>Maastakh Formation
Alazeya Beds, Segreev Creek Beds?</td></tr>
<tr><td>0.5</td><td>Lower</td><td rowspan="4">Lower</td><td>Lower</td><td>Oler Formation (Akansky Horizon)</td></tr>
<tr><td>0.78</td><td rowspan="4">Lower</td><td rowspan="3">Eopleistocene</td><td rowspan="3">Lower</td><td colspan="2" rowspan="5">Neogene</td><td rowspan="5">Oler Formation (Chukochinsky Horizon)
Kutuyakh Beds
Begunov Formation</td></tr>
<tr><td>1.24</td></tr>
<tr><td>1.8</td></tr>
<tr><td>2.5</td><td colspan="3" rowspan="2">Neogene</td><td colspan="2" rowspan="2">Neogene</td></tr>
<tr><td></td><td colspan="2">Neogene</td></tr>
</table>

Table 2. Correlation of the stratigraphic units across western Beringia

Kolyma Lowland	Yana–Indigirka Lowland	Laptev Sea coast and Lena delta
Q_{3al} Aleshkina Formation Q_{3yed} Edoma Formation	Q_{3yed}, Q_{3vor} Vorontsov Formation	Q_{3ya} Yana Formation Q_{3ovg} Oiagoss Formation
Q_{3kb} Kuobakh Beds (intergl.)		$Q_{3kr\text{-}yu}$ Krest-Yuryakh Formation
Q_{2ms} Maastakh Formation Segreev Creek Beds?	Q_{2ke} Keremesit Superhorizon Q_{2ch} Chroma Formation Q_{2d} "*Dycrostonyx*" Beds	Q_{2kch} Kuchchugui Formation Q_{2zim} Zimov'e Beds Q_{2yuk} Yukagir Formation $Q_{2?bul}$ Bulukur Formation
Q_{2alz} Alazeya beds (intergl.)	Q_{2ach} Achchagy Formation Q_{2all} Allaikha Formation Q_{2ut} Utkinskii Beds	
Q_{2ak} Oler Formation, Akansky Horizon	Q_{2ak}	
Q_{1ch} Oler Formation, Chukochinsky Horizon	Q_{ich}	
$N_2Q_{1?kut}$ Kutuyakh Beds N_{2be} Begunov Formation		

to the international scheme is in discussion (Borisov, 2009).

The modern international stratigraphic scheme for the Quaternary (Gibbard and Head, 2009a, 2009b) put the base of the Quaternary lower, at 2.58 Ma; and the most recently, at 2.5 Ma (Gibbard and Head, 2010). We follow this decision.

The main stratigraphic units of the region under study were described in the Kolyma Lowland (Sher, 1971, 1979, 1984). These units are most completely characterized by rodent and large mammal fossils, pollen, seeds, and insects. Other regional schemes are correlated with the Kolyma Lowland (Tables 1, 2). The dates of the units were corrected according to the modern stratigraphic scheme.

2b. Stratigraphy of the Studied Areas

Miocene

The oldest Neogene–Quaternary insects from western Beringia come from two sites, Ary-Mas (Berelekh River Basin, left of the Indigirka River) and a borehole on Letyatkin Cape, Kolyma Lowland (Fig. 1) (Arkhangelov et al., 1979; Elias et al., 2006; Kiselev and Nazarov, 2009; Ovander and Rybakova, 1985). Fossils are not numerous, only one sample from Ary-Mas is sufficiently representative; it includes mostly hygrophilous species. Some specimens probably belong to extinct species.

Pliocene

The Pliocene Begunov Formation is known from a section at the Krestovka River, Kolyma Lowland (Figs. 1, 2). The Begunov Formation is not characterized by mammals. The Pliocene age of the formation was proved by fossil plants, which are indicative of taiga environments, and by the stratigraphic position. The age of the next unit, Kuobakh Beds, is better know, because the unit has yielded fossil mammals; according to Sher (1997a), its age is approximately 2.5–2.0 Ma. Both Begunov Formation and Kuobakh Beds were undoubtedly inside the Pliocene in all traditional schemes. As the lower Quaternary boundary is taken for 2.58 Ma, the position of the Begunov Formation becomes uncertain. It apparently belongs to the Upper Pliocene, but probably, some part of the formation falls on the Pleistocene. Fossil insects from this unit are not numerous, they belong mostly to tundra species and one beetle, a weevil of the tribe Cleonini (subfamily Cleoninae in Kiselev, 1981), could have been a steppe–tundra indicator.

Lower and Middle Pleistocene

The lowest part of the Lower Pleistocene in the recent sense is represented by the Kutuyakh Beds. This unit was described in the same section of the Krestovka River. In previous works, it was dated Upper Pliocene (Sher et al., 1979, Sher, 1997a). First true steppe–tundra indicators, such as the pill beetle *Morychus viridis,* were found here (Kiselev, 1981).

The upper part of the Lower Pleistocene sequence is represented by the Chukochinsky Horizon of the Oler Formation. The Oler Formation was described by Sher (1971). This formation is widespread in the Kolyma Lowland. It consists of two horizons. The lower, Chukochinsky Horizon shows reversed magnetization and belongs to the Matuyama chron; the upper, Akansky Horizon shows normal magnetization and belongs to the Brunhes chron. This magnetization change marks the Lower/Middle Pleistocene boundary in the modern sense. In previous works, the Chukochinsky Horizon was described as the Upper Pliocene (Sher et al., 1979) or Eopleistocene (Sher, 1997a).

The reference sites of the Oler Formation have been studied in the Kolyma Lowland (Krestovka, Chukochya, Alazeya; Figs. 1, 2, 3) and the eastern Yana–Indigirka Lowland (Khomus-Yuryakh, Keremesit; Figs. 1, 2, 4, 5). The stratotype of the Oler Formation is a section on the Bolshaya Chukochya River. A common feature of the Oler deposits of Chukochya sites is a thick peat bed at elevation 16–18 m above the river level. Only the top unit (above the peat) belongs to the Akansky Horizon (Virina, 1997).

Fossil insects from Chukochya sites were well studied (about 40 samples) by Kiselev (1981). Most of insects belong to tundra species; steppe species play a secondary role, but their presence is permanent throughout the section. Fossil insect assemblages from the upper part of Chukochinsky Horizon (a peat) include forest species.

The unit above the Oler Formation is tiny organic free sands. This unit was described from the Chukochya River as the Middle Pleistocene Maastakh Formation (Arkhangelov, 1977). Insect samples taken from this unit are poor (Kiselev, 1981). The section is terminated by the Late Pleistocene Edoma Formation.

Another series of important sites with distinct presence of the Lower and Middle Pleistocene deposits was observed on the Alazeya River (Figs. 1, 2, 3). The principal composition of the section is similar to that of Chukochya, but some additional units were described from there (Kaplina et al., 1981, Sher, personal communication): the Alazeya Beds and Sergeev Creek Beds. Both units are situated between the Oler and Maastakh formations and their age is still problematic. The Alazeya Beds is a stratum with large ice wedge casts filled by sand and silt with pieces of wood, larch cones, and peat lenses. This structure is indicative of warm time, which was confirmed by paleontological analyses (Kaplina et al., 1981), but there are no evidence of a certain age of this interglacial or interstadial unit. It can belong to one of warm stages of the Middle Pleistocene. Even more problematic is the age of the Sergeev Creek Beds. This is an alluvial structure of coarse sand and gravel with oblique bedding. The unit is also situated between the Oler and Maastakh formations, but geological permafrost features and the insect fauna (Kuzmina, 1989) do not provide evidence of "warming." We guess that this unit could have been the lower part of the Maastakh Formation and it lies stratigraphically above the Alazeya Beds.

While Lower Pleistocene deposits are restricted to the Kolyma and Indigirka lowlands (Table 2), the Middle Pleistocene units are more widespread. In addition to the Kolyma and Yana–Indigirka lowlands, a well-developed Middle Pleistocene complex has been recorded in Lyakhovskii Island (Fig. 6) and the opposite side of the Dmitry Laptev Strait, Oiagoss Yar (Kuchchugui and Yukagir formations, Zimov'e Beds),

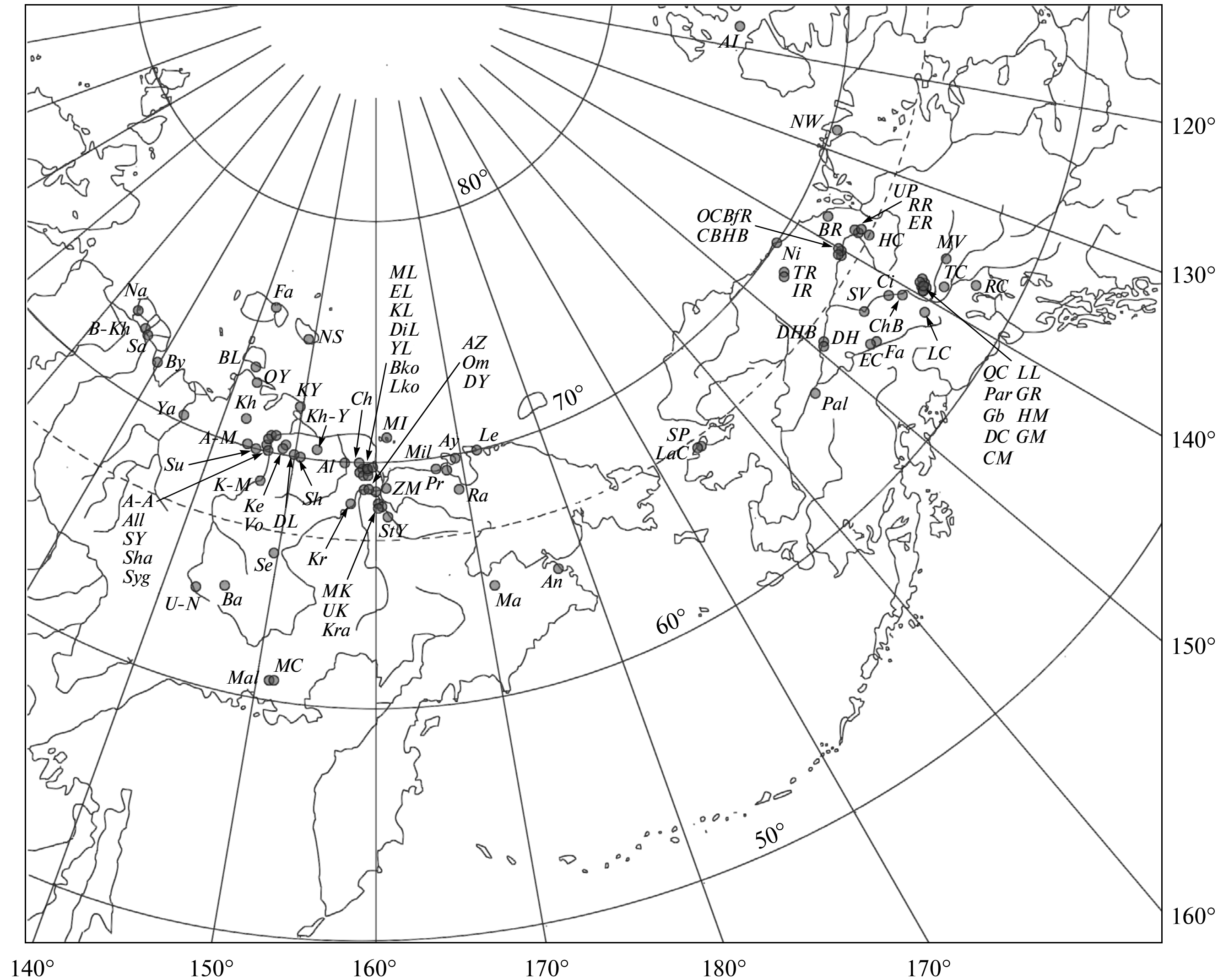


Fig. 1. Map of studied insect sites in Beringia. Designations: Western Beringia: (*A-A*) Achchagy–Allaikha, (*Ai*) Aion, (*Al*) Alazeya, (*All*) Allaikha, (*A-M*) Ary-Mas, (*An*) Anadyr, (*AZ*) Aleshkina Zaimka, (*Ba)* Badyarikha, (*Bko*) Big Kon'kovaya, (*B-Kh*) Buor-Khaya, (*BL*) Bolshoi Lyakhovskii, (*By*) Bykovsii, (*Ch*) Chukochya, (*DL*) Danila Lake, (*DiL*) Dikoe Lake, (*DY*) Duvanny Yar, (*EL*) Evety Lake, (*Fa*) Faddeevsky, (*Ke*) Keremesit, (*Kh*) Khroma, (*Kh-Y*) Khomus-Yuryakh, (*KL*) Kotelnicheskoe Lake, (*K-M*) Krest-Maior, (*Kr*) Krestovka, (*Kra*) Krasivoe, (*KY*) Khaptashinskii Yar, (*Le*) Letyatkin, (*LK*) Little Kon'kovaya, (*Ma*) Main River, (*Mal*) Maltan, (*MC*) Mamontovyi Creek, (*MI*) Medvezhyi Island, (*Mil*) Milkera, (*ML*) Mavrinskoe Lake, (*MK*) Molotkovskii Kamen', (*Na*) Nagym, (*NS*) New Siberia, (*Om*) Omolon, (*OY* Oiagoss Yar, (*Pr*) Primorskii, (*Ra*) Rauchua, (*Sa*) Samoilov, (*Se*) Sededema, (*Sh*) Shandrin, (*Sha*) Shamanovo, (*StY*) Stanchikovskii Yar, (*Su*) Suturuokha, (*SY*) Sypnoi Yar, (*Syg*) Sygannakh, (*UK*) Utkinskii Kamen', (*U-N*) Ust'-Nera, (*Vo*) Volch'ya, (*Ya*) Yana, (*YL*) Yakutskoe Lake, (*ZM*) Zelenyi Mys and Chersky. Eastern Beringia: (*AI*) Arctic Islands (Banks, Prince Patrick, Melville, Bathurst, Meighen, Ellesmer islands), (*BfR*) Bluefish River Basin (excl. Ch'ijee's and Hidden Bluff), (*BR*) Blow River, (*CB*) Ch'ijee's Bluff, (*Ci*) Circle, (*CM*) Christie Mine, (*ChB*) Chester Bluff, (*DC*) Dominion Creek, (*DH*) Dalton Highway, (*DHB*) Dalton Highway near bridge, (*EC*) Eva Creek, (*ER*) Eagle River, (*Fa*) Fairbanks, (*Gb*) Goldbottom, (*GM*) Gatenby Mine, (*GR*) Gold Run, (*HB*) Hidden Bluff, (*HC*)Hungry Creek, (*HM*) Hollis Mine, (*IR*) Ikpikpuk River, (*LaC*) Lava Camp, (*LC*) Lost Chicken, (*LL*) Lucky Lady, (*MV*) village of Mayo, (*Ni*) Niguanak, (*NW*) northwestern Territories Mainland, (*OC*) Old Crow, (*Par*) Paradise, (*Pal*) Palisades, (*QC*) Quartz Creek, (*RC*) Revenue Creek, (*RR*) Rock River, (*SP*) Seward Peninsula, (*SV*) village of Stevens, (*TC*) Thistle Creek, (*TR*) Titaluk River, (*UP*) Upper Porcupine River.

and, probably, in the Lena delta (Fig. 7) (Bulukur Formation probably has a middle Pleistocene age).

The Achchagy and Allaikha formations described from the Lower Indigirka sections (Kaplina et al., 1980) apparently correspond to the Alazeya Beds. The lower unit here is the Achchagy Formation with large and small ice wedge casts; the next is lacustrine–boggy Allaikha Formation (Fig. 1). The Middle Pleistocene upper limit of these two formations is proved by small fossil mammals from the "*Dycrostonyx*" Beds, which lie on the top of the Allaikha Formation (Kaplina et al., 1980). Insects from the Lower Indigirka sites

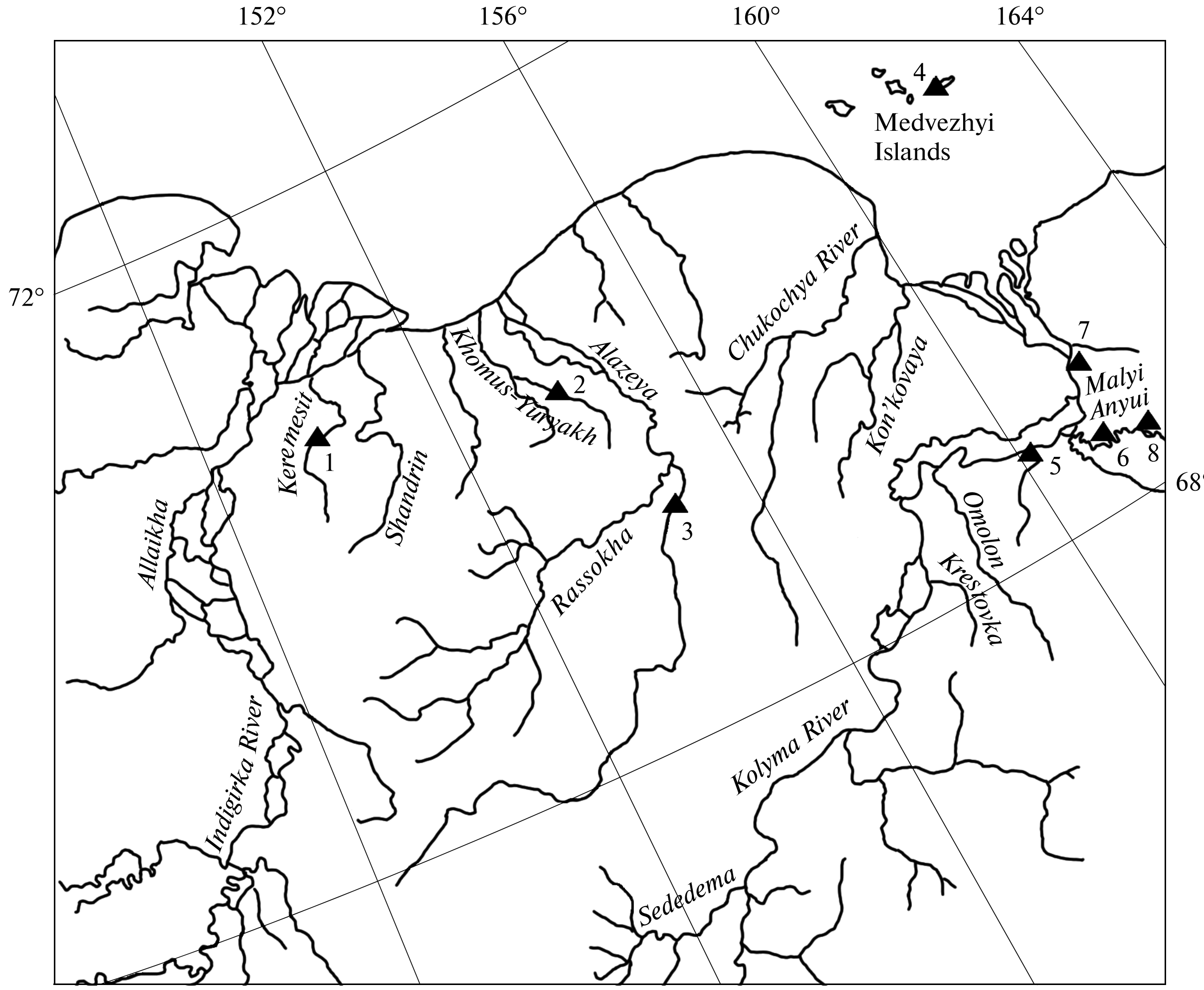


Fig. 2. Map of studied sections in the Kolyma and Indigirka lowlands. Designations: (1) Keremesit, (2) Khomus-Yuryakh, (3) Alazeya, (4) Medvezhyi Islands, (5) Duvanny Yar, (6) Stanchikovskii Yar, (7) Zelenyi Mys, (8) Molotkovskii Kamen'.

(Kiselev, 1981) indicate that only the Allaikha Formation fits to the concept of thermochron.

The sections on the Keremesit River (Fig. 4) were studied by an expedition of "Aerogeology" (Bashlavin et al., 1986, 1987) and Moscow State University; fossil insects were studied by Kiselev and, later, by the author. An extensive collection of large and small mammals supports the Middle Pleistocene age of most of the sequence. The Middle Pleistocene unit from the Keremesit River was considered as the most complete section of this age (Sher et al., 1987); thus, all other local units were included in the "Keremesit Superhorizon" and the Keremesit River became the stratotype area for the Middle Pleistocene. Interglacial beds have not been found on the Keremesit River, but they were formally assigned to the superhorizon.

Upper Pleistocene

Upper Pleistocene deposits are very common in the studied region. The main appearance of the Upper Pleistocene is a section of ice rich in sandy–silty sediments with huge ice wedges. This feature gives a common name for the typical geological structure of this age, "the Ice Complex." A more formal name is the Edoma Formation, which means the same structure (one definition of the word Edoma is "been eaten" reflects ice melting and fast erosion of the outcrop: Sher, 1997b). The stratotype of the Edoma Formation is the Duvanny Yar site (Figs. 1, 2) on the Kolyma River (Vas'kovsky, 1963). This is another source of confusion, because the term "Duvanny Yar Interval" (Colinvaux, 1985) is used for the last part of the Late Pleistocene, which is regionally correlated only with the upper part of the Edoma Formation and with the Aleshkina Formation (Fig. 1).

The Aleshkina Formation is a sandy unit described from nearby the Aleshkina Zaimka locality (Sher, 1971). It forms the second river terrace, which is lower than Edoma. The age of Aleshkina sands conforms to the last glacial maximum. These two formations are different geological bodies, but their ages overlap. Fos-

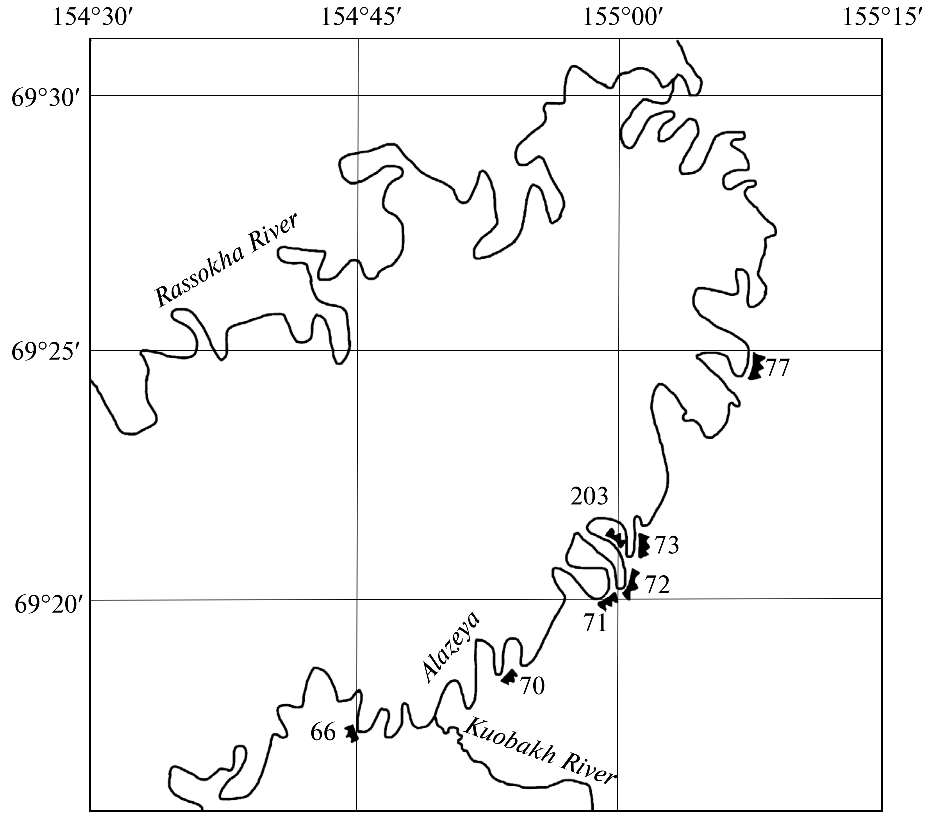


Fig. 3. Map of studied sections on the Alazeya River.

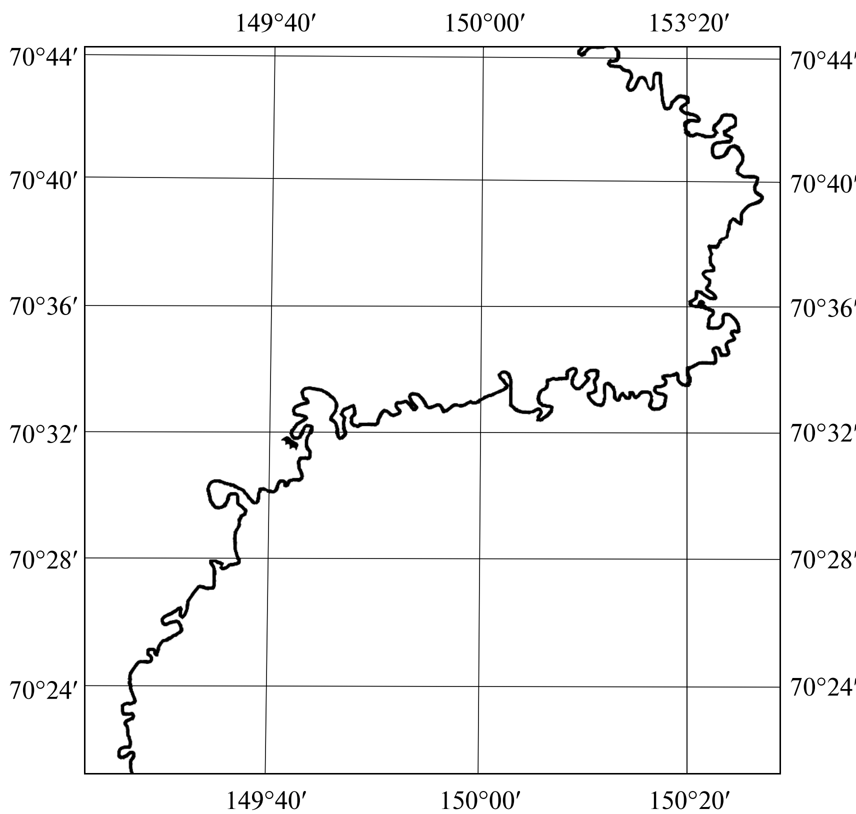


Fig. 4. Map of studied sections at the Keremesit River.

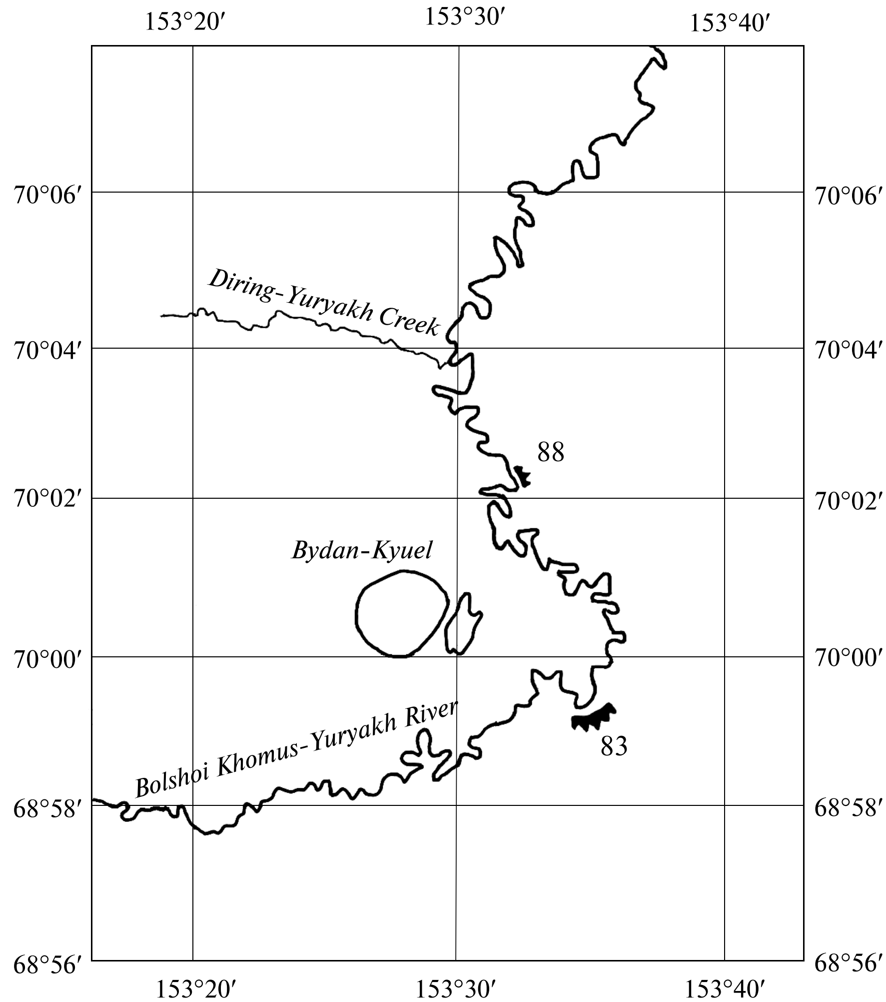


Fig. 5. Map of studied sections at the Khomus Yuryakh River.

sil insects from Duvanny Yar and Aleshkina Zaimka were studied by Kiselev (1981) and some samples from Duvanny Yar, by Kuzmina (Zanina et al., 2011).

The Edoma Formation was recorded in all parts of the region from the Lena delta to Chukotka Peninsula. Almost all sites where older deposits were described in the Kolyma and Yana–Indigirka lowlands contain The Edoma Formation near the top.

The last interglacial (MIS5), the first stage of the Late Pleistocene, could be recognized in the sections by the climate stratigraphy methods, including palynology and fossil insect study. In fact, we have only a few doubtless MIS5 sections, one of which is the Kuobakh Beds on the Alazeya River and another is the Krest-Yuryakh Formation in the Laptev Strait area. The Kuobakh Beds is a silty–sandy unit with peat layers, which is situated between the Maastakh (Q_2) and Edoma (Q_3) formations. Fossil insects from this unit are indicative of forest–tundra environments, with a steppe–tundra admixture (Kuzmina, 1989). This is a "warming" signal, although it is relatively weakly pronounced, because the modern environment of the site is also forest–tundra. It is impossible to say that the MIS5 warming was stronger than modern one in this area.

Different observation has been made in the north (Bolshoi Lyakhovskii Island, Oiagoss Yar: Fig. 1). The Krest-Yuryakh Formation represented here is a distinct unit with large ice wedge casts filled by plant debris rich in fossils: seeds, shells, ostracods, and insects (Kienast, 2011). In comparison with sediments of the lower and upper parts of the Krest-Yuryakh section, which are usually poor in organic matter, this unit contains rich accumulations. All fossils are indicative of a significant warming event. Recently, the site is situated in the arctic tundra zone; during MIS5, shrub tundra close to the forest–tundra with steppe–tundra elements occupied this area. Unlike inland situation (Alazeya site), zonal shift due to climatic changes seems more pronounced here.

Some problematic strata possibly belong to MIS5. One of the most plausible candidates is the Molotk-

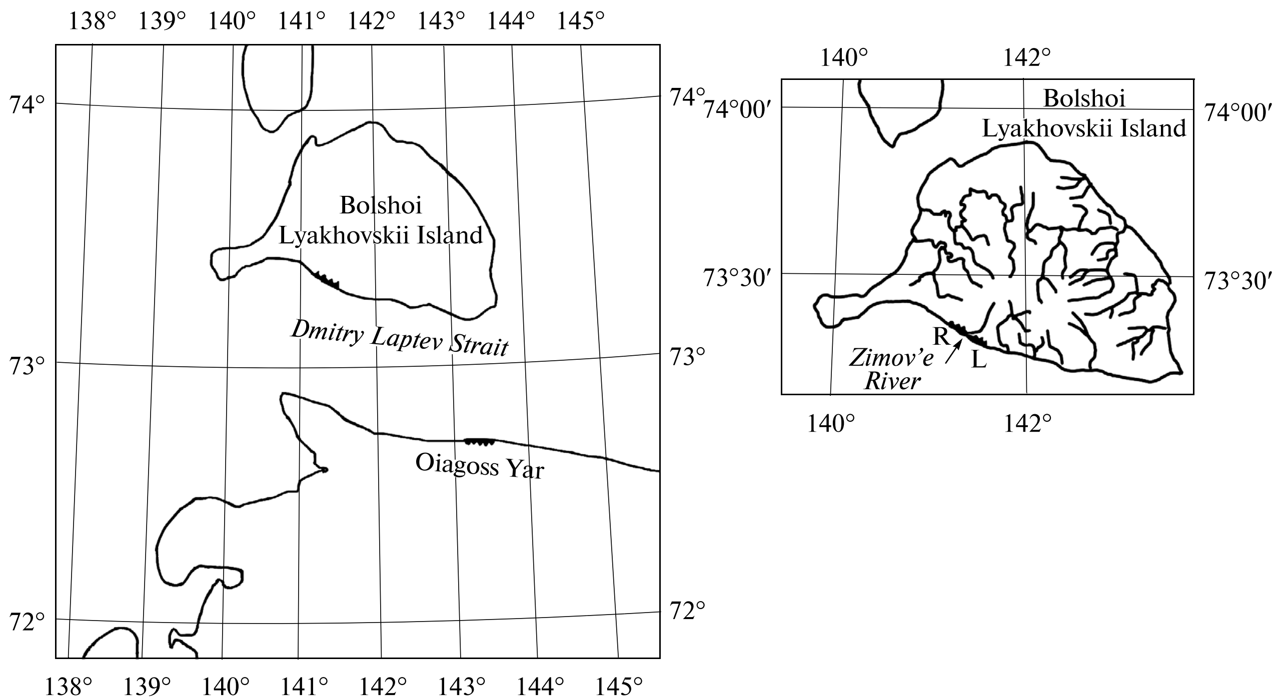


Fig. 6. Map of studied sections on Bolshoi Lyakhovskii Island.

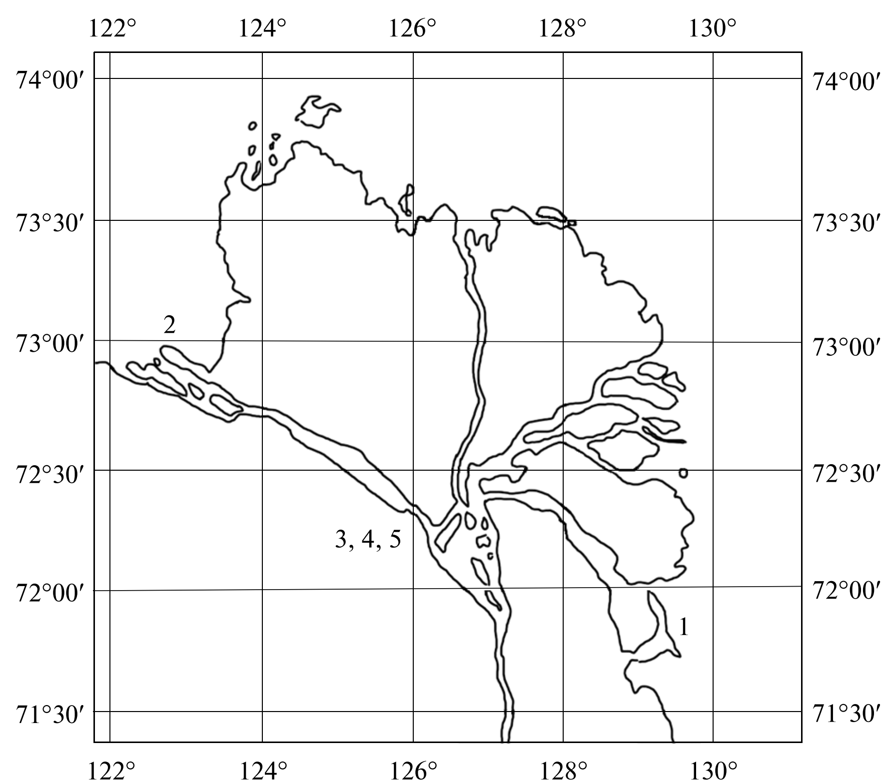


Fig. 7. Map of studied sections in the Lena delta region.

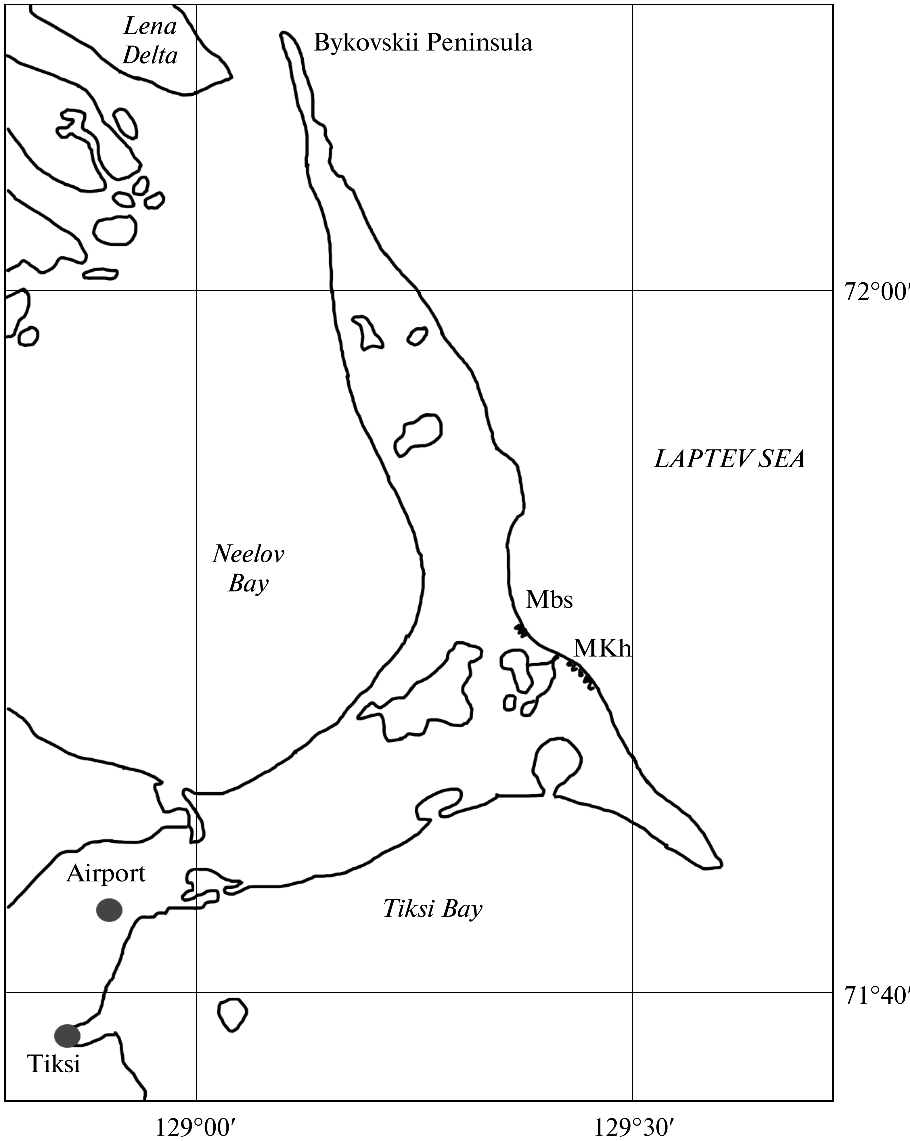


Fig. 8. Map of studied sections on the Bykovsii Peninsula.

ovskii Beds (Sher, 1971) from the Molotkovskii Kamen' site on the Malyi Anyui River (Figs. 1, 2). The section contains four peat horizons, the top one is dated Holocene, but three lower peat bodies are of uncertain age. The third peat (the second from the top) was considered as a "Karginian" unit, MIS3 (Sher, 1971; Kaplina and Giterman, 1983). The age was determined by radiocarbon data and warming signal, by pollen and insects (Kaplina and Giterman, 1983; Kiselev, 1981); thus, the Molotkovskii Beds was recommended as the regional Molotkovskii Horizon corresponding to the Middle Weichselian interstade (Shilo, 1987). The scheme of the Upper Pleistocene included the Edoma Superhorizon subdivided into the Oiagoss (lower), Molotkovskii (middle), and Sartansky (upper) horizons. The local stratigraphic units in the Kolyma Lowland were the Edoma Formation, Molotkovskii Beds, and Aleshkina Formation. Sher et al. (2005) has recently restudied and resampled the section. New radiocarbon data stay beyond the limit (over 40 ka); thus, the Molotkovskii Horizon as the Middle Weichselian (MIS3) subdivision is not valid, but it is highly probable that the unit belongs to an older warming stage, MIS5. Two lower peat levels probably belong to the Middle Pleistocene interstades or interglacial.

Holocene

The Holocene deposits are widespread in the region, but local stratigraphic names are rarely used for this time. When dealing with the Holocene,

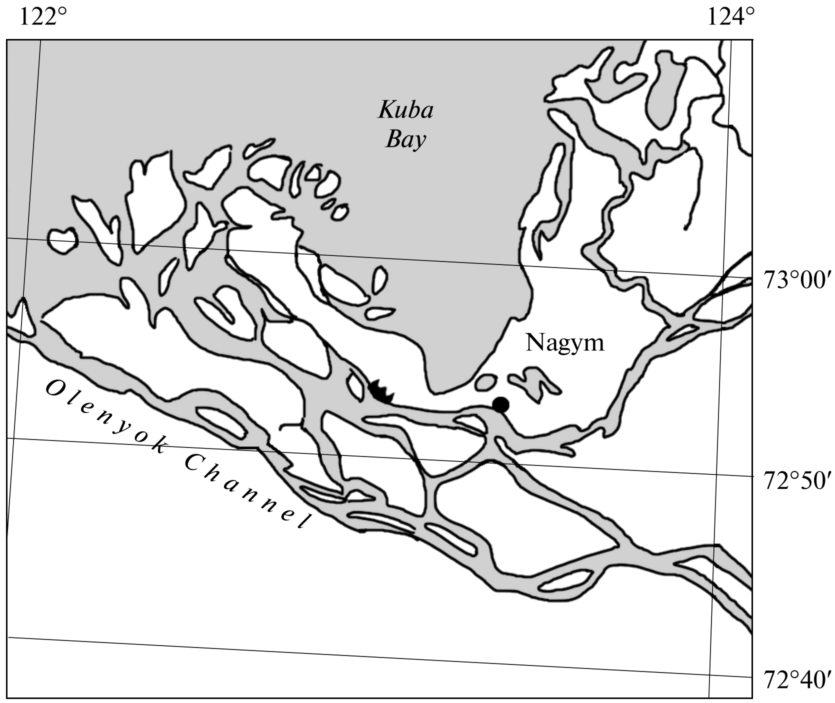


Fig. 9. Map of the Nagym site in the Lena delta.

researchers prefer the absolute age, because it fits to the range of radiocarbon method. The most interesting geological structure of this time is the "alas complex," which usually occurs on the top of the ice rich Pleistocene sections or in depressions above melted and compressed Pleistocene deposits (Kaplina and Lozhkin, 1979; Kuznetsova et al., 1999). Alas complex was named after the local term *alas,* that is, a thermokarst lake and meadow what succeed the drained lake. In the section, the alas complex appears as succession of lacustrine and boggy deposits, often with a thick peat body. The age of such structures is usually around 9–8 ka, that is, the early Holocene (boreal period). This is considered to be a regional thermal optimum of the Holocene. Fossil insects from the alas complex were usually studied in addition to the main study of the Pleistocene section (Kiselev, 1981; Kiselev and Nazarov, 2009; Wetterich, et al., 2008) or, rarely, as a self-reliant study (Kuznetsova et al., 1999; Kuzmina and Sher, 2006).

Another type of Holocene deposits that have yielded fossil insects are known on floodplain terraces. Low river terraces are usually younger, 5–1 ka. Terraces, being a separate geological structure, were studied independently (Kiselev and Nazarov, 2009; Kuzmina and Bolshiyanov, 2002; Kuzmina, 1986).

2c. Localities

We provide here information about insects and their sites studied by the author. Other insect localities were described by Kiselev (1981) and Kiselev and Nazarov (2009).

Lena Delta Area

This area is located on the northwestern side of western Beringia (Figs. 1, 7). Fossil insects from this area were collected in 1998–2001 under the German–Russian project ''The Laptev Sea System 2000.'' The most thoroughly studied area is the Bykovsii Peninsula, which is apart from the delta (Figs. 1, 7), but in fact belongs to the same formation.

Two sections were studied on the Bykovsii Peninsula (Figs. 7, 8): Mamontovyi Khayata (71°47′ N 129°26′ E) and Mamontovyi Bysagasa (71°48′ N 129°22′ E).

Other sections are situated in the Lena delta (Fig. 7): the section Nagym (72°53′ N, 123°19′ E) in the northwestern delta (Fig. 9) and three sections in the southern–central delta (Fig 10): Buor-Khaya (72°21′ N 126°30′ E, Samoilov Island (72°22′ N, 126°28′ E), and Arga-Bilir-Aryta Island (72°22′ N, 126°20′ E).

Dmitry Laptev Strait

Two sites have been studied in this area (Figs. 1, 6): the continental site of Oiagoss Yar (72°38′ N; 143°33′ E) on the southern coast of the strait and a site on its opposite side, Bolshoi Lyakhovskii Island, near the Zimov'e River mouth (73°20′ N; 141°21′ E). Fossil

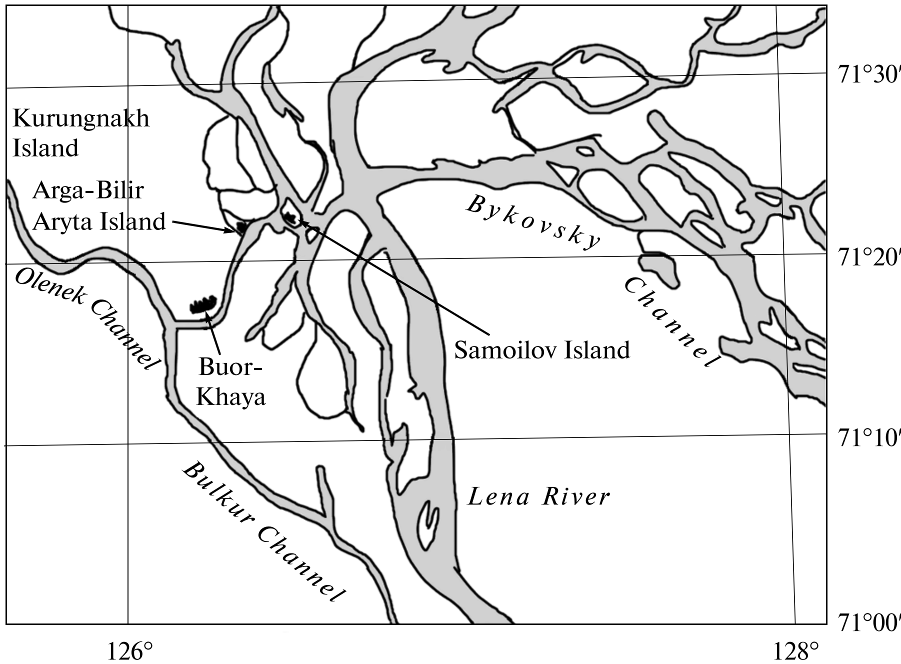


Fig. 10. Map of the Buor-Khaya and Samoilov sites in the Lena delta.

insects from the last site were collected by the author in 1999 under the German–Russian project (“The Laptev Sea System 2000”); insects from the opposite coast were studied in previous works (Kiselev and Nazarov, 2009) and one sample was collected by Frank Kienast in 2001 (Kienast et al., 2011). Samples from a few other sites: Faddeevsky Island, Novaya Sibir’ Island, and Khaptashinsky Yar have been studied by Kiselev (Kiselev and Nazarov, 2009).

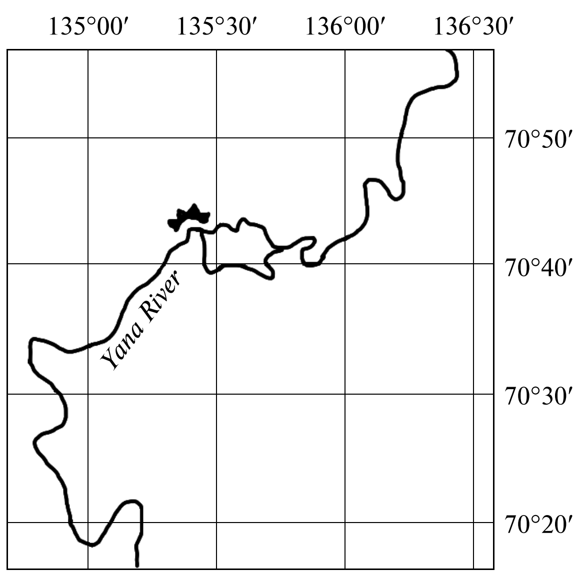


Fig. 11. Map of studied section at the Yana River.

Yana–Indigirka Lowland

Fossil insects from this area are more or less thoroughly studied. The main sections are situated on the Indigirka River low stream and nearby (Sypnoi Yar, Allaikha, Achchagy–Allaikha, Shandrin, Keremesit rivers, and others). Most of the samples have been studied by Kiselev (Kiselev and Nazarov, 2009). Samples from the Keremesit River (Figs. 2, 4) are described here. The site of Keremesit (70°32′ N, 149°41′ E; Fig. 7) is located on the left bank of the river, 5 km downstream from the Upitka Creek mouth. The samples were collected by the author in 1984.

The central and western parts of the Yana–Indigirka Lowland are worse characterized by insects. Only one small insect series from the Khroma River has been studied by Kiselev (Kiselev and Nazarov, 2009). At present, we can add another site, the Yana River. The samples were collected by Elena Pavlova in 2002. The Yana site (70°43′ N, 135°25′ E) is located on the left bank of the Yana River not far from the Kular Ridge (Figs. 2, 11).

Kolyma Lowland

The Kolyma Lowland is the best studied area in northeastern Asia. Initially, fossil insects of this region were studied by Kiselev (1981; Kiselev and Nazarov, 2009). Some new sites are described here and in my pre-

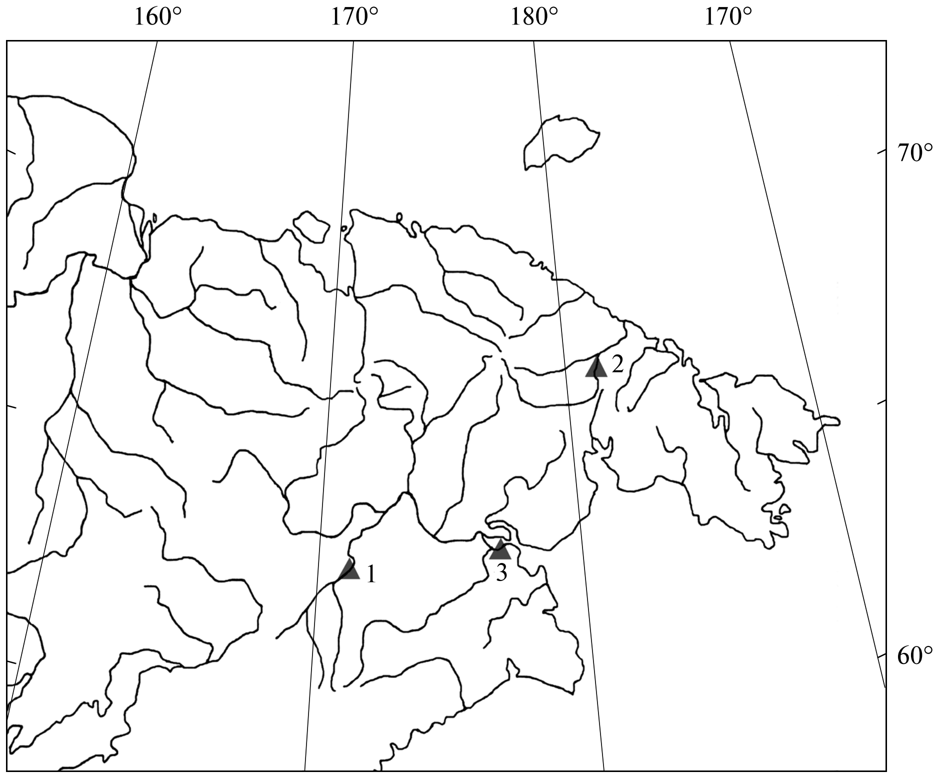


Fig. 12. Map of the sites studied on the Chukotka Peninsula: (1) Main, (2) Amguema, (3) Anadyr.

vious works (Kuzmina, 1989). The most detailed and complete insect record comes from the Alazeya River sites: sections 66 (69°17′ N, 154°45′ E), 70 (69°19′ N, 154°55′ E), 71 (69°20′ N, 155°00′ E), 72 (69°20′ N, 155°01′ E), 202 (69°21′ N, 155°00′ E), 73 (69°21′ N, 155°02′ E), 77 (69°25′ N, 155°07′ E), (Figs. 1, 2). The samples were collected by the author in 1983–1984.

Fossil insect samples described here were collected by different persons. The Medvezhyi Island locality (Kuzmina and Kolesnikov, 2000) at the Kolyma River mouth was sampled by Sergei Kolesnikov in 1985. The section is situated on the western side of the Chetyrekhstolbovoi Island (70°38′ N, 162°30′ E, Figs. 1, 2).

The site on the Bolshoi Khomus-Yuryakh River (Figs. 1, 2, 5) was sampled by Sher in 1988–1989. Two sections have been studied. Section 88 (70°02′ N, 153°32′ E) is located 2 km upstream from the Diring-Yuryakh Creek mouth; section 83 (69°59′ N, 153°35′ E) is 6 km upstream from the previous one.

Several small samples were collected by Sher in 1990 in addition to those studied by Kiselev in the section of Molotkovskii Kamen' (68°16′ N, 161°47′ E) on the Malyi Anyui River (Figs. 1, 2).

The well-known site of Duvanny Yar (Figs. 1, 2) on the Kolyma River (68°38′ N, 159°12′ E) was studied by Kiselev (1981). Additional samples were collected by Gubin and Zanina and studied by me (Gubin et al. 2003, Zanina et al., 2011). These samples are interesting because they come from paleosol layers and ground squirrel nests.

Chukotka Peninsula

The Chukotka Peninsula (Fig. 12), being the eastern part of western Beringia, is a very important region. Pleistocene insects from Chukotka (especially its eastern areas) could have provided significant information about transcontinental migrations; however, a lack of available sections block our intentions. Only the western Chukotka Peninsula (Aion Island and coastal lowland at the Chaun Bay) have been studied well (Kiselev, 1981, 1980b; Nazarov, 2009); one sample is known from the central–western Chukotka (Amguema River) and a group of sections in the central–southern part of Chukotka has been studied by Kiselev (1980a) and me (Kuzmina et al., 2011). The Holocene samples were collected in the western Chukotka Peninsula, Amguema River, and Anadyr Bay.

The Ice Bluff site (Fig. 13) is situated on the Main River, not far downstream from the village of Vaiegi, in the central–southern part of Chukotka (64°35′ N, 171°06′ E). The section was studied in detail by an expedition of the Geographical Department of Moscow State University in the 1970s (Kaplin, 1980); the

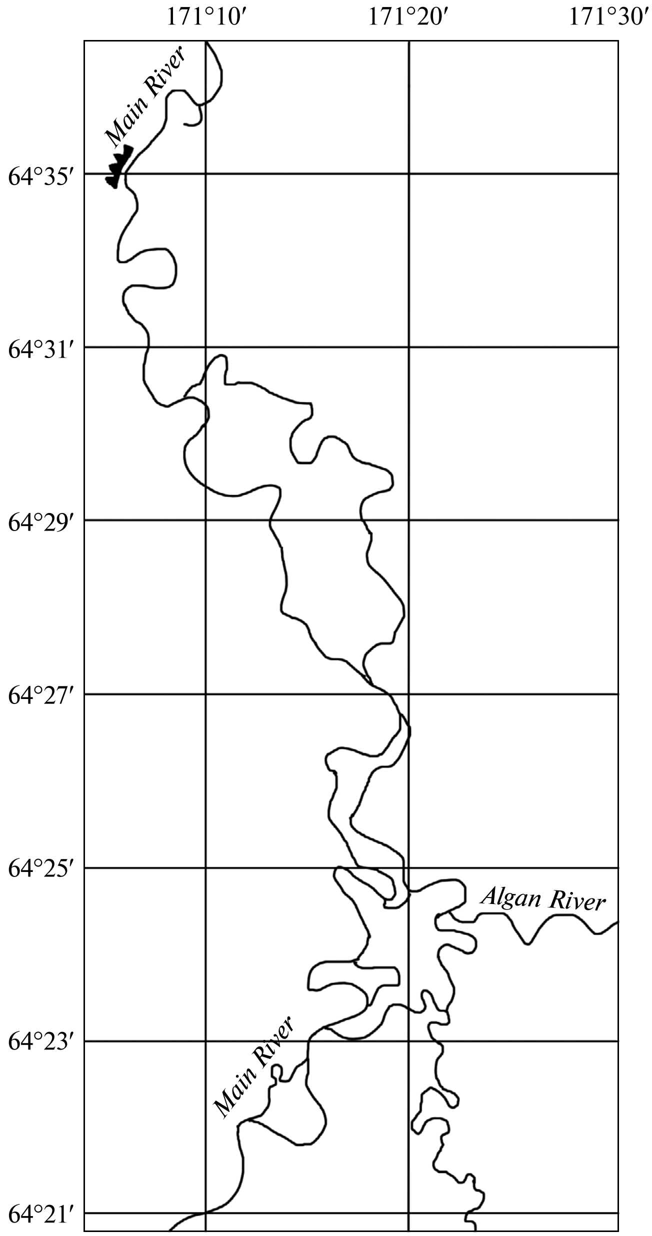


Fig. 13. Map of the Main River, Chukotka, Ledovyi Obryv (Ice Bluff) section.

entire sequence was considered to be the Middle Pleistocene Turcutsky Formation, but recently, with new evidence including radiocarbon dating, the age has been improved up to the Late Pleistocene (Kuzmina et al., 2011).

The sites on the Amguema River near the village of Tranzitnyi (67°18′ N, 178°42′ E) in the central Chukotka Peninsula were briefly visited by the author in 1988. One sample from deposits rich in ice probably of the Late Pleistocene age was taken and a few low river floodplain terraces (probably Late Holocene) were sampled. All samples come from poorly studied sections and their age is uncertain, but the purpose of the trip was preliminary survey, which, unfortunately, did not prolonged.

The section at the Anadyr Bay (64°42′ N, 177°12′ E) was also only briefly visited in 2004. This section is the closest to the eastern Beringia side, thus it seems suitable to test the paleozoogeographic effects.

CHAPTER 3. SITES AND INSECT FAUNAS

3.1. Kolyma Lowland

3.1a. Alazeya

The Alazeya River is situated in the western Kolyma Lowland (Figs. 1, 2). Several exposures of Pleistocene deposits (Figs. 14a–14d) from the Lower Pleistocene (Fig. 15) to Holocene (Fig. 16) have been studied in the middle stream of the river from the village of Andryushkino to the Bolshoi Taamar mouth. The area was described for the first time by V.E. Terekhova (Baranova and Biske, 1964). She visited some Alazeya sites in 1957 and decided that all units belong to the Upper Pleistocene. Later, in 1974, Sher and Kaplina (Kaplina et al., 1981) worked on the Alazeya sections and provided a geological description based on the mammal fauna, pollen analysis, and paleopermafrost features. They traced three main units known from the Chukochya River: Oler, Maastakh, and Edoma formations; and two local units were described, the Alazeya Beds at the top of the Oler Formation and the Kuobakh Beds at the top of the Maastakh Formation. Both units were correlated with warm periods (Kaplina et al., 1981). In 1983 and 1984, the main sections were studied in more detail by S.F. Kolesnikov, I.R. Plakht, A.V. Sher, and me; insect samples were collected (Kuzmina, 1989).

The Oler Formation is composed of gray silt with isolated peat lenses. The unit is 18–20 m thick. Lake sediments (bluish gray silt with scattered plant debris) is present in some parts of the sections. Some of such lake subunits are terminated by boggy soil. Three horizons of ice wedge casts are traced across the Oler Formation. It indicates that the sediment was frozen and unfrozen repeatedly. Paleomagnetic research made in 1984 shows that the lower part of the Oler Formation belongs to the Chukochinsky Horizon and the upper part to the Akansky Horizon (Grinenko and Minyuk, 1985).

Alazeya bed occupy on the Oler Formation. It is horizon of big ice wedge casts filled by silt, sand and large pieces of wood, larch cones and small peat lenses. The age of the unit is still uncertain; probably the Alazeya beds belong to the lower part of the Middle Pleistocene.

The Maastakh Formation from Alazeya sites includes two units. The lower one is represented by coarse sand and gravel with oblique bedding. It is alluvial in genesis. A similar unit has been found apart from the main sections (sect. 66), i.e., the Sergeev Creek Beds. The age of this locality is not clear; prob-

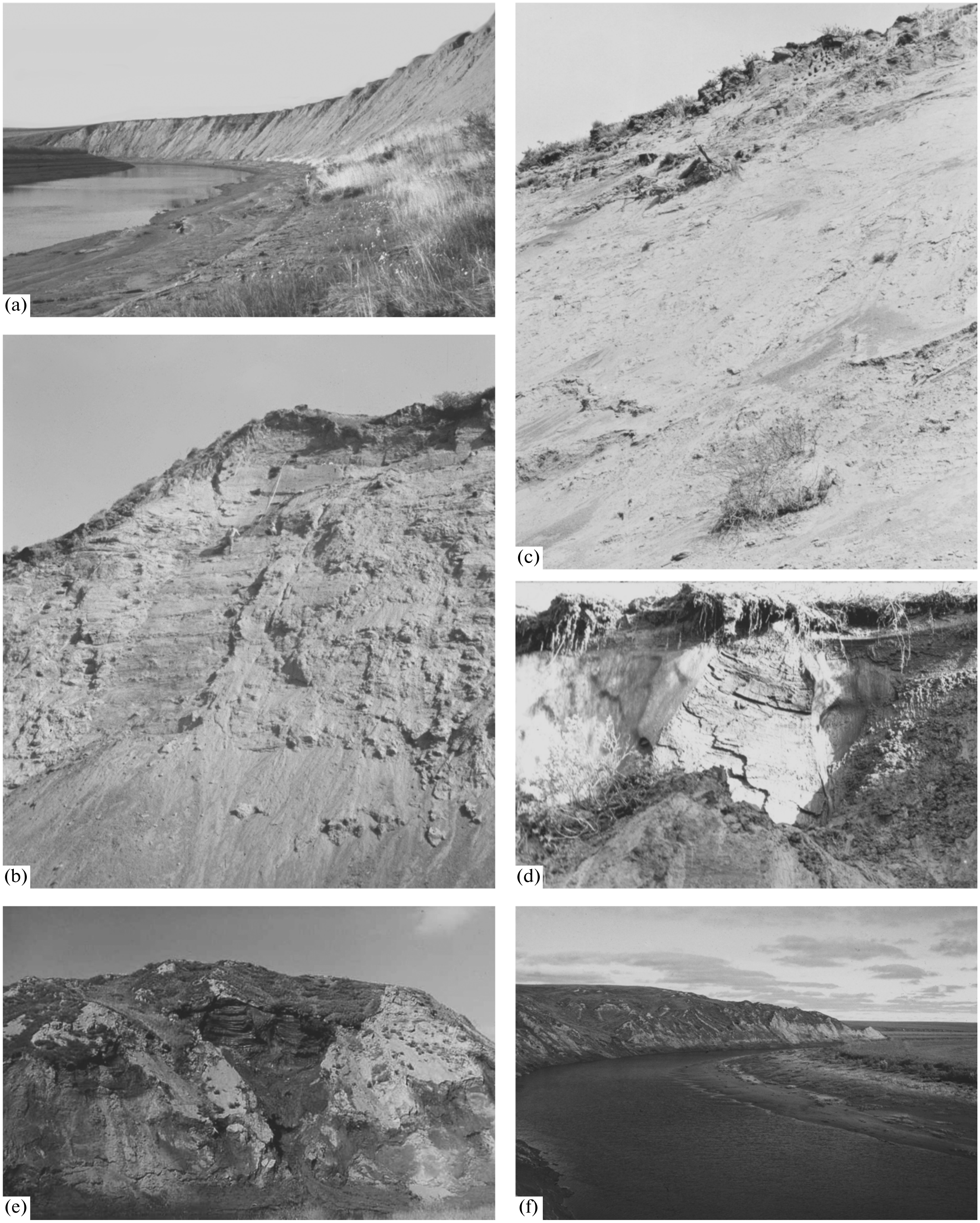


Fig. 14. Photograph of (a–d) Alazeya, (e) Khomus-Yuryakh, and (f) Keremesit sections. (a) Alazeya, section 73; general view, (b) Alazeya section 73, Oler and Maastakh formations; (c) Alazeya section 73, Kuobakh Beds with fossil wood; (d) Alazeya section 71, Edoma Formation.

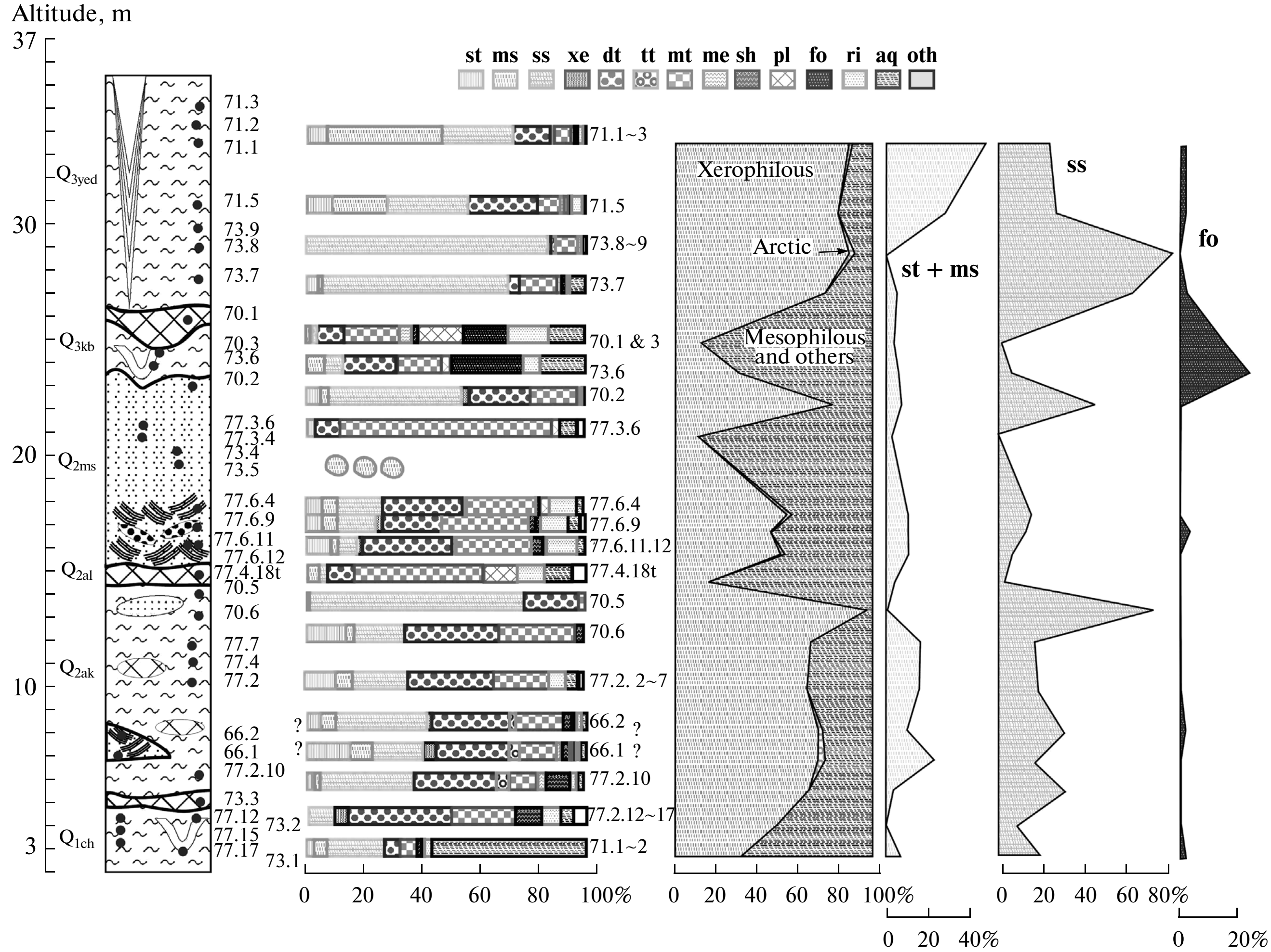


Fig. 15. Stratigraphic scheme and insect assemblages from the Pleistocene at the Alazeya River: the first column is stratigraphy, the second is distribution of ecological groups, and the thirdis correlation of the main groups: the xerophilous part includes the groups **st**, **ms**, **ss**, and **xe**, the arctic part includes the group **tt**, the mesophilous and other groups include the groups **mt**, **sh**, **me**, **pl**, **fo**, **ri**, **aq**, and **oth**. Legend: (**st**) steppe, (**ms**) meadow–steppe, (**ss**) insects of hemicryophytic steppe, (**xe**) xerophilous insects of various habitats, (**dt**) insects of dry tundra habitats, (**tt**) insects of typical and arctic tundra, (**mt**) insects of mesic tundra habitats, (**sh**) shrub, (**me**)meadow, (**pl**) plant litter, (**fo**) forest, (**ri**) riparian, (**aq**) aquatic, (**oth**) other insects; (Q_{1ch}) Chukochinsky Horizon, (Q_{2ak}) Akansky Horizon, (Q_{2al}) Alazeya Beds, (Q_{3ku}) Kuabakh Beds, (Q_{2ms}) Maastakh Formation, (Q_{3yed}) Edoma Formation. For symbols in the stratigraphic column, see Fig. 16.

ably, it should be correlated with the lower part of the Maastakh Formation. The upper part of the Maastakh Formation is similar to the stratotype on the Chukochya River, tiny sand almost without organic matter.

Between the Maastakh Formation and ice rich Edoma sediments, there is a layer of lake clay and peat lenses. The pollen spectrum of this deposits includes a high percent of shrubs and trees. This unit (Kuobakh Beds) represents the last inter glacial (Fig. 13c).

The Edoma Formation (Upper Pleistocene) on the Alazeya River is typical for coastal lowlands. The sediment is mostly brown–gray ice-rich silt with plant debris, including tiny grass roots. Huge ice wedges are a common feature for the Edoma Formation (Fig. 13d). The pollen spectrum is indicative of a relatively cold steppe–tundra environment.

Fossil insects were sampled in all units (Tables 3–5): six samples from the Chukochinsky Horizon, six from the Akansky Horizon, one from the Alazeya Beds, two from Sergeev Creek, five from Lower Maastakh, seven from Upper Maastakh, three from the Kuobakh Beds, and five from the Edoma Formation. Some samples, especially taken from Maastakh sands poor in organics, contain small amount of insects. We combined insects from some poor samples if the samples were similar in species composition and close in stratigraphic position.

The Chukochinsky Horizon of the Oler Formation has been tested in sections 73 and 77/2 (Figs. 3, 15, Table 3). Three samples were taken from section 73.

Table 3. Insects from the Alazeya sites (Oler Formation)

Age	Chukochinsky		Akansky				Akansky?		
Section	73	77/2	77/2		70		66		eco
Species/sample	1, 2	12–17	10	2–7	6	5	1	2	
Order Coleoptera									
Family Carabidae									
Subfamily Nebriinae									
Notiophilus aquaticus L.	–	2	–	–	–	–	–	1	**xe**
Subfamily Carabinae									
Carabus odoratus Motsch.	–	–	–	–	–	–	1	–	**mt**
Carabus sp.	–	2	–	1	–	–	–	–	**oth**
Subfamily Elaphrinae									
Diacheila polita Fald.	–	1	–	–	–	–	–	1	**mt**
Elaphrus riparius L.	–	1	–	–	–	–	–	–	**ri**
Subfamily Scaritinae									
Dyschiriodes melancholicus Putz.	–	–	–	1	–	–	–	–	**ri**
Subfamily Trechinae									
Bembidion (*Asioperyphus*) *umiatense* Lth.	–	1	1	–	–	–	–	–	**ri**
Bembidion (*Peryphus*) sp.	1	–	–	–	–	–	2	1	**ri**
Bembidion sp.	–	–	–	2	–	–	–	–	**ri**
Subfamily Harpalinae									
Tribe Harpalini									
Dicheirotrichus mannerheimi Sahlb.	1	1	2	4	–	–	1	–	**dt**
Harpalus affinis Schrank	–	–	–	1	–	–	–	–	**ms**
H. vittatus kiselevi Kat. et Shil.	–	–	–	–	–	–	2	3	**ms**
H. vittatus vittatus Gebl.	–	–	–	–	–	–	5	4	**ms**
Tribe Lebiini									
Cymindis arctica Kryzh. et Em.	1	–	–	–	–	–	–	–	**st**
Tribe Pterostichini									
Poecilus (*Derus*) *nearcticus* Lth.	–	3	2	1	4	12	11	11	**dt**
P. (*Cryobius*) *brevicornis* (Kby.)	–	–	2	2	–	–	2	2	**mt**
P. (*Cryobius*) *nigripalpis* Popp.	–	–	3	1	–	9	2	1	**dt**
P. (*Cryobius*) *pinguedineus* Esch.	–	5	–	2	4	–	5	7	**mt**
P. (*Cryobius*) *ventricosus* Esch.	–	–	–	1	6	1	2	8	**mt**
Pterostichus (*Cryobius*) sp.	6	–	–	2	4	11	13	10	**mt**
P. (*Lenapterus*) *agonus* Horn.	–	1	–	–	–	–	1	2	**mt**
P. (*Lenapterus*) *costatus* Men.	–	–	–	2	–	–	–	2	**mt**
P. (*Lenapterus*) *vermiculosus* Men.	–	1	–	–	–	–	–	0	**mt**
P. (*Tundraphilus*) *sublaevis* Sahlb.	–	–	–	2	–	–	2	2	**dt**
Stereocerus haematopus (Dej.)	–	2	–	1	2	–	2	4	**dt**
Tribe Zabrini									
Amara interstitialis Dej.	–	–	–	2	–	–	1	–	**dt**
Curtonotus alpinus Payk.	2	9	–	9	13	86	31	40	**dt**
Family Dytiscidae									
Subfamily Agabinae									
Agabus moestus (Curt.)	–	1	–	–	–	–	1	2	**aq**
SubfamilyColymbetinae									
Colymbetes dolabratus (Payk.)	49	1	–	–	–	–	2	1	**aq**
Subfamily Hydroporinae									
Hydroporus acutangulus Thoms.?	–	–	–	2	–	–	2	–	**aq**
Hydroporus sp.	–	–	–	–	–	–	–	1	**aq**
Dytiscidae gen. indet.	–	–	1	–	–	–	–	–	**aq**
Family Hydrophilidae									
Subfamily Helophorinae									
Helophorus splendidus Sahlb.	–	–	–	1	–	–	–	–	**aq**
Helophorus sp.	–	–	–	–	–	–	1	–	**aq**

Table 3. (Contd.)

Age	Chukochinsky		Akansky				Akansky?		
Section	73	77/2	77/2		70		66		eco
Species/sample	1, 2	12–17	10	2–7	6	5	1	2	
Family Leiodidae									
Subfamily Leiodinae									
Cyrtoplastus irregularis Rtt.?	–	–	–	–	–	–	1	–	**pl**
Subfamily Cholevinae									
Cholevinus sibiricus (Jean.)	–	1	–	3	1	1	3	1	**mt**
Family Staphylinidae									
Subfamily Tachyporinae									
Tachinus arcticus Motsch.	–	1	2	2	2	–	7	8	**mt**
Family Scarabaeidae									
Aphodius sp.	–	–	–	–	–	–	11	–	**xe**
Family Byrrhidae									
Subfamily Byrrhinae									
Morychus viridis Kuzm. et Korot.	18	4	14	14	11	452	43	82	**ss**
Family Dryopidae									
Dryopidae gen. indet.	–	–	–	–	–	–	–	1	**aq**
Family Elateridae									
Subfamily Dendrometrinae									
Denticollis varians Germ.	–	–	–	–	–	–	–	1	**fo**
Family Melyridae									
Troglocollops arcticus L. Medv.	–	–	–	–	–	3	1	3	**ms**
Family Tenebrionidae									
Upis ceramboides L.	–	–	–	–	–	–	1	–	**fo**
Family Anthicidae									
Anthicus ater Pz.	–	–	–	–	–	–	–	1	**me**
Family Cerambicidae									
Cerambicidae gen. indet.	1	–	–	–	–	–	–	–	**fo**
Family Chrysomelidae									
Subfamily Cassidinae									
Cassida sp.	–	–	–	–	–	–	1	–	**me**
Subfamily Chrysomelinae									
Chrysolina brunnicornis bermani Medv.	–	–	–	2	–	1	5	3	**st**
Ch. subsulcata Mnnh.	–	–	1	–	–	1	10	7	**tt**
Hydrothassa hannoverana F.	–	–	–	–	–	–	1	1	**ri**
Subfamily Galerucinae									
Galeruca daurica Jeann.	–	–	–	–	–	–	–	1	**st**
Family Brentidae									
Subfamily Apioninae									
Hemitrichapion tschernovi T.-M.	1	–	1	–	–	–	–	–	**dt**
Pseudoprotapion astragali Payk.?	–	–	–	–	–	–	1	1	**ms**
Family Brachyceridae									
Subfamily Erirhininae									
Notaris bimaculatus F.	–	1	–	1	–	–	1	2	**ri**
Family Curculionidae									
Subfamily Ceutorhynchinae									
Ceutorhynchus sp.	–	–	1	–	–	–	1	–	**dt**
Pelenomus velaris Gyll.	1	–	–	–	–	–	–	–	**ri**
Subfamily Entiminae									
Tribe Alophinini									
Lepidophorus thulius (Kiss.)	–	1	3	1	–	–	–	1	**dt**
Tribe Blosyrini									
Dactylotus globosus Gebl.	–	–	–	–	–	–	–	1	**mt**
Tribe Phyllobini									
Phyllobius kolymensis Kor. et Egorov	3	–	–	2	–	–	2	2	**ms**
Ph. virideaeris Laich.	–	–	1	–	–	–	–	–	**me**
Tribe Sitonini									
Sitona borealis Kor.	–	–	–	–	–	3	1	2	**dt**

Table 3. (Contd.)

Age	Chukochinsky		Akansky				Akansky?		
Section	73	77/2	77/2		70		66		eco
Species/sample	1, 2	12–17	10	2–7	6	5	1	2	
Subfamily Hyperinae									
Hypera diversipunctata Schrank.	–	–	–	–	–	–	1	2	**dt**
H. ornata Cap.	1	–	–	–	2	2	8	8	**dt**
Subfamily Lixinae									
Tribe Cleonini									
Coniocleonus astragali T.-M. et Kor.	–	–	–	–	1	–	–	–	**ms**
C. cinerascens Hochh.	1	–	–	–	–	–	6	1	**ms**
C. vinocurovi T.-M. et Kor.	–	–	–	–	–	–	2	–	**ms**
Coniocleonus sp.	–	–	–	–	1	–	–	–	**ms**
Stephanocleonus eruditus Faust	2	–	–	–	–	–	3	4	**st**
S. deportatus Chevr.	–	–	–	–	–	–	–	1	**st**
S. fossulatus Fisch.	–	–	–	–	–	–	21	2	**st**
S. incertus Ter-Min.	–	–	–	1	9	–	5	–	**st**
S. paradoxus Fahr.	–	–	–	–	–	–	1	–	**st**
S. tricarinatus F.-W.	–	–	–	–	–	–	1	–	**st**
Stephanocleonus sp.	–	–	1	5	–	–	1	–	**st**
Subfamily Molytinae									
Tribe Lepyrini									
Lepyrus nordenskioeldi Faust	1	4	4	–	2	–	10	8	**sh**
Subfamily Curculioninae									
Tribe Elliscini									
Dorytomus rufulus Maekl.	–	–	–	–	–	–	–	1	**sh**
Tribe Tichiini									
Tychius tectus LeC.	–	–	1	–	–	–	–	–	**ms**
Tribe Rhamphini									
Isochnus arcticus Kor.	–	–	1	–	–	–	–	1	**tt**
I. flagellum Erics.	–	–	–	–	–	–	–	1	**sh**
Order Heteroptera									
Family Pentameridae									
Aelia frigida Kir.	–	–	–	1	–	–	–	–	**ms**
Order Hymenoptera									
Hymenoptera gen. indet	–	–	–	–	–	4	7	5	**oth**
Order Trichoptera									
Thrichoptera gen. indet. (larvae)	–	–	–	–	–	–	–	5	**aq**
Order Diptera									
Diptera gen. indet. (puparia)	–	–	–	–	–	–	4	3	**oth**
Sum	89	43	41	69	62	582	238	250	

Sample 73-1 comes from the base of the unit, gray cloddy silt with small peat lenses; in addition to insects, the sample includes rodent and fish bones, freshwater mollusks, and ostracods. Sample 73-2 was taken 2.5 m above a small ice wedge cast filled by gray sandy silt with numerous small peat lenses and wood pieces. In addition to insects, the sample includes mollusk and ostracod shells.

The two samples are similar in taxonomic composition and we combine them in one assemblage. Sample 73-3 was taken 1 m upward in the section; it is poor in insects.

The insect fauna from samples 73-1 and 2 is dominated by the aquatic group. The diving beetle *Colymbetes dolabratus* composes more than half of individuals. This beetle is a common member of Quaternary communities, but rarely plays an important role. Extant *Colymbetes dolabratus* lives in various lentic water bodies from the forest to shrub tundra. The beetles spent winter in deep water, which remains unfrozen.

Terrestrial insects of sample 73-1,2 are represented by tundra and steppe species. Isolated fossils belong to the forest, shrub, and riparian groups. The steppe–tundra indicators are dominated in the terrestrial part of the fauna. These are: the pill beetle *Morychus viridis*

Table 4. Insects from the Alazeya sites (Alazeya Beds, Maastakh Formation)

Age	Alazeya Beds	Maastakh Formation								
Section	77/4	77/6			73		77/3		70	eco
Species/sample	18t	11, 12	9	4	5	4	4	6	2	
Order Coleoptera										
Family Gyrinidae										
Gyrinus opacus Salb.	–	1	–	–	–	–	–	–	–	**aq**
Family Carabidae										
Subfamily Nebriinae										
Notiophilus aquaticus L.	–	2	–	–	–	–	–	–	–	**xe**
Subfamily Carabinae										
Carabus sp.	1	–	–	–	–	–	–	1	–	**oth**
Subfamily Elaphrinae										
Elaphrus riparius L.	–	1	1	1	–	–	–	–	–	**ri**
Subfamily Scaritinae										
Dyschiriodes melancholicus Putz.	1	1	–	1	–	–	–	–	–	**ri**
Subfamily Trechinae										
Bembidion (*Asioperyphus*) *umiatense* Ldt.	–	3	–	1	–	–	–	–	2	**ri**
B. (*Peryphanes*) *dauricum* Motsch.	–	–	–	–	–	–	–	–	1	**dt**
Bembidion (*Peryphus*) sp.	–	–	–	1	–	–	–	–	–	**ri**
Bembidion sp.	1	–	1	–	–	–	–	–	–	**oth**
Subfamily Harpalinae										
Tribe Harpalini										
Dicheirotrichus mannerheimi Sahlb.	1	4	2	–	–	–	–	–	–	**dt**
Harpalus pusillus Motsch.	–	1	–	–	–	–	–	–	–	**st**
H. vittatus vittatus Gebl.	–	–	2	–	–	–	–	–	–	**ms**
Tribe Lebiini										
Cymindis arctica Kryzh. et Em.	–	–	–	–	–	–	–	1	–	**st**
Tribe Pterostichini										
Poecilus (*Derus*) *nearcticus* Lth.	–	4	–	5	1	–	1	–	6	**dt**
P. (*Cryobius*) *brevicornis* (Kby.)	14	6	–	5	–	–	–	1	–	**mt**
P. (*Cryobius*) *nigripalpis* Popp.	1	–	–	4	–	–	–	–	4	**dt**
P. (*Cryobius*) *pinguedineus* Esch.	1	11	3	10	–	1	–	–	8	**mt**
P. (*Cryobius*) *ventricosus* Esch.	–	2	–	5	–	–	–	1	5	**mt**
Pterostichus (*Cryobius*) sp.	–	–	6	4	–	1	–	20	16	**mt**
P. (*Lenapterus*) *agonus* Horn.	–	3	–	–	–	–	–	–	–	**mt**
P. (*Lenapterus*) *costatus* Men.	–	–	–	2	–	–	–	–	–	**mt**
P. (*Lenapterus*) *vermiculosus* Men.										**mt**
P. (*Tundraphilus*) *sublaevis* Sahlb.	–	1	1	4	–	–	–	–	–	**dt**
Stereocerus haematopus (Dej.)	–	6	1	1	1	–	–	–	–	**dt**
Tribe Zabrini										
Amara (*Amarocelia*) *interstitialis* Dej.	–	–	–	–	–	–	–	–	2	**dt**
Curtonotus alpinus Payk.	–	14	6	14	–	1	–	1	36	**dt**
C. bokori Csiki	1	–	–	1	–	–	–	–	–	**dt**
Family Dytiscidae										
Subfamily Agabinae										
Agabus moestus (Curt.)	1	–	–	–	–	–	–	–	1	**aq**
Agabus sp.	1	–	–	1	–	–	–	–	–	**aq**
SubfamilyColymbetinae										
Colymbetes dolabratus (Payk.)	1	1	–	–	–	1	–	–	–	**aq**
Subfamily Hydroporinae										
Hydroporus acutangulus Thoms.?	1	–	–	–	–	–	–	–	–	**aq**
Hydroporus sp.	–	1	–	1	–	–	–	–	–	**aq**

Table 4. (Contd.)

Age	Alazeya Beds	Maastakh Formation								
Section	77/4	77/6			73		77/3		70	eco
Species/sample	18t	11, 12	9	4	5	4	4	6	2	
Family Hydrophilidae										
Subfamily Hydrophilinae										
Hydrobius fuscipes F.	–	–	2	–	–	–	–	–	–	**aq**
Subfamily Sphaeridiinae										
Cercyon sp.	–	1	1	1	–	–	–	–	–	**ri**
Family Leiodidae										
Subfamily Leiodinae										
Cyrtoplastus irregularis Rtt.?	–	1	–	3	–	–	–	–	–	**pl**
Subfamily Cholevinae										
Cholevinus sibiricus (Jean.)	–	2	4	2	–	–	–	2	6	**mt**
Family Staphylinidae										
Subfamily Omaliinae										
Olophrum consimile Gyll.	–	1	–	–	–	–	–	–	–	**mt**
O. latum Maekl.	1	–	–	–	–	–	–	–	–	**pl**
O. rotundicolle Sahlb.	1	–	–	–	–	–	–	–	–	**pl**
Eucnecosum tenue LeC.	2	–	–	1	–	–	–	–	–	**pl**
Subfamily Tachyporinae										
Tachinus arcticus Motsch.	4	4	3	5	1	–	–	2	10	**mt**
Tachyporus sp.	1	–	–	–	–	–	–	–	–	**pl**
Subfamily Aleocharinae										
Aleochara sp.	–	–	–	–	–	–	–	1	–	**pl**
Family Scarabaeidae										
Aegali kamtschatica Motsch.	1	–	–	–	–	–	–	–	–	**ri**
Aphodius sp.	–	–	1	–	–	–	–	–	5	**xe**
Family Byrrhidae										
Subfamily Byrrhinae										
Morychus viridis Kuzm.et Korot.	1	8	7	34	3	–	–	–	123	**ss**
Family Melyridae										
Troglocollops arcticus L. Medv.	–	–	–	–	–	–	–	–	5	**ms**
Family Chrysomelidae										
Subfamily Chrysomelinae										
Chrysolina arctica Medv.	–	–	–	–	–	7	3	–	–	**ms**
Chrysolina sp.	–	1	–	–	–	–	–	–	–	**mt?**
Hydrothassa glabra Hbst.	1	–	–	–	–	–	–	–	–	**ri**
H. hannoverana F.	–	–	–	–	–	–	–	–	1	**ri**
Family Brentidae										
Subfamily Apioninae										
Hemitrichapion tschernovi T.-M.	–	1	–	2	–	–	–	–	–	**dt**
Family Brachyceridae										
Subfamily Erirhininae										
Notaris bimaculatus F.	–	3	2	7	1	1	–	2	–	**ri**
Grypus equiseti F.	–	1	–	–	–	–	–	–	–	**ri**
G. mannerheimi Faust.	–	1	–	–	–	–	–	–	–	**ri**
Family Curculionidae										
Subfamily Ceutorhynchinae										
Ceutorhynchus sp.	–	1	1	–	–	–	–	–	–	**dt**
Pelenomus velaris Gyll.	–	1	–	3	–	–	–	–	–	**ri**
Phytobius leucogaster (Marsh.)	–	–	1	–	–	–	–	–	–	**ri**

Table 4. (Contd.)

Age	Alazeya Beds	Maastakh Formation								
Section	77/4	77/6			73		77/3		70	eco
Species/sample	18t	11, 12	9	4	5	4	4	6	2	
Subfamily Entiminae										
Tribe Alophinini										
Lepidophorus thulius Kiss.	–	–	–	2	–	–	–	–	–	**dt**
Tribe Phyllobini										
Phyllobius kolymensis Kor. et Egorov.	–	1	–	1	–	–	–	–	3	**ms**
Tribe Sitonini										
Sitona borealis Kor.	–	–	–	1	–	–	–	–	1	**dt**
Subfamily Hyperinae										
Hypera ornata Cap.	1	4	–	5	–	–	–	2	6	**dt**
Subfamily Lixinae										
Tribe Cleonini										
Coniocleonus astragali T.-M. et Kor.	–	1	–	–	–	–	–	–	–	**ms**
C. vinocurovi T.-M. et Kor.	–	–	1	–	–	–	–	–	–	**ms**
Coniocleonus sp.	–	–	–	1	–	–	–	–	–	**ms**
Stephanocleonus eruditus Faust	–	–	–	–	–	–	–	–	12	**st**
S. fossulatus Fisch.	–	3	–	–	–	–	–	–	–	**st**
S. incertus Ter-Min.	–	3	–	–	–	–	–	–	–	**st**
Stephanocleonus sp.	–	3	3	–	–	–	–	–	–	**st**
Cleonini gen. indet.	2	–	–	–	–	–	–	–	–	**ms?**
Tribe Lepyrini										
Lepyrus nordenskioeldi Faust	–	4	1	–	–	–	–	–	–	**sh**
Tribe Pissodini										
Pissodes irroratus Reitt.	–	–	1	–	–	–	–	–	–	**fo**
Subfamily Curculioninae										
Tribe Rhamphini										
Isochnus arcticus Kor.	–	2	–	1	–	–	–	–	–	**tt**
I. flagellum Erics.	–	1	–	1	–	–	–	–	–	**sh**
Order Heteroptera										
Family Corixidae										
Sigara sp.	–	–	–	1	–	–	–	–	–	**aq**
Family Saldidae										
Salda sp.	1	–	–	–	–	–	–	–	–	**ri**
Order Megaloptera										
Family Sialidae										
Sialis sp. (larvae)	2	–	–	–	–	–	–	–	–	**aq**
Order Trichoptera										
Trichoptera gen. indet. (larvae)	–	–	–	–	2	–	5	–	–	**aq**
Sum	41	110	51	132	7	12	4	34	253	

(group **ss**) comprises 20% of the total number of beetles; insects of the **ms** group are the weevils *Phyllobius kolymensis* and *Coniocleonus cinerascens*; the **st** group is represented by the ground beetle *Cymindis arcticus* and the weevil *Stephanocleonus eruditus*. Tundra species play a minor role. Insects of the **dt** group are the ground beetles *Curtonotus alpinus* and *Dicheirotrichus mannerchaemi*, the weevils *Hemitrichapion tschernovi and Hypera ornata*, and the **mt** group is represented by the ground beetles *Pterostichus* (*Cryobius*) spp.

The high percent of aquatic beetles reflects local environment (a small pound). Terrestrial insects are dominated by xerophilous, especially steppe–tundra indicators. This assemblage belongs to the **TU/S-T**

Table 5. Insects from the Alazeya site (Kuobakh Beds, Holocene)

Age	Kuobakh Beds		Edoma Formation				Holocene				
Section	73	70	73		71		203				
Species/sample	6	1, 3	7	8–9	5	1–3	1	5	6	7–8	eco
Order Coleoptera											
Family Gyrinidae											
Gyrinus aeratus Steph.	–	–	–	–	–	–	–	6	3	1	**aq**
Gyrinus sp.	–	1	–	–	–	–	–	–	–	–	**aq**
Family Carabidae											
Subfamily Nebriinae											
Notiophilus aquaticus L.	–	–	–	–	–	–	1	1	–	–	**xe**
Subfamily Carabinae											
Carabus arvensis Hbst.	–	–	–	–	–	–	–	–	2	–	**fo**
C. canaliculatus Adams	–	–	–	–	–	–	–	–	2	–	**fo**
C. truncaticollis Esch.	1	–	–	–	–	–	–	–	–	–	**mt**
Carabus sp.	–	–	–	1	–	–	–	–	–	–	**oth**
Subfamily Elaphrinae											
Blethisa catenaria Brown.	–	–	1	–	–	–	–	1	1	–	**mt**
B. multipunctata (L.)							–	1	1	–	**ri**
Diacheila polita Fald.	–	1	–	–	–	–	–	3	–	–	**mt**
Elaphrus cupreus Duft.	–	–	–	–	–	–	–	1	–	–	**ri**
E. lapponicus Gyll.	–	–	–	–	–	–	–	2	–	–	**ri**
E. riparius L.	–	–	–	1	–	–	–	–	1	–	**ri**
E. splendidus Fisch.	–	–	–	–	–	–	–	1	–	–	**ri**
Subfamily Scaritinae											
Dyschiriodes melancholicus Putz.	–	–	–	–	–	–	–	4	–	1	**ri**
Subfamily Trechinae											
Bembidion (*Asioperyphus*) *umiatense* Lth.	–	–	–	–	2	–	1	–	2	3	**ri**
B. (*Bembidion*) *quadrimaculatum* L.	–	–	–	–	–	–	–	5	–	–	**ri**
B. (*Peryphanes*) *dauricum* Motsch.	–	2	–	–	–	–	1	1	–	–	**dt**
Bembidion (*Peryphus*) sp.	–	–	–	–	–	1	–	–	–	–	**ri**
Bembidion (*Plataphus*) sp.	–	–	–	–	–	–	–	–	1	–	**ri**
Subfamily Harpalinae											
Tribe Harpalini											
Dicheirotrichus mannerheimi Sahlb.	–	–	–	–	–	–	1	1	1	–	**dt**
Harpalus affinis Schrank	–	–	–	–	–	–	1	–	–	–	**ms**
H. amputatus amputatoides Mlynar	–	–	–	–	–	–	5	–	–	–	**ms**
H. cf. *pusillus* Motsch.	–	–	–	–	–	–	3	–	–	–	**st**
H. vittatus vittatus Gebl.	–	–	–	–	–	–	–	–	2	–	**ms**
Harpalus sp.	–	–	–	–	1	–	–	–	–	–	**ms**
Tribe Platynini											
Agonum quinquepunctatum Motsch.	1	–	–	–	–	–	–	4	–	–	**ri**
A. fuliginosum Panz.	–	1	–	–	–	–	–	–	–	–	**ri**
Tribe Pterostichini											
Poecilus (*Derus*) *nearcticus* Lth.	1	–	–	–	5	18	10	–	2	–	**dt**
Pterostichus (*Cryobius*) *brevicornis* (Kby.)	–	–	2	–	1	–	–	–	–	–	**mt**
P. (*Cryobius*) *nigripalpis* Popp.	–	–	–	–	–	–	3	1	–	–	**dt**
P. (*Cryobius*) *pinguedineus* Esch.	–	1	3	–	3	1	2	–	–	–	**mt**
P. (*Cryobius*) *ventricosus* Esch.	–	–	–	1	1	–	10	3	–	–	**mt**
Pterostichus (*Cryobius*) sp.	2	–	–	3	–	8	13	1	4	–	**mt**
P. (*Lenapterus*) *costatus* Men.	–	–	–	–	–	–	2	1	1	–	**mt**
P. (*Lenapterus*) *vermiculosus* Men.	1	–	–	–	–	–	–	–	–	–	**mt**
P. (*Petrophilus*) *eximius* Mor.	–	–	–	–	–	–	1	–	–	–	**dt**
P. (*Petrophilus*) *tundrae* Tschitsch.	–	–	–	–	–	–	1	–	–	–	**dt**
P. (*Tundraphilus*) *sublaevis* Sahlb.	–	–	–	1	1	–	5	–	1	–	**dt**
Stereocerus haematopus (Dej.)	1	–	–	–	–	–	–	1	–	–	**dt**
Tribe Zabrini											
Amara interstitialis Dej.	–	–	–	–	–	–	3	1	–	–	**dt**
Curtonotus alpinus Payk.	2	3	2	–	22	19	24	2	2	–	**dt**
C. bokori Csiki	–	–	–	–	–	–	3	–	–	–	**dt**

Table 5. (Contd.)

Age	Kuobakh Beds		Edoma Formation				Holocene				
Section	73	70	73		71		203				
Species/sample	6	1, 3	7	8–9	5	1–3	1	5	6	7–8	eco
Family Haliplidae											
Haliplus sp.	–	–	–	–	–	–	–	1	–	–	**aq**
Family Dytiscidae											
Subfamily Agabinae											
Agabus lapponicus (Thoms.) ?	–	–	–	–	–	–	–	5	2	2	**aq**
A. moestus (Curt.)	–	–	–	–	–	–	1	–	–	–	**aq**
A. serricornis (Payk.) ?	–	–	–	–	–	–	–	–	2	–	**aq**
A. thomsoni (J. Sach.)?	–	–	–	–	–	–	–	4	4	1	**aq**
Agabus sp.	–	–	–	–	1	–	–	–	–	–	**aq**
Subfamily Dytiscinae											
Dytiscus sp.	–	–	–	–	–	–	–	–	1	–	**aq**
Subfamily Colymbetinae											
Colymbetes dolabratus (Payk.)	1	–	1	–	–	–	3	–	–	1	**aq**
Subfamily Hydroporinae											
Hydroporus ex gr. *fuscipennis* Schaum.	–	–	–	–	–	–	–	–	1	–	**aq**
H. lapponum (Gyll.)	–	–	–	–	–	–	–	–	2	1	**aq**
Dytiscidae gen. indet.	–	1	–	–	–	–	–	–	–	–	**aq**
Family Hydrophilidae											
Subfamily Helophorinae											
Helophorus sibiricus Motsch.	–	–	1	–	–	–	–	–	1	–	**aq**
H. splendidus Sahlb.	–	–	–	–	–	–	–	3	–	–	**aq**
Helophorus sp.	–	1	–	–	1	–	–	–	–	–	**aq**
Subfamily Hydrophilinae											
Hydrobius fuscipes F.	–	2	–	–	–	–	–	2	4	–	**aq**
Subfamily Sphaeridiinae											
Cercyon sp.	–	7	–	–	–	–	1	1	–	–	**ri**
Family Leiodidae											
Subfamily Leiodinae											
Cyrtoplastus irregularis Rtt.?	–	2	–	–	–	–	–	2	–	–	**pl**
Leiodes sp.	–	2	–	–	1	–	–	–	–	–	**pl**
Subfamily Coloninae											
Colon sp.	–	–	–	–	–	–	–	1	–	–	**pl**
Subfamily Cholevinae											
Cholevinus sibiricus (Jean.)	1	1	–	1	3	3	–	1	–	–	**mt**
Family Silphidae											
Subfamily Silphinae											
Phosphuga atrata L.	–	–	–	–	–	–	–	1	–	–	**fo**
Thanatophilus dispar Hbst.	–	–	–	–	–	–	2	–	–	–	**oth**
Th. lapponicus F.	–	–	–	–	–	–	–	3	1	–	**oth**
Family Staphylinidae											
Subfamily Omaliinae											
Arpedium quadratum Gr.	–	–	–	–	–	–	–	1	–	–	**pl**
Subfamily Tachyporinae											
Tachinus arcticus Motsch.	–	10	1	5	4	2	1	1	–	–	**mt**
Tachyporus sp.	–	1	–	–	–	–	–	–	–	–	**mt**
Subfamily Oxytelinae											
Oxytellus sp.	–	–	–	–	–	–	–	1	–	–	**pl**
Subfamily Paederinae											
Lathrobium sp.	–	–	–	–	–	–	–	3	–	–	**pl**
Subfamily Staphylininae											
Philonthus sp.	–	–	1	–	–	–	–	–	–	–	**pl**
Quedius sp.	–	2	–	–	–	–	–	–	–	–	**pl**
Family Scarabaeidae											
Aphodius sp.	–	–	–	–	–	–	1	–	–	–	**xe**
Family Buprestidae											
Melanophila sp.	–	–	–	–	1	–	–	–	–	–	**fo**

Table 5. (Contd.)

Age	Kuobakh Beds		Edoma Formation				Holocene				
Section	73	70	73		71		203				
Species/sample	6	1, 3	7	8–9	5	1–3	1	5	6	7–8	eco
Family Byrrhidae											
Subfamily Byrrhinae											
Byrrhus sp.	–	1	–	–	–	–	–	–	–	–	**me**
Cytilus sericeus Forst.	–	–	–	–	–	–	–	3	2	–	**me**
Morychus viridis Kuzm. et Korot.	2	1	36	153	36	67	50	3	2	–	**ss**
Simplocaria arctica Popp.	–	1	–	–	–	–	–	4	–	–	**dt**
S. semistriata F.	–	–	–	–	–	–	–	–	–	1	**dt**
Family Heteroceridae											
Heterocerus sp.	–	–	–	–	–	–	–	–	–	1	**ri**
Family Elateridae											
Subfamily Dendrometrinae											
Berninelsonius hyperboreus (Gyll.)	–	1	–	–	–	–	–	–	–	–	**me**
Family Cantharidae											
Subfamily Cantharinae											
Cantharis sp.	–	–	–	–	–	–	–	2	–	–	**me**
Family Melyridae											
Troglocollops arcticus L. Medv.	2	1	–	–	3	9	–	1	–	–	**ms**
Family Coccinellidae											
Subfamily Coccinellinae											
Hyppodamia arctica Schneid.?	–	–	–	–	–	–	–	2	–	–	**ri**
Coccinelinae gen. indet.	–	–	–	–	–	–	1	–	–	1	**oth**
Family Lathridiidae											
Subfamily Corticariinae											
Corticaria sp.	–	5	–	–	–	1	–	1	–	1	**pl**
Family Melandryidae											
Melandrya dubia Shall.?	–	–	–	–	–	–	–	–	–	1	**fo**
Family Cerambicidae											
Cerambicidae gen. indet.	–	–	1	–	–	–	–	–	–	–	**fo**
Family Chrysomelidae											
Subfamily Donaciinae											
Donacia sp.	–	–	1	–	–	–	–	3	1	–	**ri**
Subfamily Cassidinae											
Cassida sp.	–	–	–	–	–	–	–	1	–	–	**me**
Subfamily Chrysomelinae											
Chrysolina arctica Medv.	–	–	–	–	–	2	–	–	–	–	**ms**
Ch. brunnicornis bermani Medv.	–	–	–	–	–	18	4	–	1	–	**st**
Ch. septentrionalis Men.	–	–	–	7	–	7	1	–	1	–	**mt**
Ch. subsulcata Mnnh.	–	–	–	2	–	2	1	–	1	–	**tt**
Colaphellus alpinus Gebl.	–	–	–	–	–	–	2	–	–	–	**ms**
Phaedon concinnus Steph.	–	1	–	–	1	–	–	1	–	–	**me**
Phratora polaris Schn.	–	1	–	–	–	–	–	1	–	–	**sh**
Subfamily Galerucinae											
Tribe Alticini											
Altica sp.	–	–	–	–	–	–	2	–	–	–	**fo**
Tribe Galerucini											
Galeruca daurica Jeann.	–	–	–	–	2	–	–	–	–	–	**st**
Galeruca sp.	–	–	–	–	–	–	–	–	–	1	**st?**
Tribe Luperini											
Luperus sp.	6	–	–	–	–	2	–	3	1	1	**fo**
Subfamily Eumolpinae											
Bromius obscurus L.	1	–	–	–	–	–	–	–	–	–	**me**
Family Brentidae											
Subfamily Apioninae											
Mesotrichapion wrangelianum Kor.	–	–	–	–	1	–	–	–	–	–	**dt**
Family Brachyceridae											
Subfamily Erirhininae											
Erirhinus aethiops (F.)	–	–	–	–	–	–	–	9	1	–	**ri**

Table 5. (Contd.)

Age	Kuobakh Beds		Edoma Formation				Holocene				
Section	73	70	73		71		203				
Species/sample	6	1, 3	7	8–9	5	1–3	1	5	6	7–8	eco
Notaris bimaculatus F.	1	2	–	–	–	1	3	5	–	1	**ri**
Grypus equiseti F.	–	–	–	–	–	–	–	–	1	–	**ri**
Family Curculionidae											
Subfamily Ceutorhynchinae											
Ceutorhynchus sp.	–	1	–	–	–	–	–	–	–	–	**dt**
Pelenomus velaris Gyll.	–	–	–	–	1	5	–	–	–	–	**ri**
Pelenomus sp.	–	–	–	–	–	–	–	1	–	–	**ri**
Phytobius leucogaster (Marsh.)	–	–	–	–	–	–	–	–	–	1	**ri**
Subfamily Entiminae											
Tribe Phyllobini											
Phyllobius kolymensis Kor. et Egorov.	–	–	–	–	22	98	5	–	–	–	**ms**
Ph. virideaeris Laich.	–	1	–	–	–	–	–	1	1	–	**me**
Tribe Sitonini											
Sitona borealis Kor.	2	–	–	–	–	–	–	–	–	–	**dt**
Subfamily Hyperinae											
Hypera diversipunctata Schrank.	–	–	–	–	–	–	2	–	–	–	**dt**
H. ornata Cap.	–	–	–	–	3	–	2	–	–	–	**dt**
Subfamily Lixinae											
Tribe Cleonini											
Coniocleonus cinerascens Hochh.	–	–	–	–	–	–	3	–	–	–	**ms**
C. ferrugineus Fahr.	–	–	1	–	–	–	–	–	–	–	**ms**
Coniocleonus sp.	–	–	–	–	–	1	–	1	–	–	**ms**
Stephanocleonus deportatus Chevr.	–	–	–	–	–	–	1	–	–	–	**st**
S. eruditus Faust	–	–	2	–	–	–	2	–	–	–	**st**
S. fossulatus F.-W.	–	–	–	–	–	–	4	–	–	–	**st**
Stephanocleonus sp.	–	–	–	–	9	–	–	–	–	–	**st**
Subfamily Molytinae											
Tribe Lepyrini											
Lepyrus gemellus Kby.	–	–	–	–	–	–	1	–	1	–	**sh**
L. nordenskioeldi Faust	–	–	–	–	–	–	7	1	1	1	**sh**
Tribe Pissodini											
Pissodes insignatus Boh.	–	–	–	–	–	–	1	–	–	–	**fo**
Pissodes sp.	–	–	–	–	–	–	1	–	–	–	**fo**
Subfamily Curculioninae											
Tribe Elliscini											
Dorytomus rufulus amplipennis Tourn.	–	–	–	–	–	–	–	3	–	–	**sh**
Tribe Rhamphini											
Eubrychius velutus Beck.	–	–	–	–	–	–	–	4	–	–	**ri**
Isochnus flagellum Erics.	–	–	–	–	–	–	–	–	–	2	**sh**
Order Heteroptera											
Family Corixidae											
Sigara sp.	4	4	1	–	–	1	3	1	–	–	**aq**
Family Veliidae											
Microvelia ambricola Wrobl.	–	–	–	–	–	–	–	2	–	–	**aq**
Family Saldidae											
Salda sp.	–	–	–	–	2	–	–	–	–	–	**ri**
Family Pentameridae											
Neottiglossa metallica Jak.	–	1	–	–	–	–	–	–	–	–	**fo**
Order Hymenoptera											
Family Formicidae											
Camponotus herculeanus L.	–	–	–	–	–	–	–	2	1	–	**fo**
Formica sp.	2	10	–	–	–	–	–	–	–	–	**fo**
Leptothorax acervorum F.	–	–	–	–	–	–	–	1	–	–	**fo**
Hymenoptera gen. indet	–	5	–	–	–	–	–	–	–	1	**oth**
Family Sialidae											
Sialis sp. (larvae)	–	1	–	–	–	–	–	–	–	–	**aq**
Order Trichoptera											
Thrichoptera gen. indet. (larvae)	4	–	–	–	–	–	–	–	–	3	**aq**
Sum	31	69	54	175	127	266	195	127	59	22	

type. Wood remains and individual forest insect species are indicative of the presence of trees, but the role of the forest was not very important.

Upward in the section, there is the Chukochinsky Horizon composed of gray silt with rare tiny peat layers; it was tested in section 77.2. Three samples (77.2/17, 15, and 12 were taken there, the samples come from similar altitude and contain similar insect fossils, we can combine these samples into one assemblage.

Assemblage 77.2/12,15,17 has normal proportions of aquatic and terrestrial species, so that terrestrial insects strongly prevail. This is typical for Pleistocene entomofaunas. The steppe–tundra indicators are poorly represented here (only 8.5% of the group **ss** alone). Other xerophilous species are more common, there are the ground beetle (group **xe**) *Notiophilus aquaticus* (4%) and 40% belong to the **dt** group (the ground beetles *Curtonotus alpinus, Dicheirotrichus mannerchaemi, Stereocerus haematopus, Poecilus nearcticus,* and the weevil *Lepidophorus thulius*). Indicators of the wet tundra environment (group **mt,** 30%) are represented by the ground beetles *Pterostichus* (*Cryobius*) spp., *P. vermiculosus, P. agonus, Diacheila polita*, the small carrion beetle *Cholevinus sibiricus*, and the rove beetle *Tachinus arcticus*. Assemblage 77.2/12,15,17 belongs to the **TU/XE** type. A number of relatively thermophilous species, such as *Elaphrus riparius, Notaris bimaculatus,* and *Colymbetes dolabratus*, are indicative of mild climate and environment close to forest–tundra.

The Akansky Horizon was tested in sections 70 and 77 (Fig. 15, Table 3). The paleomagnetic study has been applied to section 77 and displayed distinct boundary between the Chukochinsky and Akansky horizons. We took four samples from the Akansky Horizon of section 77: the lower sample (77.2/10) is rather rich in insects, but three higher samples (77.2/4, 7) are poor and similar; they are combined into one assemblage.

Assemblage 77.2/10 is dominated by steppe–tundra indicators: the group **ss** comprises 33%; thermophilous steppe insects are represented by the weevil *Stephanocleonus* sp. (2%). Tundra insects are not very numerous, the groups **dt** and **mt** compose 19 and 14%, respectively. The assemblage includes arctic tundra indicators (group **tt**, 5%), there are the leaf beetle *Chrysolina subsulcata* and the weevil *Isochnus arcticus*. Both species regularly occur in Pleistocene insect communities, but in this assemblage, they come in conflict with the presence of relatively thermophilous *Stephanocleonus sp.* Here, because of poor preservation of *Stephanocleonus* remains, we consider reworking of the steppe fossils. The species diversity of the assemblage is not very rich. The assemblage belongs to the **S-T/S-T** type, but the species composition and group proportions are not typical; the assemblage apparently reflects a more severe environment than usual steppe–tundra.

Assemblage 77.2/2-7 is similar to the previous one, but differs in detail. The steppe–tundra indicators play an important role here (37%) and thermophilous steppe species are more abundant. The steppe **st** group (12%) is represented by the weevils *Stephanocleonus* sp., *Stephanocleonus incertus*, and the leaf beetle *Chrysolina brunnicornis bermani*. This assemblage also includes the **ms** group (4%): the weevils *Phyllobius kolymensis* and the true bug *Aelia frigida*. Tundra insects (**dt** = 30%, and **mt,** = 22%) are rather frequent. Insects of the shrub and forest groups are absent in the assemblage, but riparian species, such as *Dyschiriodes melancholicus* and *Notaris bimaculatus*, are indicative of a relatively mild climate. The entomofauna of 77.2/2-7 is rich in species, especially in the tundra groups. The assemblage belongs to the **TU/S-T** type. Thus, a mild steppe–tundra environment with not very cold winter and relatively warm summer is reconstructed.

Two samples were taken from the Akansky Horizon in section 70. Sample 70/6 was taken from the top of gray silt unit that lies above the studied interval in section 77.2. The next sample, 70/5, was taken above, from a sandy silt unit with peat lenses. This unit underlies the Oler/Maastakh formations boundary (Fig. 15).

Assemblage 70/6 is similar to assemblage 77.2/2-7, but the role of steppe–tundra indicators is stronger (35.5%, including 14.5% of the **st** group). The assemblage belongs to the **S-T/S-T** type. The low species diversity of the entomofauna probably results from monotonous landscapes. Insect assemblage 70/5, which is youngest in the Akansky unit, differs from other samples of the Oler Formation. fossil insects are primarily concentrated in this top layer (its MNI is about 600), as compared with less than 100 in other samples. The entomofauna is strongly dominated by steppe–tundra indicators, 77% belong to the group **ss** (*Morychus viridis*) and 1%, of **ms** and **st** (*Troglocollops arcticus* and *Chrysolina brunnicornis bermani*). Insect of the wet environment are poorly represented, only 4% (*Pterostichus* (*Cryobius*) spp. *Cholevinus sibiricus*). One specimen belongs to the arctic leaf beetle *Chrysolina subsulcata*. This assemblage belongs to the **S-T/SS** type. The poor species diversity and high number of insects with a single superdominant suggest the presence of specific environments with a few factors strongly limiting the fauna and flora. At present, *Morychus viridis* lives in floristically poor places under severe conditions with contrast summer and winter temperatures and absence of the snow cover in the winter.

The unit of uncertain stratigraphic position “Sergeev Creek Beds” was tested in site 66; two insect samples, 66.1 and 66.2, were taken there. Both samples are numerous and rich with reference to the species composition. Steppe-related species prevail, in sum 42–43%. In sample 66.1, the share of the **st** group is 16%. There are *Stephanocleonus incertus, S. fossulatus, S. eruditus*, *S. tricarinatus, S. paradoxus*, *Troglocollops arcticus,* and *Chrysolina brunnicornis bermani*. Some species from this list (*Stephanocleonus incertus, S. tricarinatus, S. paradoxus*) presently live in southern Siberia and Mongolia. These species are indicative of a well-developed steppe part of steppe–tundra environment. Sample 66.2 is characterized by less prominent steppe influence, but the ecological structure is mostly the same. Both assemblages belong to the **S-T/S-T** type.

The Alazeya Beds, an interglacial unit (Fig. 15, Table 4), was tested in section 77, sample 77.18t. The sample was taken from a peat lens. Unfortunately, the sample is poor and the number of specimens is insufficient for analysis. It yields only scarce steppe–tundra indicators (*Morychus viridis*, a weevil of the tribe Cleonini); all other fossils belong to the tundra, riparian, and aquatic groups. The assemblage provides evidence of relatively wet rather than dry environments; this agrees with peat origin of the sample, but we have not found warm indicators. A small volume of the assemblage prevents reliable conclusions. We can only say that, during the time interval considered to be warm, the entomofauna still included steppe–tundra species.

The Maastakh Formation (Fig. 15, Table 4) was tested in sites 77, 73, and 70 in two different structures. The lower part of the formation composed of obliquely bedded sands with small gravel lenses was sampled in section 77, trench 6. Four samples were taken: 77.6.12, 77.6.11, 77.6.9, 77.6.4. Two lower samples come from the same elevation and are similar in species composition; thus, they are combined.

Assemblage 77.6.12,11 is dominated by tundra species: 34% belongs to the **dt** group (*Curtonotus alpinus, Poecilus nearcticus, Stereocerus haematopus, Bembidion dauricum, P. sublaevis, Dicheirotrichus mannerchemi, Hemitrichapion tschernovi, Hypera ornata*) and 26% are the **mt** group (*Pterostichus* (*Cryobius*) spp., *P. agonus*, *Cholevinus sibiricus, Olophrum consimile, Tachinus arcticus*). Steppe insects are presented mostly by the **ss**, **ms**, and **st** groups; their role is moderate, 20%. The assemblage includes a notable for the Pleistocene share of the riparian group (9%): *Elaphrus riparius*, *Dyschirius melancholicus*, *Pelenomus velaris*, *Notaris bimaculatus*, *Grypus equseti*, and *G. mannerheimi*. These riparian species are indicative of relatively warm conditions similar to modern shrub tundra or forest–tundra. The assemblage belongs to the **TU/S-T** type. The environment was steppe–tundra with domination of tundra vegetation; the climate was relatively mild.

The next sample, 77.6.9, is similar to the previous, but contains one tree-related species, the weevil *Pissodes irroratus*. We can reconstruct environment close to forest–tundra, with a high role of steppe vegetation.

The last sample from the lower part of the Maastakh Formation is 77.6.4. The steppe part of the insect fauna is better presented here, composing 30% of specimens; *Morychus viridis* (24%) plays the main role. The assemblage belongs to the **S-T/S-T** type. Thus, the proportion of steppe insects gradually increases in the sequence (Fig. 14).

The upper part of the Maastakh Formation (clear fine sand) was tested in detailed: seven samples from the 77, 73, and 70 sections were examined, although almost all samples were extremely poor. All of these isolated specimens were poorly preserved, probably as a result of transportation and local reworking. Most of the specimens belong to the leaf beetle *Chrysolina perforata* (**st** group) or *Ch. arctica* (**ms** group). The specimens differ from extant south Siberian *Chrysolina perforata* in the smaller size and finer punctation and from extant *Ch. arctica* endemic to Wrangel Island in the bright luster. Perhaps, this fossil species is an extinct relative of both modern ones. Such a strange feature, the presence of only one disrupted specimen of leaf beetle could be occasional, but the same picture was observed in two other localities: Maastakh Formation on the Chukochya River (Kiselev, 1981) and Maastakh Formation on the Keremesit River (see below). This is probably a natural feature. The environment was probably severe, dry and floristically poor.

The top sample (70.2) is sharply different. The assemblage is dominated by the **ss** group (*Morychus viridis*), 48%. All other insects are typical for the steppe–tundra entomofauna, including *Curtonotus alpinus, Poecilus nearcticus, Pterostichus sublaevis, Pterostichus* (*Cryobius*) spp., *Tachinus arcticus, Cholevinus sibiricus, Sitona borealis, Hypera ornata*, and *Phyllobius kolymensis*. Among assemblages of this age and older, strong dominance of the pill beetle *Morychus viridis* is recorded for the first time. This is usual in younger, Late Pleistocene faunas, where the proportion of this species is sometimes even higher. Anyway, the terminal stage of the Middle Pleistocene is characterized by a steppe–tundra fauna of the **S-T/S-T** type, close to **S-T/SS**.

The Kuobakh Beds (Fig. 15, Table 5) were tested in sections 73 and 70. Samples 73.6 and 70.3 were taken from ice wedge casts filled by silt with peat lenses; sample 70.1 comes from the terminal peat bed. All three samples are probably contemporaneous or very close in age.

In the Alazeya section, assemblage 73.6 is the first to contain a significant proportion of the forest group, 22%. It is correlated with high proportions of aquatic and riparian insects (28% in sum). Certain insects rare in the tundra, such as the leaf beetle *Bromius obscurus,* which feeds on willow herb, and lady birds are indirect indicators of warming. On the other hand, the assemblage contains individual steppe–tundra indicators, such as *Morychus viridis* and *Troglocollops arcticus*.

The next assemblage (70.1,3) is larger and richer in species. It is similar in structure to the previous one. A number of species are indicative of warming: the ant *Formica gagatoiges*, the true bug *Neottiglossa metallica,* and beetles, such as *Berninelsonius hyperboreus, Phaedon concinnus, Anthicus ater, Phyllobius virideaeris,* and *Byrrhus* sp. The forest (18%) and meadow (15%)

groups are more frequent than usually. Such high proportions of these groups are unique for the Pleistocene. Assemblage 70.1,3 also contains a significant proportion of the aquatic and riparian group (36% in sum). Steppe-related species are represented by the same two species, *Morychus viridis* and *Troglocollops arcticus*.

The entomofauna from the Kuobakh Beds gives clear evidence of interglacial conditions. The stratigraphic position at the base of the Upper Pleistocene suggests that the interglacial unit belongs to MIS5 (the last interglacial). The Kuobakh Beds on the Alazeya River provide a rare proven example of the last interglacial in the Kolyma Lowland. The environment was close to the northern taiga, with remains of steppe–tundra patches.

The Edoma Formation (Fig. 15, Table 5) was tested in sections 73 and 71. The lower sample (73.7) was taken directly above the Kuobakh peat, but the insect assemblage is sharply different. It is dominated by *Morychus viridis* (68%); all other ecological groups are poorly represented. Anyway, a couple of species, i.e., *Donacia* sp. and a long horn beetle, are indicative of relatively warm conditions close to the modern forest zone.

The next sample (73.8 + 73.9) is large, but more uniform ecologically. It lacks thermophilous species; the species composition is poor and includes forms common for the steppe–tundra entomofauna, such as *Curtonotus alpinus, Pterostichus sublaevis, Pterostichus* (*Cryobius*) spp. *Cholevinus sibiricus, Tachinus arcticus, Chrysolina septentrionalis*, and *Ch. subsulcata*. The assemblage is dominated by *Morychus viridis* (87%). Such incredibly domination is close to a record, but a close value has been recorded more than ones in the Late Pleistocene (see below).

Both assemblages belong to the **S-T/SS** type. The environment was short grass–sedge steppe–tundra; the climate was rather severe. A lack of moisture in the landscape, except for depressions, is reconstructed.

The Edoma unit in section 71 lies with disconformity above Maastakh sand. The lower deposits of the Edoma Formation and interglacial Kuobakh peat were probably eroded. The first sample (71.5) was taken from the lowermost part of the Edoma section. The assemblage is dominated by steppe-related species (57% in sum), but the ratio of the groups is different. The group **ss** forms only 28% of the fauna, but the role of the **st** and **ms** groups is greater. These groups include *Galeruca daurica, Stephanocleonus* sp., *Troglocollops arcticus,* and *Phyllobius kolymensis*. In addition, the assemblage contains individual thermophilous species, such as meadow *Phaedon concinnus* and forest *Melanophila* sp. The assemblage apparently corresponds to the type **S-T/S-T**. The entomofauna is richer than the previous one and probably reflects a less severe steppe–tundra environment, with various habitats.

The last Edoma assemblage (71.1-3) is also dominated by steppe-related insects (73% in sum); the groups **ss, st,** and **ms** compose 25, 7, and 41%, respectively (one specimen of *Coniocleonus* sp. and numerous *Phyllobius kolymensis*). A high proportion of the **ms** group allows the assignment of this fauna to the **S-T/MS** type. This is not a very frequent type of steppe–tundra faunas, but it has been recorded in some other localities. All assemblages of the **S-T/MS** type are dominated by *Phyllobius kolymensis* (*Ph. crassus* in Kiselev, 1981). This is a rare extant species, with little studied ecology, so that it is impossible to provide accurate reconstruction based on the type. The environment was quite unique and has no modern analogues. There is an interesting fact that Duvanny Yar on the Kolyma River, the stratotype sequence of the Edoma Formation, is characterized by a similar succession of insect assemblages: **S-T/SS** at the base and **S-T/MS** near the top (Kiselev, 1981).

3.1a1. Alazeya, Holocene

The Holocene was tested in section 203, which is situated between sections 72 and 73. The section is the first river floodplain terrace. We took five samples (Fig. 16, Table 5); three of them have yielded a sufficient number of specimens. Sample 203.1 comes from the lower obliquely bedded sand unit with peat lenses. The insect assemblage is rich and diverse. Unexpectedly, the sample yields high percent of steppe insects; the groups **ss**, **st**, and **ms** compose 28, 8, and 9%, respectively. Most of the specimens recorded here belong to the following species typical for the Pleistocene: *Stephanocleonus eruditus, S. fossulatus, S. deportatus, Chrysolina brunnicornis bermani, Phyllobius kolymensis, Coniocleonus cinerascens, Hypera ornata, H. diversipunctata,* and *Poecilus nearcticus*. At the same time, some species, for example, *Pissodes insignatus* and *Altica* sp. are indicative of forest environment. One species, the carrion beetle *Thanatophilus lapponicus,* is common in the modern fauna, but has never been recorded in the Pleistocene. Thus, it is probably an index species of the Holocene. The assemblage reflects transitional time of the early Holocene. It is possible that some fossils, especially heavy Cleonini weevils were reworked from the nearby Pleistocene sections.

The next sample (203.5) was taken from a silt unit with plant debris layers. The plant debris includes shrub twigs and larch cones. The deposits were formed in less dynamic conditions in comparison with the previous alluvial unit, so that the possibility of fossil transportation is considerably lower here.

The assemblage is dominated by aquatic and riparian insects. These insects are represented by various species, in contrast with the above-described assemblage from the Lower Oler, and includes *Agabus thomsoni, A. lapponicus, Haliplus* sp., *Helophorus splendidus, Hydrobius fuscipes*, *Sigara* sp. *Microvelia ambri-*

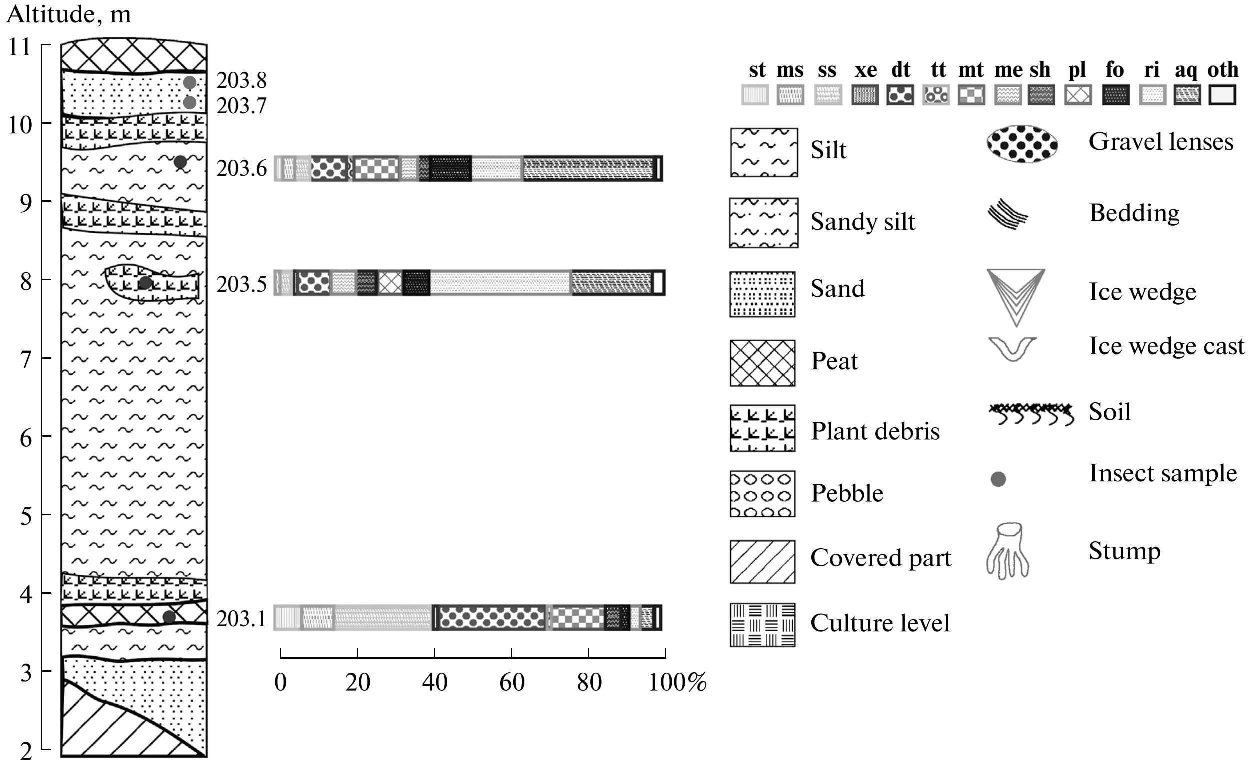


Fig. 16. Stratigraphic scheme and insect assemblages from the Holocene at the Alazeya River.

cola, Blethisa multipunctata, Elaphrus lapponicus, E. splendidus, Dyschiriodes melancholicus, Agonum quinquepunctatum, Donacia sp., *Hyppodamia arctica, Notaris aethiops, N. bimaculatus, Eubrychius velutus,* and others. These species are aquatic and riparian and, hence, rarely live outside the forest zone. There are also true forest indicators, such as *Phosphuga atrata, Luperus* sp., and *Camponotus herculeanus*. The plant litter inhabitants, such as *Oxytellus* sp., *Lathrobium* sp., *Cyrtoplastus irregularis, Corticaria* sp., are taken for indirect indicators of the forest environment. A number of species is limited mostly to the Holocene: *Cytilus sericeus, Thanatophilus dispar, Cantharis* sp., *Cassida* sp., and *Dorytomus rufulus amplipennis*. At the same time, the assemblage still includes singular steppe–tundra indicators, such as *Morychus viridis, Troglocollops arcticus,* and *Coniocleonus* sp.

Assemblage 203.5 clearly corresponds to a forest environment. The prevalence of aquatic and riparian species is a distinctive feature of such assemblages (Kiselev and Nazarov, 2009); it could be explained by the barrier role of rich riparian vegetation in the warm periods.

The next sample (203.6) was taken from the same layer, 1.5 m above the previous one. The two insect assemblages are similar in ecological composition. Almost half of the specimens are aquatic and riparian species: *Hydroporus* ex gr. *fuscipennis*, *Hydroporus* sp., *Agabus serricornis?, A. thomsoni, Dytiscus* sp., *Gyrinus aeratus*, *Helophorus sibiricus, Hydrobius fuscipes*, *Blethisa multipunctata, Elaphrus riparius*, *Donacia* sp., *Grypus equiseti*, and *Notaris aethiops*. A number of thermophilous insects (*Carabus arvensis, C. canaticulatus*, *Luperus* sp., *Cytilus sericeus*) are indicative of quite mild climate; among them, the carpenter ant *Camponotus herculeanus* is a direct indicator of the forest environment. At the same time, the assemblage differs from extant forest or even tundra–forest insect communities of the region. There are two main differences. First, the fossil assemblage includes the same arctic species, such as *Pterostichus costatus* and *Chrysolina subsulcata,* which presently live far northerly from the tree line. The second feature is the presence of the relict Pleistocene ground beetle *Poecilus nearcticus* and steppe beetles, such as *Chrysolina brunnicornis bermani, Stephanocleonus* sp., and *Morychus viridis*. These steppe–tundra relicts were still members of the early Holocene entomofauna.

Two top samples come from the upper sandy layer. The samples are poor, but contain species (*Heterocerus* sp. *Luperus* sp. *Dyschiriodes melancholicus*) clearly indicative of a mild climate.

Most of the samples studied from the Holocene site on the Alazeya River suggest that there was a relatively warm and wet climate, may be even warmer than today. The older assemblage reflects transitional time from the Pleistocene steppe–tundra to modern tun-

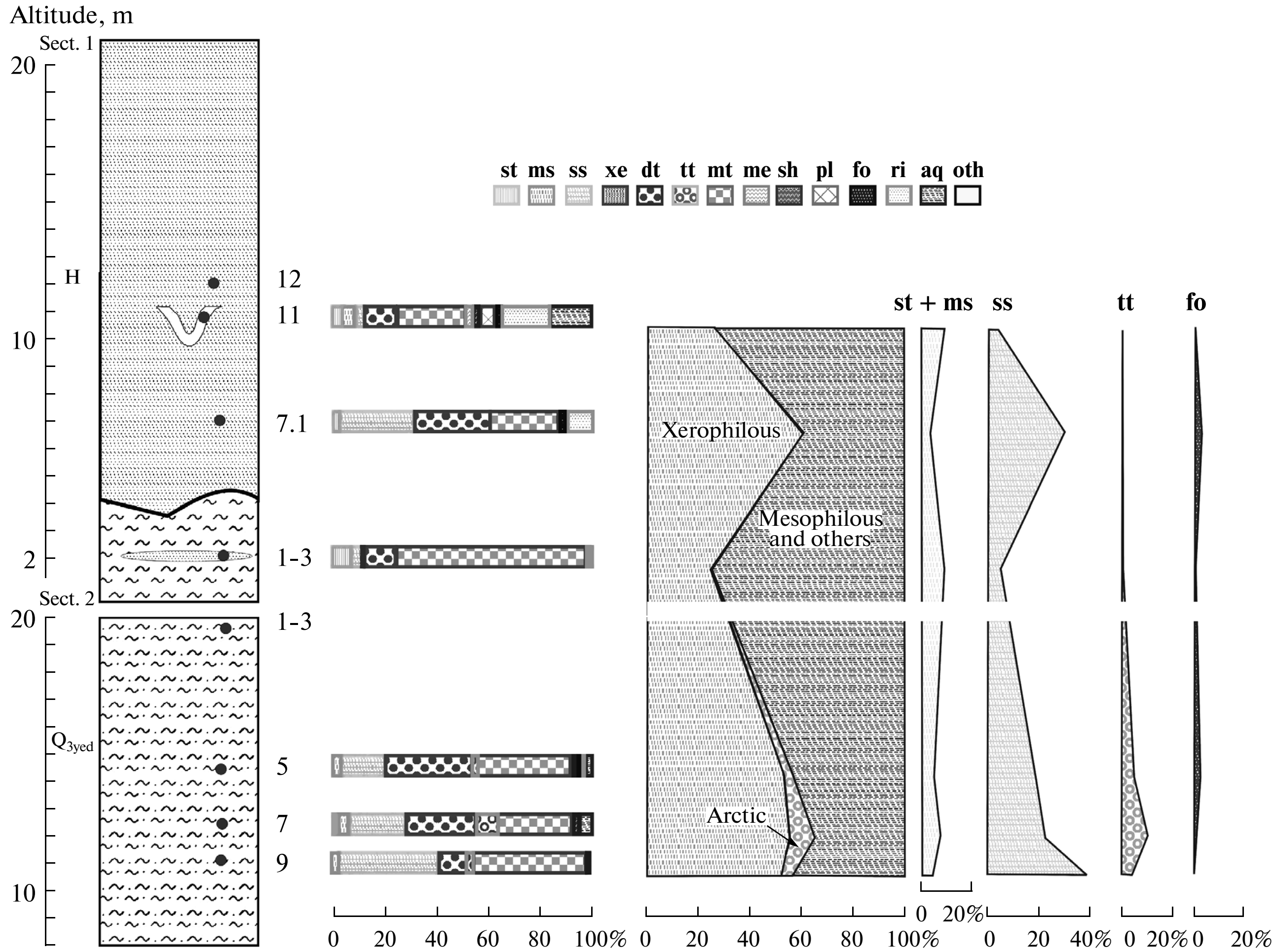


Fig. 17. Stratigraphic scheme and insect assemblages from the Medvezhyi Islands site. For legend, see Figs. 15 and 16.

dra–forest. The younger assemblages also include steppe–tundra relicts.

The floodplain terrace close to section 203 has been described before. Radiocarbon dating (Rybakova and Chernyshova, 1979) shows that the lower peat bed in this outcrop was formed around 8.4 ka. The pollen spectrum from the lower part of the section is dominated by grasses, *Artemisia,* and Chenopodiaceae; pollen of shrub birch and shrub alder play a secondary role. Upward in the section, the spectrum changes towards shrub–tree domination. The first appearance is birch tree, then, spruce, larch, and tall alder. Thus, the palynological spectrum confirms the results of the insect study.

3.1b. Medvezhyi Island

Insect samples from this region were collected by Kolesnikov in 1985 (Kuzmina and Kolesnikov, 2000). The sections studied are located on Chetyrekhstolbovoi Island (Figs. 1, 2), near altitude mark 41.4 m. Fossil insects were found in 12 samples from one Upper Pleistocene (section 2) and one Holocene (section 1) sections.

The Upper Pleistocene is represented by a monotonous 30-m-thick unit of ice rich sandy silt with plant debris. The large ice wedges and geomorphologic position suggest that this unit is comparable to the Edoma Formation of the Kolyma Lowland. Insect samples were taken from the top part of the unit (Fig. 17, Table 6).

Assemblage 2/9 is poor. Tundra mesohygrophilous species are best presented here (**mt** = 47%); the second position belongs to *Morychus viridis* (40%). Other groups are represented by individual specimens. Assemblage 2.9 is close to the **TU/XE** type.

The second sample (2/7) contains more abundant fossils. The tundra groups (**dt** = 33% and **mt** = 27%) compose about half of the assemblage. In addition, the assemblage includes a significant proportion of arctic tundra insects (**tt** = 8%), such as the leaf beetle *Chrysolina subsulcata* and the weevil *Isochnus arcticus.* The steppe–tundra indicators are poorly represented; the group **st** composed 2% (the leaf beetle *Chrysolina brunnicornis bermani*) and the group **ms,** 4.5% (weevil

Table 6. Insects from Medvezhii Islands

Age	Edoma Formation				Holocene				
Section	2				1				
Species/sample	9	7	5	1.3	1–3	7.1	11	12	eco
Order Coleoptera									
Family Gyrinidae									
Gyrinus opacus Salb.	–	–	–	–	–	–	1	1	**aq**
Family Carabidae									
Subfamily Nebriinae									
Notiophilus aquaticus L.	–	–	–	–	1	–	–	–	**xe**
Subfamily Carabinae									
Carabus sp.	–	–	–	–	–	–	–	1	**mt?**
Subfamily Elaphrinae									
Blethisa catenaria Brown.	–	–	–	–	–	–	3	–	**mt**
Elaphrus riparius L.	–	–	–	–	–	–	2	–	**ri**
Subfamily Trechinae									
Bembidion (*Asioperyphus*) *umiatense* Lth.	–	–	–	1	–	–	4	1	**ri**
Bembidion (*Plataphus*) sp.	–	–	–	–	–	–	2	–	**ri**
Subfamily Harpalinae									
Tribe Harpalini									
Harpalus sp.	–	–	–	–	–	–	2	–	**ms**
Tribe Platynini									
Agonum fuliginosum Panz.	–	–	–	–	–	–	–	1	**ri**
Tribe Pterostichini									
Poecilus (*Derus*) *nearcticus* Lth.	–	1	1	–	–	–	2	–	**dt**
P. (*Cryobius*) *brevicornis* (Kby.)	–	2	–	–	9	–	5	4	**mt**
P. (*Cryobius*) *pinguedineus* Esch.	–	1	–	–	2	1	2	–	**mt**
P. (*Cryobius*) *ventricosus* Esch.	3	1	–	–	–	2	2	–	**mt**
Pterostichus (*Cryobius*) sp.	–	3	7	1	4	–	3	–	**mt**
P. (*Lenapterus*) *costatus* Men.	2	4	2	–	–	–	3	–	**mt**
P. (*Tundraphilus*) *sublaevis* Sahlb.	1	–	–	–	–	–	2	–	**dt**
Stereocerus haematopus (Dej.)	1	2	–	–	–	–	3	–	**dt**
Tribe Zabrini									
Curtonotus alpinus Payk.	2	10	12	2	10	4	–	–	**dt**
Family Dytiscidae									
Subfamily Agabinae									
Agabus moestus (Curt.)	–	2	1	–	–	–	3	6	**aq**
SubfamilyColymbetinae									
Colymbetes dolabratus (Payk.)	–	–	–	–	–	–	6	–	**aq**
Subfamily Hydroporinae									
Hydroporus lapponicum (Gyll.)	–	–	–	–	–	–	2	1	**aq**
Hydroporus sp.	–	2	–	–	–	–	–	–	**aq**
Family Hydrophilidae									
Subfamily Helophorinae									
Helophorus splendidus Sahlb.	–	1	1	–	–	–	2	1	**aq**

Table 6. (Contd.)

Age	Edoma Formation				Holocene				
Section	2				1				
Species/sample	9	7	5	1.3	1–3	7.1	11	12	eco
Subfamily Hydrophilinae									
Hydrobius fuscipes F.	–	–	–	–	–	–	1	–	**aq**
Subfamily Sphaeridiinae									
Cercyon sp.	–	–	–	–	–	–	–	1	**ri**
Family Leiodidae									
Subfamily Leiodinae									
Cyrtoplastus irregularis Rtt.?	–	–	–	–	–	–	1	1	**pl**
Subfamily Cholevinae									
Cholevinus sibiricus (Jean.)	4	6	4	–	12	1	2	–	**mt**
Family Staphylinidae									
Subfamily Omaliinae									
Eucnecosum tenue LeC.	–	–	–	–	–	–	2	2	**pl**
Olophrum consimile Gyll.	–	–	–	–	–	–	1	3	**mt**
O. latum Maekl.	–	–	–	–	–	–	2	–	**pl**
Subfamily Tachyporinae									
Tachinus arcticus Motsch.	7	7	15	3	56	6	2	–	**mt**
T. brevipennis Sahlb.	–	1	–	1	–	–	–	–	**mt**
Tachyporus sp.	–	–	–	–	–	–	1	–	**pl**
Subfamily Steninae									
Stenus sp.	–	–	–	–	–	–	1	–	**ri**
Family Byrrhidae									
Subfamily Byrrhinae									
Morychus viridis Kuzm. et Korot.	14	19	13	2	5	11	3	–	**ss**
Simplocaria arctica Popp.	–	–	1	–	–	–	3	–	**dt**
S. semistriata F.	–	–	–	–	–	–	1	–	**dt**
Family Bostrichidae									
Stephanopachys sp.	–	–	1	–	–	–	–	–	**fo**
Family Ptinidae									
Subfamily Anobiinae									
Caenocara bovistae Hoffm.	–	–	–	–	–	–	1	–	**fo**
Family Melyridae									
Troglocollops arcticus L. Medv.	–	–	–	–	–	–	3	–	**ms**
Family Chrysomelidae									
Subfamily Cassidinae									
Cassida sp.	–	–	–	–	–	–	1	–	**me**
Subfamily Chrysomelinae									
Chrysolina brunnicornis bermani Medv.	–	2	–	–	8	–	1	–	**st**
Ch. subsulcata Mnnh.	1	2	–	–	–	–	–	–	**tt**
Ch. bungei Jac.	–	1	–	–	–	–	–	–	**tt**
Phaedon concinnus Steph.	–	–	–	–	1	–	1	–	**me**
Phratora polaris Schn.	–	–	–	–	–	–	–	1	**sh**

Table 6. (Contd.)

Age	Edoma Formation				Holocene				
Section	2				1				eco
Species/sample	9	7	5	1.3	1–3	7.1	11	12	
Subfamily Galerucinae									
Altica sp.	–	–	–	–	–	–	1	–	**fo**
Family Brentidae									
Subfamily Apioninae									
Mesotrichapion wrangelianum Kor.	–	2	–	–	–	–	–	–	**dt**
Family Brachyceridae									
Subfamily Erirhininae									
Notaris bimaculatus F.	–	–	1	–	–	3	4	–	**ri**
Family Curculionidae									
Subfamily Ceutorhynchinae									
Ceutorhynchus sp.	–	1	–	–	–	–	–	–	**dt**
Pelenomus velaris Gyll.	–	–	–	–	1	1	–	–	**ri**
Subfamily Entiminae									
Tribe Phyllobini									
Phyllobius virideaeris Laich.	–	–	–	–	1	–	–	1	**me**
Tribe Sitonini									
Sitona borealis Kor.	–	–	1	–	–	–	–	–	**dt**
Subfamily Hyperinae									
Hypera diversipunctata Schrank.	–	3	3	–	–	3	–	–	**dt**
H. ornata Cap.	–	5	6	–	3	4	–	–	**dt**
Subfamily Lixinae									
Tribe Cleonini									
Coniocleonus sp.	1	4	2	–	–	–	–	–	**ms**
Stephanocleonus eruditus Faust	–	–	–	–	–	–	2	–	**st**
Stephanocleonus sp.	–	–	–	–	–	1	–	–	**st**
Subfamily Molytinae									
Tribe Lepyrini									
Lepyrus nordenskioeldi Faust	1	3	1	–	–	–	1	1	**sh**
Tribe Hylobiini									
Hylobius piceus DeG.	–	–	–	–	–	1	–	–	**fo**
Subfamily Curculioninae									
Tribe Elliscini									
Dorytomus imbecillus Faust	–	–	–	–	–	–	1	–	**sh**
Dorytomus rufulus amplipennis Tourn.	–	–	–	–	–	–	–	1	**sh**
Tribe Rhamphini									
Isochnus arcticus Kor.	–	4	2	–	–	–	–	–	**tt**
Order Heteroptera									
Family Corixidae									
Sigara sp.	–	–	–	–	–	–	3	–	**ri**
Order Hymenoptera									
Family Formicidae									
Leptothorax acervorum F.	–	–	–	–	–	–	–	1	**fo**
Hymenoptera gen. indet.	–	–	–	2	–	–	–	–	**oth**
Order Diptera									
Chironomidae gen. indet (larvae)	–	–	–	10	–	–	–	–	**aq**
Sum	37	89	74	10	113	38	88	28	

Coniocleonus sp.), but the presence of cold resistant steppe–tundra indicator, the pill beetle *Morychus viridis* is more important (group **ss** = 21%). The poor species composition and absence of thermophilous species suggest a severe environment with relatively cold and dry summer. This assemblage belongs to the **TU/S-T** type.

Sample 2.5, taken from the middle part of the section, shows an increase in the role of tundra insects. The tundra groups make up two-thirds of the assemblage (**dt** = 30%, **mt** = 40%, and **tt** = 4%). Steppe–tundra indicators are represented mostly by the **ss** group (16.5%); meadow–steppe insects are singular and true steppe species are absent. The assemblage belongs to the **TU/XE** type. This assemblage is interesting in the presence of individual taiga species (a false powderpost beetle, *Stephanopachys* sp.) and relatively thermophilous riparian weevil *Notaris bimaculatus*. In addition, cold resistant species, such as the ground beetle *Pterostichus costatus* and the rove beetle *Tachinus arcticus* have been found in the assemblage. Such a combination is difficult to explain; probably, the sample includes a layer formed during a short warming period. The method of insect sampling in the permafrost area allows this opportunity, because we can take up to a 20-cm-thick sediment body.

The samples from the upper part of the section (2.1, 2.1, and 2.3) were taken close to each other and they are similar in insects, so that we can combine them. All the samples are poor in terrestrial insects, most of remains belong to head capsules of aquatic larvae, such as caddis flies and aquatic dipterans. Rare terrestrial beetles are represented mostly by mesic tundra species *Cholevinus sibiricus*; steppe–tundra indicators are represented by singular *Morychus viridis*. The number of specimens is insufficient for environmental conclusions; the type of assemblage is probably close to the previous one.

The Holocene site is located in the lake-thermokarst depression. The section is 18 m thick. The lower part is represented by greenish gray silt with ferriferous spots, plant debris, and small sand lenses. The upper part is composed of fine horizontally bedded sands with ice wedge casts.

A total of seven samples have been collected in the section (Fig. 17, Table 6). Samples 1.1, 1.2, and 1.3 come from the lower part; they are similar in species composition, so that they are combined in one assemblage. Assemblage 1.1–3 is dominated by the tundra mesohygrophilous group (**mt** = 74%); most of the specimens belong to the rove beetle *Tachinus arcticus*. Xerophilous insects play a secondary role: the groups **dt** = 11.5%, **xe** = 1%, **st** = 7%, and **ss** = 4%. A relatively high proportion of steppe insects in this tundra-like assemblage and the stratigraphic position of the unit (below thermokarst lake deposits, which probably results from melting and compression of Pleistocene deposits) suggest that Pleistocene and Holocene insects were mixed together in these strata. On the other hand, the upper insect samples, taken from obvious Holocene, contain an even higher share of steppe species.

Samples 1.7 and 1.10 were taken from the lower part of the sandy unit. The samples are similar in species composition, so that they are combined. The insect assemblage (surprise for the Holocene) is dominated by xerophilous insects, including the **ss** group (32%) and singular steppe insects, the weevil *Stephanocleonus* sp. One beetle is from the taiga group *Pissodes* sp. This assemblage is similar to the Pleistocene ones; however, the few number of specimens makes the conclusion doubtful. It is interesting that a weevil of the typical steppe genus *Stephanocleonus* first appeared in the insect record of Medvezhyi Island in the Holocene.

Sample 1.11 comes from an ice wedge cast from the middle part of the section. This assemblage is rather rich and has a typical Holocene character. The role of tundra insects is significant: **mt** = 27% and **dt** = 11%, but an unusually important role belongs to aquatic (**aq** = 18%) and riparian (**ri** = 13%) species. The assemblage includes insects from the group others (**oth** = 4%), which is represented by plant litter inhabitants: *Agathidium* sp., *Deliphrum* sp., *Tachyporus* sp., and individual meadow, shrub, and taiga insects. The steppe–tundra indicators, such as *Morychus viridis, Troglocollops arcticus*, *Chrysolina brunnicornis bermani,* and *Stephanocleonus eruditus* are also present here. The role of the steppe group is high for the Holocene, **st** = 7%. Assemblage 1.11 includes a number of relatively thermophilous species, such as *Blethisa catenaria, Olophrum consimile, Colymbetes dolabratus, Notaris bimaculatus, Elaphrus riparius,* and *Caenocara bovistae*. The insect assemblage is indicative of a warmer climate than at present: shrub tundra close to the tree line with steppe patches.

The last sample (1.12) of the Holocene section was taken in the upper ice wedge cast. This sample is poor in fossil specimens, but species diversity is relatively high. This assemblage does not include steppe species. Some thermophilous insects, such as the ant *Leptothorax acervorum* and the weevil *Dorytomus rufulus septentrionalis,* are indicative of environments close to shrub tundra or forest–tundra.

The insect fauna of Medvezhyi Island was formed in a relatively severe climate. The role of steppe insects during the Late Pleistocene was lower than in the southern sites, but the role of moisture-loving species was higher. The Pleistocene/Holocene transition is not sharp in this site. Steppe insects continued (even increased) their role in the early Holocene. A similar situation was described for west Chukotka fossil insect faunas (Kiselev and Nazarov, 2009). An interesting feature of the site is the permanent high role of the rove beetle *Tachinus arcticus* in Late Pleistocene and early Holocene insect assemblages. This beetle is usually not abundant in Quaternary faunas. It could be an example of a long-lived local species.

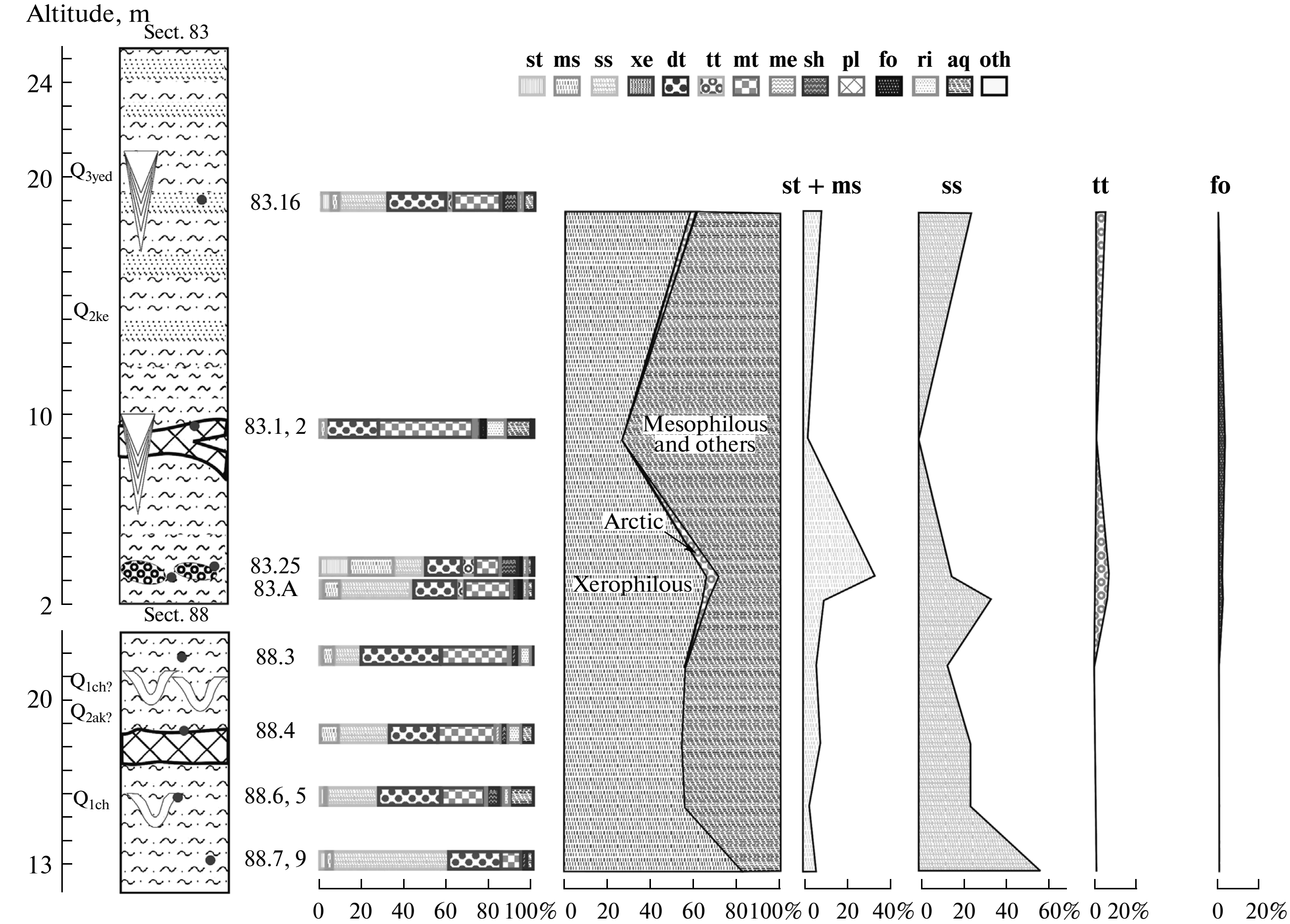


Fig. 18. Stratigraphic scheme and insect assemblages from the Khomus-Yuryakh site. For legend, see Figs. 15 and 16.

3.1c. Khomus-Yuryakh

The sites in question are located at the upper reaches of the Bolshoi Khomus-Yuryakh River, between the Alazeya and Indigirka rivers (Figs. 1, 2, 14e). A Quaternary sequence from the Lower to Upper Pleistocene was observed here. The sections were studied by an expedition of the Academy of Science of the USSR, with participation of A.V. Sher, A.Ya. Druk, and D.A. Gilichinsky in 1988 and 1989; a number of fossil insect samples were collected and transferred to me.

The Khomus-Yuryakh locality was mentioned in several papers (Lozhkin, 1977; Lozhkin and Anderson, 1995; Sher, 1997a; Virina, 1997), but complete results of investigation still remain unpublished. The insect samples were taken from section 88 (eight samples from the Oler Formation) and section 83 (three samples from the Keremesit Superhorizon and one from the lower part of the Edoma Formation) (Figs. 5, 18; Table 7).

The Oler Formation in section 83 is characterized by positive magnetics and belongs to the Akansky Horizon. In section 88, paleomagnetic studies were only performed in trenches 1 and 2. The results show that most (about two-thirds) of the Oler Formation belongs to the magnetic reverse Chukochinsky Horizon and the top belongs to the Akansky Horizon (Fig. 18).

The Keremesit Superhorizon is represented here by the local unit Khomus Horizon (Virina, 1997), composed of sandy deposits with peat layers in the lower part and, at the top, sand poor in organics, similar to the Maastakh Formation. The Edoma Formation is represented by typical silty deposits with large ice wedges.

The Chukochinsky Horizon of the Khomus-Yuryakh site was tested in section 88. Several samples were taken (9, 7, 5, 5a, 6: Fig. 18, Table 7). Samples 9 and 7 come from the lower part of the section; they are similar in species composition and, hence, combine in one assemblage. The insect assemblage is not rich, but the species composition is quite distinctive. The steppe–tundra indicators play an important role here. More than half of specimens (60%) are represented by *Morychus viridis*; steppe and meadow–steppe insects are singular. The second place (24%) belongs to the

Table 7. Insects from the Khomus-Yuryakh site

Age	Chukochinsky Horizon		Chukochinsky? Akansky? Horizon		Keremesit Horizon			Edoma Formation	
Section	88				83				
Species/sample	7, 9	5, 6	4	3	A	25	1, 2	16	eco
Order Coleoptera									
Family Gyrinidae									
Gyrinus opacus Salb.	–	5	–	–	–	–	–	–	**aq**
Family Trachypachidae									
Trachypachus zetterstedtii Gyll.	–	–	–	–	–	1	–	–	**fo**
Family Carabidae									
Subfamily Nebriinae									
Nebria frigida Sahlb.	–	–	–	–	–	–	–	1	**ri**
Notiophilus aquaticus L.	–	–	–	–	2	15	–	–	**xe**
N. semistriatus Say	–	–	–	–	1	–	–	–	**xe**
Subfamily Carabinae									
Carabus truncaticollis Esch.	–	1	–	–	1	13	–	–	**mt**
Subfamily Elaphrinae									
Blethisa catenaria Brown	–	–	–	–	–	6	–	–	**mt**
B. multipunctata (L.)	–	–	–	–	–	–	2	–	**ri**
Diacheila polita Fald.	–	–	1	–	–	3	2	–	**mt**
Elaphrus lapponicus Gyll.	–	–	–	–	–	7	–	–	**ri**
E. riparius L.	–	–	–	–	–	7	–	–	**ri**
Subfamily Trechinae									
Bembidion (*Asioperyphus*) *umiatense* Lth.	–	2	1	2	5	20	–	–	**ri**
B. (*Peryphanes*) *dauricum* Motsch.	–	–	–	1	–	7	4	2	**dt**
B. (*Peryphanes*) *grapii* Gyll.	–	–	1	–	–	16	–	–	**dt**
Bembidion (*Peryphus*) sp.	–	4	–	–	–	–	4	–	**ri**
Bembidion (*Plataphus*) sp.	–	–	–	4	–	10	–	–	**ri**
Subfamily Harpalinae									
Tribe Harpalini									
Dicheirotrichus mannerheimi Sahlb.	2	8	2	7	1	16	–	–	**dt**
Harpalus amputatus amputatoides Mlynar	–	–	–	1	2	–	–	–	**ms**
H. cf. *pusillus* Motsch.	–	–	–	–	–	2	–	4	**st**
H. vittatus alaskensis Lth.	–	–	–	–	4	–	–	–	**ms**
H. vittatus kiselevi Kat. et Shil.	–	2	–	2	–	120	–	–	**ms**
H. vittatus vittatus Gebl.	–	–	–	–	–	3	–	–	**ms**
Harpalus sp.	–	–	–	–	–	–	2	–	**ms**
Tribe Lebiini									
Cymindis arctica Kryzh. et Em.	–	–	–	–	–	3	–	3	**st**
Tribe Pterostichini									
Poecilus (*Derus*) *nearcticus* Lth.	2	10	–	3	4	99	–	–	**dt**
Pterostichus (*Cryobius*) *brevicornis* (Kby)	–	2	–	6	4	37	–	–	**mt**
P. (*Cryobius*) *nigripalpis* Popp.	–	1	–	3	–	12	–	–	**dt**
P. (*Cryobius*) *pinguedineus* Esch.	1	5	2	2	13	81	–	–	**mt**
P. (*Cryobius*) *ventricosus* Esch.	–	10	2	8	3	229	–	–	**mt**
Pterostichus (*Cryobius*) sp.	2	17	–	6	13	137	22	34	**mt**
P. (*Lenapterus*) *agonus* Horn.	–	1	–	2	1	3	2	–	**mt**
P. (*Lenapterus*) *costatus* Men.	–	–	–	–	1	37	–	3	**mt**
P. (*Lenapterus*) *vermiculosus* Men.	–	–	–	–	1	2	3	–	**mt**
P. (*Tundraphilus*) *sublaevis* Sahlb.	2	9	1	4	3	14	2	3	**dt**
Stereocerus haematopus (Dej.)	–	4	–	1	2	33	6	2	**dt**
Tribe Zabrini									
Amara interstitialis Dej.	–	–	–	–	–	2	–	–	**dt**
Curtonotus alpinus Payk.	2	25	4	20	26	503	5	30	**dt**
C. bokori Csiki	–	–	–	–	–	25	–	–	**dt**

Table 7. (Contd.)

Age	Chukochinsky Horizon		Chukochinsky? Akansky? Horizon		Keremesit Horizon			Edoma Formation	
Section	88				83				
Species/sample	7, 9	5, 6	4	3	A	25	1, 2	16	eco
Family Dytiscidae									
Subfamily Agabinae									
Agabus moestus (Curt.)	–	2	1	–	3	105	3	5	**aq**
A. thomsoni (J. Sach.)?	–	–	–	–	–	–	2	–	**aq**
Subfamily Colymbetinae									
Colymbetes dolabratus (Payk.)	1	6	–	–	1	11	2	1	**aq**
Subfamily Hydroporinae									
Hydroporus acutangulus Thoms.?	–	10	–	–	1	19	–	2	**aq**
Hydroporus sp.	–	–	1	–	–	–	–	–	**aq**
Oreodytes sanmarkii Sahl.	–	–	–	–	1	–	–		**aq**
Dytiscidae indet.	–	–	–	–	–	12	–	–	**aq**
Family Hydrophilidae									
Subfamily Helophorinae									
Helophorus splendidus Sahlb.	–	1	–	1	3	13	–	3	**aq**
Subfamily Hydrophilinae									
Hydrobius fuscipes F.	–	–	–	–	–	4	2	–	**aq**
Subfamily Sphaeridiinae									
Cercyon sp.	–	–	–	–	1	3	–	–	**ri**
Coelostoma orbiculare F.	–	–	–	–	–	1	–	–	**ri**
Family Leiodidae									
Subfamily Leiodinae									
Cyrtoplastus irregularis Rtt.?	–	3	–	1	–	4	–	–	**pl**
Subfamily Cholevinae									
Cholevinus sibiricus (Jean.)	–	3	2	9	8	42	–	3	**mt**
Family Staphylinidae									
Subfamily Omaliinae									
Olophrum consimile Gyll.	–	1	–	1	–	–	1	–	**mt**
Omaliinae gen. indet.	–	–	–	–	–	1	–	–	**pl**
Subfamily Tachyporinae									
Tachinus arcticus Motsch.	–	2	1	2	4	58	2	7	**mt**
T. brevipennis Sahlb.	–	–	1	2	1	–	–	–	**mt**
Subfamily Paederinae									
Lathrobium sp.	–	–	–	–	–	–	1	–	**pl**
Subfamily Staphylininae									
Quedius fuliginosus (Grav.)	–	–	–	–	1	–	–	–	**pl**
Quedius sp.	–	–	–	–	–	11	–	–	**pl**
Family Scarabaeidae									
Scarabaeidae gen. indet.	–	–	–	–	–	–	1	–	**oth**
Family Byrrhidae									
Subfamily Byrrhinae									
Morychus viridis Kuzm. et Korot.	18	52	8	15	87	885	–	45	**ss**
Subfamily Syncalyptinae									
C*urimopsis cyclolepidia* Muenst.	–	1	–	4	1	24	–	3	**dt**
Family Elateridae									
Subfamily Dendrometrinae									
Berninelsonius hyperboreus (Gyll.)	–	–	–	1	–	2	–	1	**me**
Family Melyridae									
Troglocollops arcticus L. Medv.	–	–	–	–	–	5	–	–	**ms**
Family Anthicidae									
Anthicus ater Pz.	–	–	–	–	–	1	–	–	**me**
Family Chrysomelidae									
Subfamily Donaciinae									
Donacia sp.	–	–	–	–	–	–	1	–	**ri**

Table 7. (Contd.)

Age	Chukochinsky Horizon		Chukochinsky? Akansky? Horizon		Keremesit Horizon			Edoma Formation	
Section	88				83				
Species/sample	7, 9	5, 6	4	3	A	25	1, 2	16	eco
Subfamily Cassidinae									
Cassida sp.	–	–	–	–	–	2	–	–	**me**
Subfamily Chrysomelinae									
Chrysolina arctica Medv.	–	–	–	–	–	1	–	–	**ms**
Ch. brunnicornis bermani Medv.	–	–	–	1	–	129	–	1	**st**
Ch. purpurata Fald.?	–	–	–	–	–	2	–	–	**st**
Ch. septentrionalis Men.	–	2	–	1	8	28	–	–	**mt**
Ch. subsulcata Mnnh.	–	–	–	–	8	236	–	1	**tt**
Ch. tolli Jac.	–	–	–	–	1	95	–	4	**tt**
Chrysolina sp. (nov.?)	–	–	–	–	1	3	–	–	**mt?**
Chrysomela blaisdelli V. D.?	–	–	–	–	–	28	–	–	**sh**
Ch. collaris L.	–	–	–	–	–	9	–	–	**sh**
Colaphellus alpinus Gebl.	–	–	–	–	1	28	–	–	**ms**
Gastrophysa viridula Deg.	–	–	–	–	1	–	–	–	**me**
Hydrothassa hannoverana F.	–	–	–	–	–	2	–	–	**ri**
Phaedon concinnus Steph.	–	–	–	–	1	7	1	–	**me**
Phratora polaris Schn.	–	1	–	–	–	8	–	–	**sh**
Ph. vulgatissima L.	–	–	–	–	–	7	–	–	**sh**
Subfamily Eumolpinae									
Bromius obscurus L.	–	–	–	–	–	4	–	–	**me**
Family Brentidae									
Subfamily Apioninae									
Hemitrichapion tschernovi T.-M.	–	–	–	–	2	30	–	1	**dt**
Mesotrichapion wrangelianum Kor.	–	–	–	–	5	3	–	–	**dt**
Pseudoprotapion astragali Payk.?	–	–	–	–	1	9	–	–	**ms**
Apioninae gen. indet.	–	–	–	–	–	3	–	–	**oth**
Family Brachyceridae									
Subfamily Erirhininae									
Erirhinus aethiops (F.)	–	–	–	–	–	2	–	–	**ri**
Notaris bimaculatus F.	–	–	–	–	1	54	–	1	**ri**
Grypus equiseti F.	–	–	–	–	–	6	–	–	**ri**
Family Curculionidae									
Subfamily Ceutorhynchinae									
Ceutorhynchus sp.	–	2	–	1	–	22	–	1	**dt**
Pelenomus sp.	–	–	–	–	–	–	–	1	**ri**
Subfamily Entiminae									
Tribe Alophinini									
Lepidophorus thulius (Kiss.)	–	1	–	–	–	13	–	–	**dt**
Tribe Phyllobini									
Phyllobius kolymensis Kor. et Egorov.	–	–	–	2	5	795	–	3	**ms**
Ph. virideaeris Laich.	–	1	1	–	–	61	–	–	**me**
Tribe Sitonini									
Sitona borealis Kor.	–	1	–	2	1	108	–	2	**dt**
S. lineellus Bonsd.	–	–	–	–	–	1	–	–	**me**
Subfamily Hyperinae									
Hypera diversipunctata Schrank.	–	–	–	–	7	4	–	5	**dt**
H. ornata Cap.	–	2	–	1	–	78	1	6	**dt**
Subfamily Lixinae									
Tribe Cleonini									
Coniocleonus astragali T.-M. et Kor.	–	–	–	–	–	47	–	1	**ms**
C. cinerascens Hochh.	–	–	1	–	3	143	–	–	**ms**

Table 7. (Contd.)

Age	Chukochinsky Horizon		Chukochinsky? Akansky? Horizon		Keremesit Horizon			Edoma Formation	
Section	88				83				eco
Species/sample	7, 9	5, 6	4	3	A	25	1, 2	16	
C. ferrugineus Fahr.	–	–	–	–	–	21	–	2	**ms**
C. vinocurovi T.-M. et Kor.	–	–	–	–	–	–	–	1	**ms**
C. zherichini T.-M. et Kor.	–	–	–	–	1	–	–	–	**dt**
Coniocleonus sp.	1	–	2	2	4	15	–	–	**ms**
Stephanocleonus eruditus Faust	1	5	–	–	5	683	–	3	**st**
S. incertus Ter-Min.	–	–	–	–	–	3	–	–	**st**
Subfamily Molytinae									
Tribe Hylobiini									
Hylobius piceus DeG.	–	–	–	–	–	2	1	–	**fo**
Tribe Lepyrini									
Lepyrus gemellus Kby.	–	–	–	–	2	–	–	–	**sh**
L. nordenskioeldi Faust	1	11	1	2	5	474	–	10	**sh**
Tribe Pissodini									
Pissodes sp.	–	–	–	–	1	–	–	–	**fo**
Subfamily Curculioninae									
Tribe Elliscini									
Dorytomus rufulus amplipennis Tourn.	–	–	–	1	–	1	–	–	**sh**
Dorytomus sp.	–	1	–	–	–	–	–	–	**sh**
Tribe Rhamphini									
Isochnus arcticus Kor.	–	–	–	–	–	39	–	1	**tt**
I. flagellum Erics.	–	–	–	–	–	13	–	3	**sh**
Subfamily Scolytinae									
Scolytinae gen. indet.	–	–	–	–	–	2	1	–	**fo**
Order Heteroptera									
Family Saldidae									
Salda sp.	–	–	1	1	–	3	–	–	**ri**
Order Hymenoptera									
Family Formicidae									
Leptothorax acervorum F.	–	–	–	–	–	1	–	–	**fo**
Hymenoptera gen. indet.	–	1	–	–	–	–	–	–	**oth**
Order Homoptera									
Cicadellidae gen. indet	–	1	–	–	–	–	–	–	**me**
Order Megaloptera									
Family Sialidae									
Sialis sp.	–	3	–	2	–	–	–	–	**aq**
Order Trichoptera									
Thrichoptera larvae	–	5	1	3	–	–	–	–	**aq**
Order Diptera									
Family Chironomidae									
Chironomidae gen. indet.	–	7	–	1	–	–	–	–	**aq**
Diptera fam. indet. (puparia)	–	2	–	1	–	–	–	–	**oth**
Sum	33	214	34	122	263	5889	73	199	

dt group; wet tundra insects are rare (9%). Assemblage 88.7+9 belongs to the **S-T/SS** type.

The next sample comes from trench 3+4 in section 88. It is impossible to determine with certainty the age of deposits, because this trench has not been tested by the paleomagnetic method, but according to the sedimentological structure, it probably belongs to the Chukochinsky Horizon. Sample 88.5+6 is rather rich. Steppe-related insects form 27% of the assemblage; most of them belong to the **ss** group (*Morychus viridis* composes 24%). True steppe (*Stephanocleonus eruditus*) and meadow–steppe (*Harpalus vittatus kiselevi*) insects are rare. The tundra groups form almost equal portions of the assemblage: **dt** = 28% and **mt** = 23%. The assemblage contains a relatively high proportion of aquatic beetles (11%).

The assemblage belongs to the **TU/S-T** type. The rich species composition and presence of some thermophilous species (*Olophrum consimile, Colymbetes dolabratus, Dorytomus* sp., *Phyllobius virideaeris, Cyr-*

toplastus irregularis) are indicative of relatively moderate environments.

The next sample (88.4) from site 88, trench 3+4 is relatively poor, but has a similar species composition.

The last sample (88.3) from site 88, trench 3+4 comes from a peat layer, which belongs to the upper Chokochinsky or lower Akansky horizons. The fossil insect assemblage is dominated by the tundra groups: **mt** = 35% and **dt** = 34%. The steppe groups play a secondary role, among them, 13% is *Morychus viridis*; steppe (*Chrysolina brunnicornis bermani*) and meadow–steppe (*Harpalus vittatus kiselevi, Phyllobius kolymensis*) insects are singular. The assemblage includes relatively thermophilous species, such as the shrub weevil *Dorytomus rufulus amplipennis*, meadow click beetle *Berninelsonius hyperboreus,* and plant litter *Cyrtoplastus irregularis*.

Assemblage 88.3 also belongs to the **TU/S-T** type, but the steppe influence is less evident here. The assemblage reflects mild and not very dry climate; steppe habitats were restricted.

Section 83 was sampled less detailed, but one outstanding fossil insect assemblage has been found here. This is sample 83.25 from a silty sandy unit, with gravel lenses and plant debris beds. The sampled layer belongs to the uppermost part of the Akansky Horizon. The deposits show positive magnetics; its local name is the Khomus-Yuryakh Horizon (Virina, 1997). Samples 83.25 and 83.25c from the nearby parts of the same level were screened in a search for rodent teeth; the combined sample is larger than usual and, in addition, it is overfull with insects.

To date, the insect fauna from 83.25 is the largest in Beringia. It has yielded more than 10000 specimens, which correspond to MNI about 6000. Such an extensive collection of well-preserved fossils allows the establishment of several new and probably extinct species.

Almost half of entomofauna 83.25 (49%) belong to steppe-related species. The group **ss** forms 15% and the group **st**, 14% (*Cymindis arctica, Troglocollops arcticus Chrysolina brunnicornis bermani, Stephanocleonus eruditus, S. incertus*); the group **ms** comprises 20% (*Harpalus vittatus, H.* cf. *pusillus, Colaphellus alpinus, Phyllobius kolymensis, Coniocleonus ferrugineus, C. cinerascens, C. astragali,* and others). We can see that the steppe and meadow–steppe groups are not only abundant, but also diverse.

The tundra groups play a secondary role: **dt** = 15% and **mt** = 13%. An interesting feature of this steppe-dominated assemblage is a significant proportion of cold resistant species of the group **tt** (6%). There are the arctic leaf beetles *Chrysolina subsulcata* and *Ch. tolli* and the arctic willow weevil *Isochnus arcticus*. The presence of these species is in conflict with the steppe part of the fauna, but, in fact, this is not a unique case. The combination of species, the modern temperature ranges of which do not overlap, is a distinctive feature of the steppe–tundra fauna (see remarks in Section 5.5).

Because of the extremely large sample, the species list is longer than usually, but not so much as could have been expected. Almost all recorded species fit into a common steppe–tundra biota. Some less numerous Holocene faunas are even more diverse in species composition.

Assemblage 83.25 belongs to the **S-T/S-T** type. It corresponds to continental climate with cold winter and relatively warm summer; the absence of Mongolian or south Siberian species is indicative of relatively low summer temperatures.

Sample 83.1+2 was taken from a thick peat bed with wood pieces. The assemblage is dominated by wet tundra species; the group **mt** composes 46% (*Pterostichus* (*Cryobius*) spp., *P. vermiculosus, P. agonus, Blethisa catenaria, Diacheila polita, Olophrum consimile, Tachinus arcticus*). The second most common group is dry tundra, **dt** = 24%; the contribution of aquatic and riparian species is similar, 21%. Steppe-related insects are only represented by tentatively meadow–steppe ground beetles of the genus *Harpalus*. On the other hand, the assemblage contains a number of thermophilous species, including tree-related weevil *Hylobius piceus* and a bark beetle.

Assemblage 83.1+2 belongs to the **TU/TU** type. The environment is considered to be close to forest–tundra. This peat bed, according to its stratigraphic position and insect fauna, is probably correlated with the Alazeya Beds on the Alazeya River.

The Edoma Formation was tested only by one sample (83.16) from the silty–sandy beds in the lower part of the unit. The assemblage is rather rich. It shows an increase in the proportion of steppe-related species. The groups **ss** and **st** comprise 22 and 5%, respectively (*Cymindis arctica, Chrysolina brunnicornis bermani, Stephanocleonus eruditus*); **ms** = 4% (*Phyllobius kolymensis, Coniocleonus ferrugineus, C. astragali, C. vinocurovi*). The tundra group plays a similar role, **dt** = 27% and **mt** = 25%.

Assemblage 83.16 belongs to the **S-T/S-T** type. Even the proportion of steppe species is not very high, the assemblage is certainly indicative of a steppe–tundra environment, which is typical for the Late Pleistocene.

3.1d. Molotkovskii Kamen'

The section Molotkovskii Kamen' on the Malyi Anyui River (Figs. 1, 2) was first mentioned by Alekseev (1970, 1978). Sher (1971) studied this section in detail in 1966 and collected the first insect samples there; in 1974, the section was studied by Kaplina (Kaplina and Giterman, 1983). Molotkovskii Kamen' is a 24-m-high river bluff with distinct peat beds (Fig. 18). These thick peat bodies attract attention of researchers intended to describe the interglacial units,

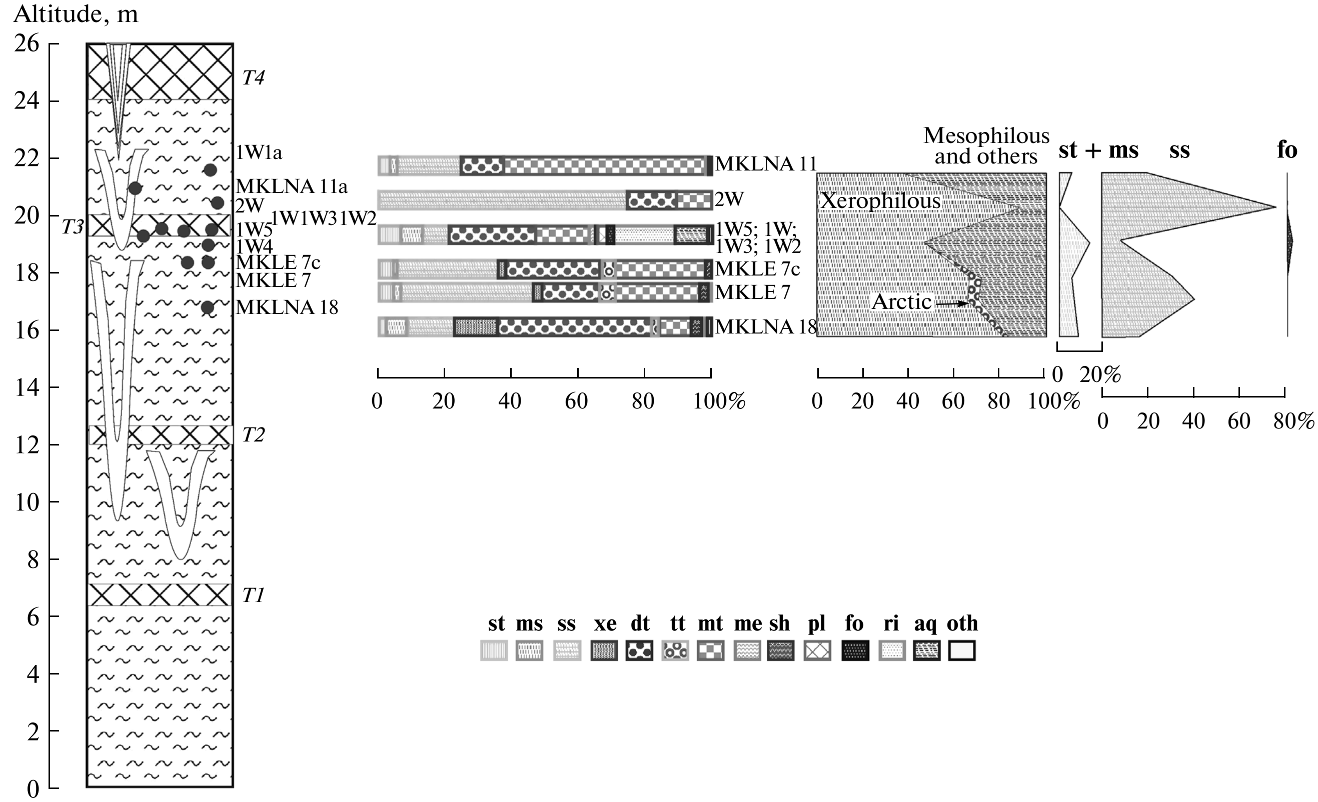


Fig. 19. Stratigraphic scheme and insect assemblages from the Molotkovskii Kamen' site. (*T1 T2 T3 T4*) peat layers; for explanation, see the text. For legend, see Figs. 15 and 16.

which are rare in the Kolyma Lowland. There are four peat beds; the first (T1) is situated a few meters above the river level and might be covered by hillside waste. It was correlated with the Middle Pleistocene Utkinskii Beds from the nearby section Utkinskii Kamen' (Sher, 1971). The age of the second peat bed (T2) remains uncertain, probably early Late Pleistocene; the third (T3) is dated Late Pleistocene. The fourth (T4) was formed in the Holocene (radiocarbon dates are 7920 and 8350: Kaplina and Giterman, 1983). According to Kaplina and Giterman (1983), the radiocarbon data established for T2 were 34400 ± 1000 and 42.80 ± 400 ka and T3 was dated 28.100–24.550 ka, i.e., the Karginian interval of the Late Pleistocene (MIS3). The pollen spectrum and plant macrofossils collected in either unit (T2 and T3) are indicative of a forest environment and relatively warm climate. Silty sandy deposits between the peat beds are characterized by grassy vegetation reflecting a cold climate (Kaplina and Giterman, 1983). With such a detailed study, the site of Molotkovskii Kamen' has become the type section of the Molotkovskii Horizon corresponding to the Karginian interstade (Shilo, 1987).

In 1992, A.V. Sher and W. Eisner visited the section with special purpose to trace environmental changes from "late Karginian warming" to the Holocene, but the main goal has not been reached, because fresh samples from T3 provide radiocarbon data over 40 ka. So, the previous conclusions were probably wrong; thus, the stratigraphy of the section should be revised (Sher et al., 2005).

The first insect samples from this problematic section were collected by Sher in 1966 and studied by Kiselev; there are four samples from T1 and one from T3. Several small samples from T3 were collected by Sher in 1992 and studied by me.

At present, we can add more information on the record of T3, which probably corresponds to the last interglacial.

The insect sequence (Fig. 19, Table 8) shows environmental changes recorded in the section. The Pleistocene peat beds, except for T2 which was not tested, could have corresponded to a warming and the silt units between them are characterized by steppe–tundra insect assemblages. Detailed analysis has disclosed a more complex picture. The first two fossil insect samples studied by Kiselev come from the lower part of the section just below T3. The combined assemblage is dominated by the **ss** group (62%), but also contains forest species probably reflecting a transitional time. The samples taken from T1 are different. According to insects, peat unit T1 is similar to the last interglacial Kuobakh Beds from the Alazeya River: 12% belong to

Table 8. Insects from the Molotkovskii Kamen' site, 1992

Species/sample MK-	MKLNA 18	MKLE 7	MKLE 7c	1W4	1W5	1W	1W3	1W2	2W	1W1a	MKLNA 11à	eco
Order Coleoptera												
Family Gyrinidae												
Gyrinus sp.	–	–	–	–	1	1	–	1	–	–	–	**aq**
Family Carabidae												
Subfamily Nebriinae												
Notiophilus aquaticus L.	–	6	3	–	–	–	–	–	–	–	–	**xe**
Subfamily Elaphrinae												
Blethisa catenaria Brown.	–	–	–	–	1	1	–	–	–	–	–	**mt**
Elaphrus riparius L.	–	–	–	–	1	–	–	–	–	–	–	**ri**
Subfamily Trechinae												
Bembidion (*Asioperyphus*) *umiatense* Lth.	–	–	–	–	–	2	–	6	–	–	1	**ri**
B. (*Peryphanes*) *dauricum* Motsch.	–	–	–	–	–	–	1	1	–	–	–	**dt**
Bembidion (*Peryphus*) sp.	–	–	–	–	1	–	–	–	–	–	–	**ri**
Subfamily Harpalinae												
Tribe Harpalini												
Dicheirotrichus mannerheimi Sahlb.	–	–	–	–	1	–	–	1	–	–	–	**dt**
Harpalus amputatus amputatoides Mlynar	–	–	–	–	–	–	1	–	–	–	–	**ms**
H. cf. *pusillus* Motsch.	–	–	–	1	–	–	–	–	–	–	–	**st**
H. vittatus alaskensis Lth.	1	–	–	–	–	–	–	–	–	–	–	**ms**
H. vittatus vittatus Gebl.	–	–	–	–	1	–	2	–	–	–	–	**ms**
Tribe Platynini												
Agonum sp.	–	–	–	1	–	–	–	–	–	–	–	**ri**
Tribe Pterostichini												
Poecilus (*Derus*) *nearcticus* Lth.	–	–	3	1	–	–	2	2	3	1	2	**dt**
Pterostichus (*Cryobius*) *brevicornis* (Kby.)	–	5	–	–	–	–	2	–	1	–	2	**mt**
P. (*Cryobius*) *nigripalpis* Popp.	–	2	6	–	–	–	–	–	6	–	4	**dt**
P. (*Cryobius*) *pinguedineus* Esch.	–	2	3	–	–	2	–	–	2	–	4	**mt**
P. (*Cryobius*) *ventricosus* Esch.	7	20	7	–	3	2	–	8	–	–	8	**mt**
Pterostichus (*Cryobius*) sp.	–	6	3	–	2	–	–	–	–	2	3	**mt**
P. (*Petrophilus*) *abnormis* Sahlb.	–	–	2	–	–	–	–	–	–	–	1	**dt**
P. (*Tundraphilus*) *sublaevis* Sahlb.	–	1	–	–	1	1	–	1	–	–	–	**dt**
Pterostichus (*Steropus*) sp.?	1	–	–	–	–	–	–	–	–	–	–	**oth**
Stereocerus haematopus (Dej.)	–	9	1	–	–	–	–	–	–	–	1	**dt**
Tribe Zabrini												
Amara (*Amarocelia*) *interstitialis* Dej.	–	–	–	–	2	1	–	–	–	–	–	**dt**
Curtonotus alpinus Payk.	7	18	18	1	7	7	4	8	6	2	8	**dt**
C. fodinae Mnnh.	–	–	–	–	–	–	–	1	–	–	–	**ms**
Family Dytiscidae												
Subfamily Agabinae												
Agabus moestus (Curt.)	–	–	–	–	–	–	–	2	–	–	–	**aq**
Agabus sp.	–	–	–	–	–	3	–	–	–	–	–	**aq**
Subfamily Colymbetinae												
Colymbetes sp.	–	–	–	–	1	3	–	2	–	–	–	**aq**
Subfamily Hydroporinae												
Hydroporus acutangulus Thoms.?	–	–	–	–	–	–	–	1	–	–	–	**aq**
H. lapponum (Gyll.)	–	–	–	–	1	–	–	–	–	–	–	**aq**
Subfamily Laccophilinae												
Laccophilus sp.	–	–	–	–	–	–	–	1	–	–	–	**aq**
Family Hydrophilidae												
Subfamily Helophorinae												
Helophorus splendidus Sahlb.	–	–	–	–	–	–	–	–	–	–	1	**aq**
Subfamily Sphaeridiinae												
Cercyon sp.	–	–	–	–	2	–	–	2	–	–	–	**ri**

Table 8. (Contd.)

Species/sample MK-	MKLNA 18	MKLE 7	MKLE 7c	1W4	1W5	1W	1W3	1W2	2W	1W1a	MKLNA 11à	eco
Family Leiodidae												
Subfamily Leiodinae												
Cyrtoplastus irregularis Rtt.?	–	–	–	–	–	–	–	1	–	–	–	**pl**
Leiodes sp.	–	–	–	–	–	–	–	1	–	–	–	**pl**
Subfamily Cholevinae												
Cholevinus sibiricus (Jean.)	–	7	4	1	1	–	2	–	–	4	28	**mt**
Family Silphidae												
Subfamily Silphinae												
Aclypea opaca (L.)	–	–	–	–	–	–	1	1	–	–	–	**oth**
Family Staphylinidae												
Subfamily Tachyporinae												
Tachinus arcticus Motsch.	1	17	10	–	–	–	–	1	–	4	35	**mt**
T. brevipennis Sahlb.	–	–	–	–	–	–	–	–	9	–	–	**mt**
Subfamily Steninae												
Stenus sp.	–	1	–	–	–	–	–	–	–	–	–	**ri**
Subfamily Paederinae												
Lathrobium brunniceps F.	–	–	–	–	–	–	–	3	–	–	–	**pl**
Family Scarabaeidae												
Aphodius sp.	11	–	–	–	–	–	–	–	–	–	–	**xe**
Family Byrrhidae												
Subfamily Byrrhinae												
Morychus viridis Kuzm. et Korot.	11	89	42	3	1	2	5	5	82	9	24	**ss**
Subfamily Syncalyptinae												
Curimopsis cyclolepidia Muenst.	–	4	2	–	–	–	–	–	–	–	–	**dt**
Family Elateridae												
Subfamily Dendrometrinae												
Denticollis varians Germ.	–	–	–	–	–	–	–	1	–	–	–	**fo**
Family Melyridae												
Troglocollops arcticus L. Medv.	–	1	–	1	–	–	–	–	–	2	2	**ms**
Family Chrysomelidae												
Subfamily Chrysomelinae												
Chrysolina arctica Medv.	–	–	–	–	–	–	–	–	–	–	1	**ms**
Ch. brunnicornis bermani Medv.	–	8	6	–	–	–	3	–	–	–	3	**st**
Ch. septentrionalis Men.	–	–	11	–	–	–	1	1	–	–	–	**mt**
Ch. subsulcata Mnnh.	–	11	–	–	–	–	–	–	–	–	–	**tt**
Ch. tolli Jac.	2	–	4	–	–	–	–	–	–	–	–	**tt**
Phaedon armoraciae L.	–	–	–	–	–	–	–	1	–	–	–	**me**
Subfamily Galerucinae												
Psylliodes cupreus (Koch)	–	–	–	–	–	–	–	1	–	–	–	**me**
P. attenuatus (Koch)	–	–	–	–	–	–	–	1	–	–	–	**me**
Subfamily Eumolpinae												
Bromius obscurus L.	–	–	–	1	–	–	–	–	–	–	–	**me**
Family Brentidae												
Subfamily Apioninae												
Mesotrichapion wrangelianum Kor.	–	–	–	–	–	1	–	–	–	–	–	**dt**
Family Brachyceridae												
Subfamily Erirhininae												
Notaris acridulus L.	–	–	–	–	–	4	–	3	–	–	–	**ri**
Notaris bimaculatus F.	–	–	–	–	2	2	1	5	–	1	–	**ri**
Family Curculionidae												
Subfamily Entiminae												
Tribe Sitonini												
Sitona borealis Kor.	1	2	3	–	–	–	1	–	–	1	–	**dt**

Table 8. (Contd.)

Species/sample MK-	MKLNA 18	MKLE 7	MKLE 7c	1W4	1W5	1W	1W3	1W2	2W	1W1a	MKLNA 11à	eco
Subfamily Hyperinae												
Hypera diversipunctata Schrank.	28	2	4	–	–	–	–	1	–	1	1	**dt**
H. ornata Cap.	1	–	1	–	–	–	1	–	1	–	–	**dt**
Subfamily Lixinae												
Tribe Cleonini												
Coniocleonus ferrugineus Fahr.	–	–	–	–	–	–	–	3	–	–	–	**ms**
C. vinocurovi T.-M. et Kor.	–	–	–	–	–	1	–	–	–	–	–	**ms**
Coniocleonus sp.	–	4	1	–	–	–	1	–	–	–	–	**ms**
Stephanocleonus eruditus Faust	1	1	–	1	–	1	3	1	–	–	2	**st**
S. fossulatus F.-W.	–	–	–	–	1	–	–	2	–	–	–	**st**
Subfamily Molytinae												
Lepyrus nordenskioeldi Faust	3	6	2	–	–	–	1	–	–	–		**sh**
Tribe Pissodini												
Pissodes piniphilus Hbst.	–	–	–	–	–	–	–	1	–	–	–	**fo**
Subfamily Curculioninae												
Tribe Rhamphini												
Isochnus arcticus Kor.	–	–	1	–	–	–	–	–	–	–	–	**tt**
Order Heteroptera												
Family Saldidae												
Salda littoralis L.	1	–	–	–	–	–	–	–	–	–	–	**ri**
Family Pentatomidae												
Aelia frigida Kir.	5	–	–	–	–	–	–	–	–	–	–	**ms**
Aelia sp.?	–	–	–	–	1	–	–	–	–	–	–	**ms**
Order Hymenoptera												
Family Formicidae												
Formica gagatoides Ruzs.	–	–	–	–	–	–	–	1	–	–	–	**fo**
Camponotus sp.	–	–	–	1	–	–	–	–	–	–	–	**fo**
Hymenoptera gen. indet.	4	1	–	–	–	–	–	–	–	–	1	**oth**
Order Homoptera												
Cicadellidae gen. indet	–	–	–	–	–	–	–	–	–	–	1	**me**
Order Trichoptera												
Thrichoptera gen. indet. (larvae)	–	1	–	–	–	–	–	–	–	–	–	**aq**
Order Diptera												
Family Chironomidae												
Chironomidae gen. indet.	–	–	–	–	–	–	–	–	–	–	1	**aq**
Diptera fam. indet. (puparia)	1	1	–	–	–	–	–	–	–	–	–	**oth**
Crustacea, order Cladocera												
Daphnia sp.	1	–	–	–	–	–	–	–	–	–	–	**aq**
Sum	81	222	137	12	31	34	32	71	110	27	131	

the forest group and small satellite groups, such as meadow, plant litter, shrub, aquatic and riparian play a significant role (47% in sum). At the same time, xerophilous steppe–tundra insects are also present. Despite similarity, we cannot correlate T1 with the Kuobakh Beds, because fossil bones found in the lower units of the section suggest the Middle Pleistocene age of the deposits. Thus, this could have been the Middle Pleistocene warm time MIS11 or MIS7.

The data of T3 and surrounding sediments show that the warm signal of that time was weaker. Forest species (*Denticollis varians, Pissodes piniphilus, Formica gagatoides*) are present, but they are fewer (3%), while indirect indicators (*Gyrinus* sp., *Colymbetes* sp., *Elaphrus riparius*, *Leiodes* sp., *Lathrobium brunniceps*, *Psylliodes cupreus, P. attenuates, Notaris acridulus*) are evidence of a relatively warm environment. The groups **me**, **pl**, **sh**, **aq**, **ri**, and **oth** play a greater role than usually, but less important than in the previous warm assemblage (34% in sum). The assemblage includes equal proportions of xerophilous and nonxerophilous groups and the share of the group **st** is even the largest in the Molotkovskii locality (7%).

The following succession of the faunal types is observed: **S-T/SS**, **TU/S-T** with **fo** (gap around T2), **TU/S-T**, **S-T/ST**, **S-T/ST**, **TU/S-T** with **fo**, **S-T/SS**, **TU/S-T**. Returning to the Alazeya reference site and other rich localities included in the QUINSIB database, it is evident that strong steppe–tundra types, such as **S-T/SS** and **S-T/ST** are rare in the pre-Late Pleistocene time. Thus, three factors prevent the correlation of T3 with the Last Interglacial (MIS5e); the environment before T3 was more typical for the Late Pleistocene steppe–tundra; the warming signal provided by assemblages from peat bed T3 is not strong; the next stage is characterized by a cold steppe–tundra environment. This interval probably belongs to the MIS5a stage. This guess fits to the scheme of the early Late Pleistocene climatic changes: relatively cold MIS5b, relatively warm MIS5a, and cold MIS4. The entire interglacial MIS5e time is missed in the section, but it could have been present in the T2 bed.

3.1e. Duvanny Yar

The Duvanny Yar section (Figs. 1, 2) is one of the most attractive sites in the Kolyma Lowland. The outcrop is about 9 km long and up to 55 m high, representing the typical Ice Complex deposits with huge ice wedges. It was repeatedly visited by many researchers. The easy access to the site, interesting geological structure, and extensive paleontological material provide complex study of the section (Baranova, 1957; Biske, 1957; Vas'kovsky, 1963; Kaplina and Kuznetsova, 1975; Kaplina et al., 1978; Kaplina, 1981; Sher, 1971; Sher et al., 1979; Tomirdiaro, 1980; Tomirdiaro and Chernen'ky, 1987; Konishchev, 1983; Gubin, 1984; Gubin et al., 2003; Vasil'chuk et al., 1988; Igarashi et al., 1995; Zanina et al., 2011).

Fossil insects from the section were studied by Kiselev (1981). The insect samples come from (1) the lowermost part of the section, silt with ice wedge casts filled by plant debris (four small samples); (2) the main body of the ice complex (eight rich samples); (3) the Holocene alas peat (four small samples).

Additional insect samples were taken by the research team headed by S. Gubin, who worked at the section since 1979. Gubin and, later, O. Zanina, a member of the team, focused on the study of paleosols (Gubin, 1984) and fossil ground squirrel nests (Gubin et al., 2003, Zanina et al., 2011). They screened many small samples from the soil horizons and ground squirrel borrows mostly for fossil seeds. This is unique material, primarily because the finds of arctic ground squirrel nest are very rare in western Beringia; Duvanny Yar and nearby sections are the only area where such fossils have been found (Zanina et al., 2011). In addition, fossil insects from the nests are characterized by excellent preservation, since they were buried in situ, and rare species, specific to the nest habitats (Zazula et al., 2007, 2011, Zanina et al., 2011). Three paleosol beds described as "Late Karginian" (Zanina et al., 2011) were discovered in the middle part of the section.

Stratigraphic features allow the first samples studied by Kiselev and the new ones to be correlated (Fig. 20). The sequence starts from the Kiselev's samples from the lower unit of the section, the horizon with ice wedge casts. A permafrost feature, such as the ice wedge cast, is considered to be an indicator of warming, but the fossil insect assemblage does not confirm this assumption. The assemblage is sharply xerophilous; it is dominated by *Morychus viridis* and also includes some cold resistant species (the weevil *Isochnus arcticus*) as well as some more thermophilous shrub leaf beetles *Chrysomela lapponica* and *Gastrolina* sp. (Kiselev, 1981). The warming episode was probably short and weak; we cannot correlate it with any main warming events of the Late Pleistocene scale.

The next samples taken below the first paleosol show even more influence of typical steppe–tundra species, the share of st and ms groups could rich 20% (significant amount for the steppe–tundra assemblage) and ss group could rich 70%.

The fossil insect assemblage from the first paleosol (Table 9) is also xerophilous, but includes more tundra species, such as the ground beetles *Poecilus* (*Derus*) *nearcticus, Pterostichus* (*Cryobius*) *ventricosus, P.* (*Cryobius*) *pinguedineus, P.* (*Petrophilus*) *abnormis, P.* (*Tundraphilus*) *sublaevis, Curtonotus alpinus, C. bokori*, the rove beetle *Tachinus brevipennis*, the weevils *Mesotrichapion wrangelianum, Coniocleonus zherichini, Hypera ornata,* and *H. diversipunctata*. The steppe and meadow–steppe groups remain their position, but the share of *Morychus viridis* decreases to 10–15%. The death-watch beetle (feeding on puffballs) *Caenocara bovistae,* which is more typical of the forest zone, was also found in the paleosol. We can notice the environment changes during the time of the first paleosol accumulation, but it is hard to say that it was a warming signal. More likely, the climate became slightly less continental and the specific landscape "cryoxerophilous steppe" did not play a prominent role.

Several samples studied by Kiselev apparently come from between the first and second paleosols (according to elevation and stratigraphy). The insect assemblages are xerophilous, the **ss** group returns its effect, but does not rich the previous superdominant position.

Two samples taken from the second paleosol are small, but we cannot combine them, because the difference in ecological structure is evident even, although the number of fossils is insufficient for accurate analysis. The first fossil beetle assemblage (the lower sample) is dominated by *Morychus viridis*. The

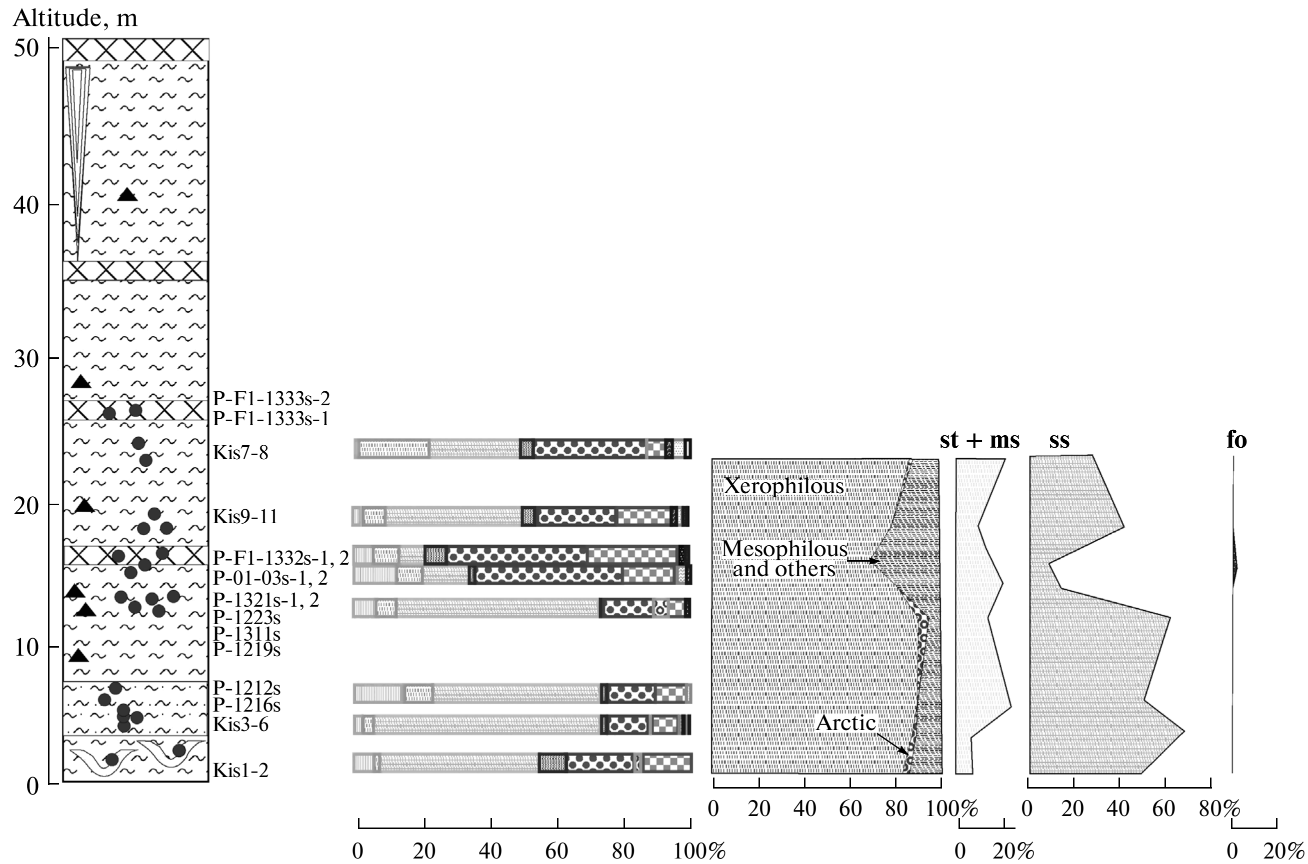


Fig. 20. Stratigraphic scheme and insect assemblages from the Duvanny Yar site (Edoma Formation). For legend, see Figs. 15 and 16; triangles are ground squirrel nests.

second sample includes only a few *M. viridis* specimens, but some tundra beetles, e.g., *Pterostichus* (*Cryobius*) spp. and *Curtonotus alpinus,* are better presented, along with aquatic beetles, *Agabus moestus* and *Helophorus splendidus,* and *Lepyrus volgensis* (associated with shrub willow). The first assemblage apparently reflects a steppe–tundra environment; the second contains more tundra species. Thus, this soil was probably formed under relatively wet conditions, but the lower horizon includes melted and compressed material from the preceding beds. The third paleosol has not been tested with reference to insects.

The sequence of fossil insect assemblages of Duvanny Yar is indicative of more or less permanently existing o dry and quite severe steppe–tundra environments (Fig. 20). Individual weak "warming" signals associated with the paleosol beds are insufficient to correlate the entire unit with the Karginian interval (MIS3). Despite the discussion whether the climate of MIS3 was warm, temperate, or cold in western Beringia (Sher et al., 2005), there is a problem with the age determination in Duvanny Yar. The lower part of the section (Vasil'chuk et al., 1988) probably belongs to MIS4, the radiocarbon age is below the limit (over 53 ka). The radiocarbon dates from the middle part of the section are uncertain. According to Zanina et al. (2011), the interval is dated 37–33 ka; Vasil'chuk et al. (1988) characterized the same unit as a partly reversed sequence, dated from 43 to 33 ka. In other recent studies, the lower part of the section includes dates 40–41 ka (Straus et al., 2010) and 29–32 ka in the upper 30-m-thick part (Straus et al., 2010; Spector et al., 2010). According to new unpublished data, all samples from the middle part fall beyond the radiocarbon method limit. Such miscorrelation prevents doubtless conclusions. We can trust only the upper dates. Probably, a part of the middle section unit is actually older than MIS3. The unit between the second and third paleosols, which has not been tested, may be younger and the top unit is clearly dated 13 ka (MIS2) (Zanina et al., 2011).

The ground squirrel nests (Tables 11, 12) were found mostly in the lower units, but a few were in the middle part and one nest was near the top of the section. Fossil insects from the nests are not numerous and this information does not help much in the environment reconstruction. In Alaska and Yukon, the finds of the nests are sprightly correlated with "cold" stages MIS4 and MIS2 (Zazula et al., 2007, 2011). Although we believe that some of nests from Duvanny

Table 9. Insects from Duvanny Yar paleosol

Age	Late Pleistocene									
Section	Duvanny Yar									
Species/sample	P-1216s	P-1212s	P-1321s-1	P-1321s-2	P-1219s	P-01-03s-1	P-01-03s-2	P-1311s	P-1232s	eco
Order Coleoptera										
Family Carabidae										
Subfamily Trechinae										
Bembidion (*Plataphus*) sp.	–	1	–	–	–	–	–	–	–	**ri**
Subfamily Harpalinae										
Tribe Harpalini										
Dicheirotrichus mannerheimi Sahlb.	–	4	–	–	–	–	–	–	–	**dt**
Harpalus vittatus kiselevi Kat. et Shil.	–	5	–	–	–	–	–	–	–	**ms**
H. obtusus obtusus Gebl.	–	–	–	–	1	–	–	–	–	**ms**
Tribe Lebiini										
Cymindis arctica Kryzh. et Em.	–	2	–	–	–	–	1	–	–	**st**
Tribe Pterostichini										
Poecilus (*Derus*) *nearcticus* Lth.	–	2	–	–	–	–	7	–	–	**dt**
Pterostichus (*Cryobius*) *brevicornis* (Kby.)	–	2	–	–	–	–	4	–	–	**mt**
Pterostichus (*Cryobius*) sp.	–	5	–	–	–	–	1	–	1	**mt**
P. (*Petrophilus*) *abnormis* Sahlb.	–	–	–	–	–	–	1	–	–	**dt**
Stereocerus haematopus (Dej.)	–	–	–	–	–	1	–	–	–	**dt**
Tribe Zabrini										
Curtonotus alpinus Payk.	–	6	1	–	–	1	8	–	6	**dt**
Family Leiodidae										
Subfamily Cholevinae										
Cholevinus sibiricus (Jean.)	–	–	1	–	–	–	–	–	–	**mt**
Family Staphylinidae										
Subfamily Tachyporinae										
Tachinus arcticus Motsch.	–	1	–	–	–	2	–	–	–	**mt**
T. brevipennis Sahlb.	–	–	1	–	–	–	–	–	–	**mt**
Family Scarabaeidae										
Aphodius sp.	–	1	1	–	–	–	1	–	–	**xe**
Family Byrrhidae										
Subfamily Byrrhinae										
Morychus viridis Kuzm. et Korot.	1	46	–	–	–	–	6	1	38	**ss**
Family Chrysomelidae										
Subfamily Chrysomelinae										
Chrysolina arctica Medv.	–	2	–	–	–	–	–	–	1	**ms**
Ch. subsulcata Mnnh.	–	–	–	–	–	–	–	–	1	**tt**
Ch. tolli Jac.	–	–	–	1	–	–	–	–	–	**tt**
Phratora polaris Schn.	–	–	–	–	–	–	–	–	1	**sh**

Table 9. (Contd.)

Age	Late Pleistocene									
Section	Duvanny Yar									
Species/sample	P-1216s	P-1212s	P-1321s-1	P-1321s-2	P-1219s	P-01-03s-1	P-01-03s-2	P-1311s	P-1232s	eco
Family Brachyceridae										
Subfamily Erirhininae										
Notaris bimaculatus F.	–	1	–	–	–	–	–	–	–	**ri**
Family Brentidae										
Subfamily Apioninae										
Mesotrichapion wrangelianum Kor.	–	–	–	–	–	–	–	–	1	**dt**
Family Curculionidae										
Subfamily Entiminae										
Tribe Phyllobini										
Phyllobius kolymensis Kor. et Egorov	1	–	–	–	–	1	–	–	1	**ms**
Ph. virideaeris Laich.	–	–	–	–	–	–	1	–	–	**me**
Subfamily Hyperinae										
Hypera ornata Cap.	–	2	–	–	–	–	1	–	1	**dt**
Subfamily Lixinae										
Tribe Cleonini										
Coniocleonus vinokurovi T.-M. et Kor.	–	–	–	–	–	–	–	–	1	**ms**
Coniocleonus sp.	–	–	–	–	–	–	2	–	–	**ms**
Stephanocleonus eruditus Faust	–	10	–	–	–	–	4	–	3	**st**
Stephanocleonus sp.	2	–	–	–	–	–	–	–	1	**st**
Subfamily Molytinae										
Tribe Lepyrini										
Lepyrus nordenskioeldi Faust	–	–	–	–	–	1	–	–	–	**sh**
Subfamily Curculioninae										
Tribe Rhamphini										
Isochnus arcticus Kor.	–	–	1	–	–	–	–	–	–	**tt**
Order Heteroptera										
Family Pentatomidae										
Pentatomidae gen. indet.	–	–	–	–	–	–	1	–	–	**oth**
Sum	4	90	5	1	1	6	38	1	56	

Yar belong to MIS4, anyway, there are nests that undoubtedly come from the MIS3 unit. We can explain the difference by a stable persistance of the steppe–tundra environment in western Beringia throughout the Late Pleistocene.

Fossils excavated from the nests are perfectly preserved. Storage behavior of the ground squirrel allowed keeping the freeze temperature of their food, which includes mostly seeds with admixture of insects. Insects got into the burial following different ways. Maybe some of them were collected by the nest hosts as protein source (ground squirrels eat insects in captivity), but most of insects were occasion visitors from surrounding landscapes. Rodent borrows are good shelters for many insects; some of them could be associated with the host animal. The species composition

Table 10. Insects from Duvanny Yar, Stanchikovskii Yar, and Chersky-Zelenyi Mys paleosol

Age	Late Pleistocene										
Section	Duvanny Yar				Stanchikovskii Yar				Chersky		
Species/sample	P-1332s-1	P-1332s-2	P-1333s-1	P-1333s-2	P-1304	P-08-03	P-09-03	P-978	Ch-2003	P-1211	eco
Order Coleoptera											
Family Carabidae											
Subfamily Trechinae											
Bembidion (*Peryphus*) *dauricum* Motsch.	–	–	–	–	–	2	–	–	1	–	**dt**
Subfamily Harpalinae											
Tribe Harpalini											
Dicheirotrichus mannerheimi Sahlb.	–	–	–	–	–	13	–	–	–	–	**dt**
Harpalus pusillus Motsch.	–	–	–	–	–	2	–	–	–	–	**st**
H. obtusus obtusus Gebl.	–	–	–	–	–	3	–	–	–	–	**ms**
Tribe Lebiini											
Cymindis arctica Kryzh. et Em.	–	1	–	–	–	2	–	–	–	–	**st**
Tribe Pterostichini											
Poecilus (*Derus*) *nearcticus* Lth.	–	1	–	–	–	3	–	2	1	4	**dt**
Pterostichus (*Cryobius*) *brevicornis* (Kby.)	–	–	–	–	–	68	2	2	7	–	**mt**
P. (*Cryobius*) *pinguedineus* Esch.	6	1	–	–	–	–	–	–	–	–	**mt**
P. (*Cryobius*) *ventricosus* Esch.	–	2	–	–	–	–	–	1	–	–	**mt**
Pterostichus (*Cryobius*) sp.	–	–	–	6	1	12	5	–	7	1	**mt**
P. (*Lenapterus*) *agonus* Horn.	–	–	–	–	–	–	–	–	1	–	**mt**
P. (*Petrophilus*) *abnormis* Sahlb.	1	–	–	–	–	7	1	1	–	–	**dt**
P. (*Petrophilus*) *tundrae* Tschitsch.	–	–	–	–	–	4	1	–	–	–	**dt**
P. (*Tundraphilus*) *sublaevis* Sahlb.	1	–	–	–	–	3	1	–	–	–	**dt**
Stereocerus haematopus (Dej.)	–	–	–	–	–	–	–	–	1	–	**dt**
Tribe Zabrini											
Curtonotus alpinus Payk.	3	6	–	4	4	88	5	2	4	–	**dt**
C. bokori Csiki	1	–	–	–	–	–	–	–	–	–	**dt**
Family Dytiscidae											
Subfamily Agabinae											
Agabus moestus (Curt.)	–	1	–	2	1	–	–	–	–	–	**aq**
Family Hydrophilidae											
Subfamily Helophorinae											
Helophorus splendidus Sahlb.	–	–	–	1	–	1	–	–	2	1	**aq**
Subfamily Hydrophilinae											
Cymbiodyta marginella (F.)	–	–	–	–	–	–	–	5	–	–	**aq**
Subfamily Sphaeridiinae											
Coelostoma orbiculare F.	–	–	–	–	–	–	–	4	–	–	**pl**
Family Leiodidae											
Subfamily Leiodinae											
Cyrtoplastus irregularis Rtt.?	–	–	–	–	–	1	–	–	–	–	**pl**
Subfamily Cholevinae											
Cholevinus sibiricus (Jean.)	–	–	–	–	–	3	3	–	–	–	**mt**
Family Silphidae											
Subfamily Silphinae											
Aclypea altaica (Gebl.)	–	–	–	–	–	21	–	–	–	–	**ms**
Family Staphylinidae											
Subfamily Tachyporinae											
Tachinus arcticus Motsch.	–	–	–	–	4	–	–	–	1	–	**mt**
T. brevipennis Sahlb.	–	4	1	1	–	1	–	1	–	–	**mt**
Family Scarabaeidae											
Aphodius sp.	–	3	–	2	1	8	3	–	–	1	**xe**
Family Byrrhidae											
Subfamily Byrrhinae											
Morychus viridis Kuzm. et Korot.	2	2	12	4	12	31	22	8	17	44	**ss**
Family Ptinidae											
Subfamily Anobiinae											
Caenocara bovistae Hoffm.	–	1	–	–	–	–	–	–	–	–	**pl**
Family Melyridae											
Troglocollops arcticus L. Medv.	–	–	1	–	–	1	–	–	–	–	**ms**

Table 10. (Contd.)

Age	Late Pleistocene										
Section	Duvanny Yar				Stanchikovskii Yar				Chersky		
Species/sample	P-1332s-1	P-1332s-2	P-1333s-1	P-1333s-2	P-1304	P-08-03	P-09-03	P-978	Ch-2003	P-1211	eco
Family Elateridae											
Subfamily Dendrometrinae											
Denticollis varians Germ.	–	–	–	–	–	1	–	–	–	–	**fo**
Family Cerambicidae											
Acmaeops pratensis Leach.	–	–	–	–	–	2	–	–	–	–	**me**
Family Chrysomelidae											
Subfamily Cassidinae											
Cassida sp.	–	–	–	–	–	–	–	–	1	–	**me**
Subfamily Chrysomelinae											
Chrysolina arctica Medv.	–	–	–	–	–	1	–	–	–	–	**ms**
Chrysolina brunnicornis bermani Medv.	–	–	–	–	–	1	–	–	–	–	**st**
Chrysolina septentrionalis Men	–	–	–	–	–	2	–	–	2	1	**mt**
Ch. tolli Jac.	–	–	–	–	1	–	1	–	–	–	**tt**
Chrysomela blaisdelli Van Dyke	–	–	–	–	–	1	–	–	–	–	**sh**
Family Brachyceridae											
Subfamily Erirhininae											
Notaris bimaculatus F.	–	–	–	–	1	–	–	–	1	–	**ri**
Family Brentidae											
Subfamily Apioninae											
Mesotrichapion wrangelianum Kor.	–	1	–	–	–	–	1	1	–	–	**dt**
Pseudoprotapion astragali Payk.?	–	–	–	–	–	1	–	–	–	–	**me**
Family Curculionidae											
Subfamily Entiminae											
Tribe Otiorhynchini											
Otiorhynchus cribrosicollis Boh. ?	–	–	–	–	–	–	–	–	2	–	**ms**
Tribe Phyllobini											
Phyllobius virideaeris Laich.	–	–	–	–	–	18	–	–	–	–	**me**
Tribe Sitonini	–	–	–	–	–	–	–	–	–	–	
Sitona borealis Kor.	–	–	–	–	2	–	1	4	–	2	**dt**
Subfamily Hyperinae											
Hypera diversipunctata Schrank.	–	3	–	–	–	17	1	–	–	–	**dt**
H. ornata Cap.	–	1	–	–	–	17	1	–	–	–	**dt**
Subfamily Lixinae											
Tribe Cleonini											
Coniocleonus cinerascens Hochh.	–	1	–	–	–	3	–	–	–	–	**ms**
C. ferrugineus Fahr.	–	–	–	–	–	4	–	–	–	–	**ms**
C. zherichini T.-M. et Kor.	1	2	–	–	–	–	–	–	–	–	**dt**
Coniocleonus sp.	–	–	–	–	–	1	–	–	1	–	**ms**
Stephanocleonus eruditus Faust	–	–	–	–	–	6	–	–	–	2	**st**
S. fossulatus F-W.	1	1	–	–	–	–	–	–	–	1	**st**
Subfamily Molytinae											
Tribe Lepyrini											
Lepyrus canadensis Casey	–	–	–	–	–	–	–	1	–	–	**sh**
L. gemellus Kby.	–	–	–	–	–	2	–	–	–	–	**sh**
L. nordenskioeldi Faust	–	–	–	–	–	15	1	1	3	–	**sh**
Lepyrus sp.	–	–	–	–	–	–	–	–	1	–	**sh**
L. volgensis Fst.	–	–	–	1	–	–	–	–	–	–	**sh**
Curculionidae gen. indet.	–	–	–	–	–	3	–	–	–	–	**oth**
Order Heteroptera											
Family Pentatomidae											
Aelia frigida Kir.	–	–	–	–	–	281	–	–	–	–	**ms**
Pentatomidae gen. indet.	2	1	–	–	–	33	–	–	–	–	**oth**
Order Homoptera											
Cicadellidae gen. Indet	–	–	–	–	–	–	–	1	–	–	**me**
Sum	18	32	14	21	27	683	49	33	53	57	

Table 11. Insects from Duvanny Yar ground squirrel nests

Age	Late Pleistocene										
Section	Duvanny Yar										
Species/sample	B-Dyb	P-1212b-1	P-1212b-2	P-1212b-3	P-1213b	P-1321b-1	P-1321b-2	P-1075b-1	P-1075b-2	P-1334b	eco
Order Coleoptera											
Subfamily Harpalinae											
Tribe Harpalini											
Dicheirotrichus mannerheimi Sahlb.	–	–	–	2	–	–	–	–	–	–	**dt**
Harpalus vittatus kiselevi Kat. et Shil.	–	–	–	2	–	–	–	–	–	–	**ms**
Tribe Lebiini											
Cymindis arctica Kryzh. et Em.	–	–	–	1	–	–	–	–	–	–	**ri**
Tribe Pterostichini											
Pterostichus (*Cryobius*) sp.	–	–	–	–	–	1	–	1	–	–	**dt**
Curtonotus alpinus Payk.	–	1	–	1	–	–	–	–	–	–	**dt**
Family Scarabaeidae											
Aphodius sp.	–	–	–	–	–	3	1	–	–	–	**xe**
Family Byrrhidae											
Subfamily Byrrhinae											
Morychus viridis Kuzm. et Korot.	1	–	–	–	1	–	–	–	–	–	**ss**
Family Curculionidae											
Subfamily Lixinae											
Tribe Cleonini											**dt**
Coniocleonus sp.	–	–	–	2	–	–	–	–	–	–	**ms**
Stephanocleonus eruditus Faust	–	–	1	–	–	–	–	–	–	–	**st**
Stephanocleonus sp.	–	–	–	–	–	–	–	–	1	–	**st**
Order Diptera											
Diptera gen. indet (pseudopupia)	–	–	–	–	–	1	–	1	–	1	**oth**
Order Lepidoptera											
Lepidoptera larvae head	–	–	–	–	–	–	1	–	–	–	**oth**
Sum	1	1	1	8	1	4	1	1	1	0	

of fossil insects from the nests (Table 11, 12) only slightly differ from the total insect sample of the region, but for the high proportion of well-preserved dung beetles of the genus *Aphodius*. These beetles probably lived in the ground squirrel nests feeding on dung and other rodent products.

Looking at the insect assemblage of Duvanny Yar, we can notice the best presentation of steppe–tundra communities. All studied assemblages are xerophilous, with a significant role of steppe–tundra indicators. The sequence of the types is as follows: **S-T/SS, S-T/SS, S-T/SS, S-T/SS, S-T/S-T, TU/S-T, S-T/S-T, S-T/S-T.** We can see sustained presence of the extreme type **S-T/SS** at the early stages; the change towards the moderate steppe–tundra type **S-T/S-T** before the first paleosol accumulation, the tundra dominated type **TU/S-T** in the soil, and the moderate steppe–tundra type **S-T/S-T** returning in the interval between the paleosols. It is plausible that the unit before the first paleosol belongs to MIS4 and the unit which includes all three paleosols belongs to MIS3. Both stages of the Late Pleistocene show imaging prosperity of the steppe–tundra environment.

Several occasional samples from paleosols and ground squirrel nests were taken from the section of Stanchikovskii Yar on the Malyi Anyui River and sections near the towns of Chersky and Zelenyi Mys at the top of the Kolyma River delta (Figs. 1, 2, Tables 10, 12). The principal composition of insect assemblages is close to Duvanny Yar samples.

Table 12. Insects from Duvanny Yar, Stanchikovskii Yar (Stan), and Zelenyi Mys (Zel. Mys) ground squirrel nests

Age	Late Pleistocene									
Section	Duvanny Yar						Stan	Zel. Mys		
Species/sample	P-1335b	P-1311b-1	P-1311b-2	P-1326b	P-1325b	P-01-03-2003b	P-1010	P-921	P-923	eco
Order Coleoptera										
Family Carabidae										
Subfamily Harpalinae										
Tribe Pterostichini										
Pterostichus (*Cryobius*) *brevicornis* (Kby.)	–	–	–	–	–	1	–	–	–	**mt**
Pterostichus (*Cryobius*) sp.	–	–	–	–	–	–	–	1	–	**mt**
Curtonotus alpinus Payk.	–	–	–	–	1	–	–	–	–	**dt**
Family Scarabaeidae										
Aphodius sp.	1	14	4	–	17	–	–	–	–	**xe**
Family Byrrhidae										
Subfamily Byrrhinae										
Morychus viridis Kuzm. et Korot.	–	–	–	1	–	1	–	–	–	**ss**
Family Melyridae										
Troglocollops arcticus L. Medv.	–	–	–	–	–	–	–	1	–	**ms**
Family Chrysomelidae										
Subfamily Chrysomelinae										
Chrysolina brunnicornis bermani Medv.	1	–	–	–	–	–	–	–	–	**st**
Ch. septentrionalis Men	1	–	–	–	–	–	–	–	–	**mt**
Family Curculionidae										
Subfamily Entiminae										
Tribe Phyllobini										
Phyllobius kolymensis Kor. et Egorov	4	–	–	–	–	–	–	1	–	**ms**
Ph. virideaeris Laich.	–	–	–	1	–	–	–	–	–	**me**
Subfamily Hyperinae										
Hypera diversipunctata Schrank.	–	–	–	–	–	–	1	–	–	**dt**
Order Diptera										
Diptera gen. indet (pseudopupia)	–	–	–	–	–	–	–	1	3	**oth**
Sum	7	14	4	2	18	2	1	3	0	

The most interesting insect assemblage is P-08-03 from Stanchikovskii Yar (Table 10). This assemblage is very rich (MNI = 683) and more than one-third of specimens belong to true bugs of the family Pentatomidae (*Aelia frigida* and a closely related species). Only one fossil insect sample from Beringia is dominated by bugs. In addition, the assemblage belongs to rare **S-T/MS** type. The meadow–steppe group includes abundant *Aelia frigida* and *Harpalus obtusus obtusus, Aclypea altaica, Troglocollops arcticus, Chrysolina arctica, Coniocleonus cinerascens,* and *C. ferrugineus*.

3.2. Yana–Indigirka Lowland

3.2a. Keremesit

The sections on the Keremesit River (Figs. 1, 2, 4, 14f) represent a complete sequence from the Lower to Upper Pleistocene (Fig. 21). These sections were studied in detail by an expedition of "Aerogeologia" company in 1978–1981 with participation of D.K. Bashlavin, S.N. Zhigulevtseva, and M.G. Ovander (Bashlavin et al., 1986, 1987). During fieldwork, six small insect samples were taken and transferred to Kiselev for studying, but results have not been published. It is known than the samples come from section 1502 from the Middle Pleistocene unit and insect assemblages contains steppe–tundra species (Kiselev, personal communication).

In 1984, the site was visited by an expedition of Moscow State University, with A.V. Sher, I.R. Plakht, and me. The main goal was a complex study of Middle Pleistocene deposits, but other units were also sampled and 18 insect samples were screened. The results of this and previous fieldworks allow the establishment of the Keremesit Superhorizon as the regional stratotypic unit of the Middle Pleistocene (Sher et al., 1987).

A paleomagnetic study performed in 1984 (Virina, 1997) has shown that the lower part of the section is correlated with the Chukochinsky Horizon (Lower Pleistocene). The next unit has an uncertain polarization and mixed rodent fauna; it was tentatively names an "eroded horizon." Positive magnetic deposits with a Middle Pleistocene rodent fauna (Keremesit Superhorizon) overlie the "eroded" horizon. The Edoma unit with ice wedges terminates the section. Some strata are missed in the section, i.e., the Akansky Horizon (lower Middle Pleistocene) and the last interglacial unit.

We took seven insect samples from the Chukochinsky Horizon (Table 13); two lower samples come from the same bed. The lower assemblages (K-8 and K-12) are dominated by the mesophilous tundra group (**mt**), composing about 50% of individuals. It includes common tundra species, such as *Pterostichus* (*Cryobius*) spp., *P. vermiculosus, Diacheila polita*, *Cholevinus sibiricus*, and *Tachinus arcticus*. The xerophilous tundra group (**dt**) is diverse (*Curtonotus alpinus, Poecilus nearcticus, Pterostichus haematopus, P. sublaevis, Amara glacialis, Trichocellus mannerheimi, Simplocaria arctica, Hemitrichapion tschernovi, Hypera ornate*), but the share of this group is less than 20%; and individual insect specimens represent the arctic group (**tt**), the leaf beetle *Chrysolina subsulcata*. All of these species, except the relict ground beetle *Poecilus nearcticus* are typical for northern shrub tundra. The steppe–tundra indicators are not abundant, the sum of **st**, **ms**, and **ss** groups is only 4–6%, that is, low for the Pleistocene. The secondary group **xe** (polyzonal xerophilous) plays an unusually high role in the assemblage, about 10%. The group is represented by the ground beetle *Notiophilus aquaticus*, which can live on open dry ground in the tundra, forest, or steppe.

The assemblage contains a number of thermophilous species: *Elaphrus* sp., *Dyschiriodes melancholicus, Lathrobium* sp., *Berninelsonius hyperboreus*, *Corticaria* sp., *Notaris bimaculatus,* and *Grypus mannerheimi*, but true forest insects are absent. Larch cones and pieces of wood found in the sediment indicate that forest was growing locally; the insect assemblage corresponds to the environment near the tree line.

Samples K-6 and K-5 come from the sandy-silt bed with small ice wedge cast. The assemblages are similar, but K-5 is richer. Tundra species dominate here; **mt** = 39% (*Pterostichus* (*Cryobius*) *pinguedineus, P.* (*Cryobius*) *ventricosus, P. costatus, Diacheila polita, Tachinus arcticus, Cholevinus sibiricus, Chrysolina septentrionalis*) and **dt** = 28% (*Curtonotus alpinus, Poecilus nearcticus, Stereocerus haematopus, Pterostichus sublaevis, Hemitrichapion tschernovi, Hypera ornata,* and others). Aquatic and riparian species play a significant role, 17% in sum. The steppe–tundra indicators are poorly represented. The assemblage is similar to the previous ones, but includes a thermophilous species. All four assemblages belong to the **TU/S-T** type.

Two next samples (K-7 and K-18) were taken from the uppermost sands in the Chukochinsky Horizon. Both samples are dominated by xerophilous species; the role of steppe–tundra indicators increases dramatically. Assemblage K-7 contains 30% of the group **ss**, 1% of **st** (the leaf beetle *Chrysolina brunnicornis bermani*), and 9% of **ms** (*Colaphellus alpinus*, *Phyllobius kolymensis, Coniocleonus ferrugineus, C. astragali*). The tundra groups are represented equally: **mt** = 21% and **dt** = 20%. The assemblage includes individual arctic (*Chrysolina subsulcata*) and forest (*Hylobius piceus*) species. Such a strange combination is not rare in steppe–tundra assemblages. Tree-related insects and cold-resistant arctic insects are found occasionally in Pleistocene steppe–tundra community. Trees were certainly present on the open grassy land, but there was not a well-developed forest biocenose.

Sample K-18 is quite similar, but the role of true steppe insects (*Stephanocleonus eruditus, S. incertus*) is higher here, 17%. Weevils of the genus *Stephanocleonus* appear for the first time in Keremesit. These beetles need a high ground temperature and their presence is indicative of a relatively warm summer, at least 12°C in July (Alfimov and Berman, 2001; Alfimov et al., 2003). This temperature is higher than modern one of the locality. The closest weather station Chokurdakh (situated south of the site) shows mean July t 7°C (Melnikova, 1965). The summer temperature for the "cold" stage of the Early Pleistocene is estimated as at least 5° higher than the modern one. This is understandable taking into account the inner continental position of the site during the Pleistocene due to a great sea regression and waste northern land instead of the modern shelf. Both last assemblages belong to the **S-T/S-T** type.

We took three samples from the problematic "eroded" horizon. This unit is composed of oblique sands with gravel and plant debris; deposits of this sort are usually very rich in fossils, including rodents and insects. Some rodent and insect fossils were reworked, but anyway, this rich bed provides important information. The three insect samples are similar to each other and resemble lower tundra assemblages. The first sample (K-3) comes from the base of the eroded horizon. The assemblage is dominated by the **mt** group (48%). The steppe–tundra indicators are represented by *Phyllobius kolymensis*, *Coniocleonus* sp., and *Morychus viridis* (15%); true steppe species are absent.

Table 13. Insects from the Keremesit site, Oler Formation

Age	Chukochinsky Horizon						Akansky? Horizon			
Section	16	16'	16			2	7	10	12	
Species/sample K-	8	12	6	5	7	18	3	1	2	eco
Order Coleoptera										
Family Carabidae										
Subfamily Nebriinae										
Notiophilus aquaticus L.	9	24	1	8	4	–	9	1	1	**xe**
Subfamily Carabinae										
Carabus odoratus Motsch.	–	–	–	1	–	–	–	–	–	**dt**
C. truncaticollis Esch.	–	–	–	–	–	–	1	–	–	**mt**
Subfamily Elaphrinae										
Blethisa catenaria Brown.	–	–	–	–	–	–	–	1	–	**mt**
Diacheila polita Fald.	1	–	–	1	1	1	–	2	2	**mt**
Elaphrus riparius L.	–	–	–	–	–	–	1	–	–	**ri**
Elaphrus sp.	1	–	–	–	–	–	–	–	–	**ri**
Subfamily Scaritinae										
Dyschiriodes melancholicus Putz.	1	–	–	–	–	–	1	–	–	**ri**
Subfamily Trechinae										
Bembidion (*Asioperyphus*) *umiatense* Lth.	4	–	–	1	1	–	5	–	–	**ri**
B. (*Peryphanes*) *grapii* Gyll.	–	2	–	–	–	–	–	1	–	**dt**
Bembidion (*Plataphodes*) *arcticum* L.	–	–	–	1	–	–	1	–	–	**ri**
Subfamily Harpalinae										
Tribe Harpalini										
Dicheirotrichus mannerheimi Sahlb.	1	4	–	2	1	–	3	–	1	**dt**
Harpalus vittatus kiselevi Kat. et Shil.	–	–	–	–	–	–	–	1	1	**ms**
Tribe Lebiini										
Cymindis vaporariorum L.?	–	–	–	–	1	–	–	–	–	**dt**
Tribe Pterostichini										
Poecilus (*Derus*) *nearcticus* Lth.	1	–	1	1	1	2	–	–	1	**dt**
Pterostichus (*Cryobius*) *brevicornis* (Kby.)	8	12	–	–	3	–	12	7	21	**mt**
P. (*Cryobius*) *nigripalpis* Popp.	2	3	–	2	1	–	2	4	3	**dt**
P. (*Cryobius*) *pinguedineus* Esch.	5	23	6	4	5	5	5	6	10	**mt**
P. (*Cryobius*) *ventricosus* Esch.	5	10	2	11	4	3	14	6	6	**mt**
Pterostichus (*Cryobius*) sp.	31	42	3	18	–	–	19	16	9	**mt**
P. (*Lenapterus*) *agonus* Horn.	–	–	2	–	–	–	–	–	–	**mt**
P. (*Lenapterus*) *costatus* Men.	–	–	–	2	–	–	4	1	4	**mt**
P. (*Lenapterus*) *vermiculosus* Men.	2	–	–	–	1	–	3	1	3	**mt**
P. (*Tundraphilus*) *sublaevis* Sahlb.	2	2	–	1	–	–	3	1	3	**dt**
Stereocerus haematopus (Dej.)	1	6	2	5	2	1	4	5	–	**dt**
Tribe Zabrini										
Amara glacialis Mnnh.	–	2	–	–	–	–	–	–	–	**dt**
A. interstitialis Dej.	–	–	–	1	2	–	1	1	2	**dt**
Curtonotus alpinus Payk.	10	21	2	21	6	5	4	8	14	**dt**
C. bokori Csiki	–	–	–	1	–	–	–	–	1	**dt**
Family Dytiscidae										
Subfamily Agabinae										
Agabus moestus (Curt.)	1	–	–	–	–	–	2	1	3	**aq**
SubfamilyColymbetinae										
Colymbetes dolabratus (Payk.)	–	–	–	–	1	2	–	1	1	**aq**
Subfamily Hydroporinae										
Hydroporus acutangulus Thoms.?	1	–	–	–	–	–	1	2	–	**aq**
Hydroporus sp.	–	–	–	2	–	–	–	–	1	**aq**
Family Hydrophilidae										
Subfamily Helophorinae										
Helophorus splendidus Sahlb.	–	–	–	–	1	–	–	–	–	**aq**
Subfamily Hydrophilinae										
Hydrobius fuscipes F.	–	–	–	–	–	–	1	–	–	**aq**
Subfamily Sphaeridiinae										
Cercyon sp.	–	–	–	–	1	–	–	–	–	**ri**

Table 13. (Contd.)

Age	Chukochinsky Horizon						Akansky? Horizon			
Section	16	16'	16			2	7	10	12	
Species/sample K-	8	12	6	5	7	18	3	1	2	eco
Family Leiodidae										
Subfamily Cholevinae										
Cholevinus sibiricus (Jean.)	1	–	–	1	2	–	3	3	2	**mt**
Family Staphylinidae										
Subfamily Tachyporinae										
Tachinus arcticus Motsch.	13	7	–	5	3	–	5	4	–	**mt**
T. brevipennis Sahlb.	1	1	–	2	–	–	2	1	–	**mt**
Subfamily Paederinae										
Lathrobium sp.	1	–	–	–	–	–	–	–	–	**pl**
Subfamily Staphylininae										
Quedius sp.	–	–	–	–	–	–	1	–	–	**pl**
Family Scarabaeidae										
Aphodius sp. nov.?	–	–	–	–	–	–	–	–	1	**xe**
Family Byrrhidae										
Subfamily Byrrhinae										
Byrrhus sp.	–	–	–	–	–	–	–	–	1	**me**
Morychus viridis Kuzm.et Korot.	7	11	1	7	29	15	23	18	16	**ss**
Simplocaria arctica Popp.	–	2	–	–	–	–	3	–	2	**dt**
S. semistriata F.	–	1	–	–	–	–	–	–	–	**dt**
Family Elateridae										
Subfamily Dendrometrinae										
Berninelsonius hyperboreus (Gyll.)	1	–	–	–	–	–	–	–	–	**me**
Family Lathridiidae										
Corticaria sp.	–	2	–	–	–	–	–	–	–	**pl**
Family Chrysomelidae										
Subfamily Cassidinae										
Cassida sp.	–	–	–	–	–	–	–	–	1	**me**
Subfamily Chrysomelinae										
Chrysolina arctica Medv.	–	–	–	–	–	–	–	1	–	**ms**
Ch. brunnicornis bermani Medv.	–	1	3	2	1	–	–	1	1	**st**
Ch. septentrionalis Men.	–	–	2	4	–	2	–	–	–	**mt**
Ch. subsulcata Mnnh.	1	2	–	–	3	–	–	2	2	**tt**
Ch. tolli Jac.	–	–	–	–	–	–	–	–	1	**tt**
Chrysolina sp.	–	–	–	–	–	–	2	–	–	**mt?**
Colaphellus alpinus Gebl.	–	–	–	–	1	–	–	–	–	**ms**
Hydrothassa hannoverana F.	–	–	–	–	–	–	–	–	1	**ri**
Phratora polaris Schn.	1	1	–	–	–	–	–	–	–	**sh**
Family Brentidae										
Subfamily Apioninae										
Hemitrichapion tschernovi T.-M.	2	2	–	1	2	–	2	–	–	**dt**
Family Brachyceridae										
Subfamily Erirhininae										
Notaris bimaculatus F.	10	16	8	17	2	8	6	5	21	**ri**
Grypus mannerheimi Faust	–	1	–	–	–	–	–	–	–	**ri**
Grypus sp.	1	–	–	–	–	–	–	–	–	**ri**
Family Curculionidae										
Subfamily Ceutorhynchinae										
Pelenomus sp.	–	–	–	–	–	–	1	–	–	**ri**
Subfamily Entiminae										
Tribe Phyllobini										
Phyllobius kolymensis Kor. et Egorov.	–	1	–	1	4	2	1	2	2	**ms**
Tribe Sitonini										
Sitona borealis Kor.	–	–	–	–	2	–	–	1	2	**dt**
Subfamily Hyperinae										
Hypera ornata Cap.	1	1	–	1	2	2	2	3	3	**dt**

Table 13. (Contd.)

Age	Chukochinsky Horizon						Akansky? Horizon			
Section	16	16'	16			2	7	10	12	
Species/sample K-	8	12	6	5	7	18	3	1	2	eco
Subfamily Lixinae										
Tribe Cleonini										
Coniocleonus astragali T.-M. et Kor.	–	–	–	–	2	1	–	–	–	**ms**
C. cinerascens Hochh.	–	–	–	–	–	–	–	–	2	**ms**
C. ferrugineus Fahr.	–	–	–	–	2	3	–	–	1	**ms**
Coniocleonus sp.	–	1	–	1	–	–	1	2	5	**ms**
Stephanocleonus eruditus Faust	–	–	–	–	–	3	–	1	4	**st**
S. fossulatus F.-W.	–	–	–	–	–	–	–	–	3	**st**
S. incertus Ter-Min.	–	–	–	–	–	10	–	–	1	**st**
Stephanocleonus sp.	–	–	–	–	–	–	–	–	3	**st**
Subfamily Molytinae										
Tribe Hylobiini										
Hylobius piceus DeG.	–	–	–	–	2	–	–	–	1	**fo**
Tribe Lepyrini										
Lepyrus nordenskioeldi Faust	1	4	2	2	3	11	4	11	19	**sh**
Tribe Pissodini										
Pissodes sp.	–	–	–	–	–	–	–	–	1	**fo**
Subfamily Curculioninae										
Tribe Elliscini										
Dorytomus rufulus amplipennis Tourn.	–	–	–	–	1	–	1	–	–	**sh**
Dorytomus sp.	–	–	–	–	–	–	–	1	–	**sh**
Tribe Rhamphini										
Isochnus arcticus Kor.	–	–	–	–	–	–	–	1	–	**tt**
Order Heteroptera										
Family Pentatomidae										
Aelia frigida Kir.	–	–	–	–	–	–	–	1	–	**ms**
Order Hymenoptera										
Family Formicidae										
Camponotus herculeanus L.	–	–	–	–	–	–	–	–	2	**fo**
Hymenoptera gen. indet	–	–	1	–	1	1	–	1	2	**oth**
Order Megaloptera										
Family Sialidae										
Sialis sp.	–	–	–	–	–	–	–	–	1	**aq**
Order Diptera										
Diptera fam. indet. (puparia)	–	–	–	–	–	4	–	–	–	**oth**
Sum	127	205	35	127	97	76	153	124	185	

Sample K-1 from the middle part of the unit is more diverse. The assemblage includes individual arctic insects (*Chrysolina subsulcata* and *Isochnus arcticus*) and steppe *Chrysolina brunnicornis* and *Stephanocleonus eruditus* (2%).

The last assemblage from the unit contains more steppe species (6%), including *Chrysolina brunnicornis bermani, Stephanocleonus eruditus, S. fossulatus,* and *S. incertus*. Thus, the weevil genus *Stephanocleonus* is present again. In addition, the assemblage contains individual forest, tree-related species, i.e., the weevils *Hylobius piceus* and *Pissodes* sp., which feed on conifers and the carpenter ant *Camponotus herculeanus*.

Despite the possibility of mixing, these three assemblages show a gradually increasing steppe influence. Two upper assemblages belong to the **S-T/S-T** type and the lower one is close to this type.

Next eight samples were taken from the Keremesit Superhorizon (Fig. 21, Table 14). Two lower samples (K-9 and K4) come from a gravel lens with plant debris. Sample K-9 is poor; it includes tundra and steppe species. Sample K-4 is much richer. It is the largest sample in the section, MNI is almost 600 (Table 14).

The assemblage includes mostly xerophilous species. The largest group is **ss** (34%). Two other steppe groups, **st** (*Chrysolina brunnicornis bermani Stephanocleonus fossulatus, S. incertus*) and **ms** (*Harpalus vittatus kiselevi, Carabus kolymensis, Colaphellus alpinus, Phyllobius kolymensis, Coniocleonus ferrugineus,*

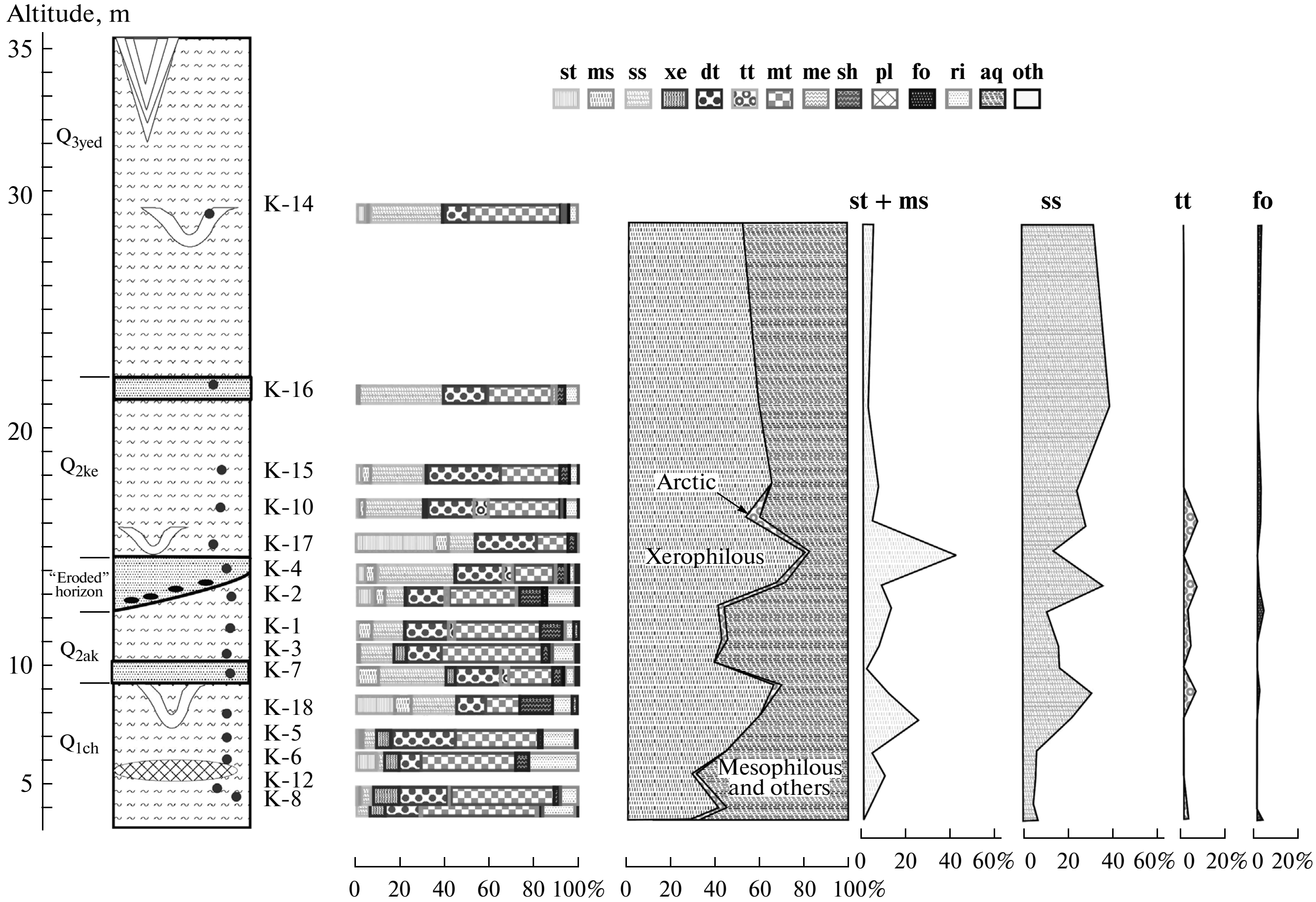


Fig. 21. Stratigraphic scheme and insect assemblages from the Keremesit site. For legend, see Figs. 15 and 16. (Q_{1ch}) Chukochinsky Horizon, (Q_{2ak}) Akansky Horizon, (Q_{2ke}) Keremesit Formation, (Q_{3yed}) Edoma Formation.

C. cinerascens) compose 3 and 6%, respectively; they are diverse and include relatively thermophilous species. The tundra groups **dt** and **mt** are represented almost equally (19 and 18%). The assemblage contains arctic species (5%), such as *Chrysolina subsulcata*, *Ch. tolli,* and *Isochnus arcticus* and rare forest (tree-related) species, *Pissodes insignatus* and *Camponotus herculeanus*.

The assemblage belongs to the **S-T/S-T** type. It reflects a mild steppe–tundra environment with various habitats.

Sample K-17 was taken from other trench from sandy bed with gravel lenses; stratigraphically, it is positioned slightly above K-4. Assemblage K-17 is clearly dominated by xerophilous, mostly steppe insects. The first most abundant group is **st** (36%); most of the specimens belong to the weevil *Stephanocleonus eruditus* and a few, to *S. fossulatus* and *S. incertus*. Meadow–steppe insects (5%) are also not diverse, including *Chrysolina arctica, Phyllobius kolymensis,* and *Coniocleonus ferrugineus*. The group **ss** composes 12% of the assemblage. This assemblage belongs to the strongly steppe type **S-T/ST**; it shows a decrease in species and ecological group diversity. The environment was more uniform, probably a grassy *Artemisia* steppe, with tundra-like depressions.

Sample K-10 comes from a sandy bed with plant debris. The assemblage is dominated by tundra species, primarily mesophilous tundra (**mt** = 36%) (*Pterostichus* (*Cryobius*) spp.*, P. costatus, Blethisa catenaria, Diacheila polita, Cholevinus sibiricus*, *Tachinus arcticus*); xerophilous tundra taxa play a secondary role (17%). The arctic group (7%) is represented by *Chrysolina subsulcata* and *Isochnus arcticus*. The steppe–tundra indicators are also recorded in the assemblage. This is primarily *Morychus viridis* (26%). The assemblage contains individual steppe and meadow–steppe species and rare forest insects, such as *Hylobius piceus, Pissodes irroratus,* and *Formica gagatoides*.

The assemblage belongs to the **S-T/S-T** type, close to **S-T/TU**, with a high role of mesophilous and hydrophilous species and ecological diverse.

A small sample from the middle part of the Keremesit Superhorizon K-11 contains only a few speci-

Table 14. Insects from the Keremesit site (Keremesit Horizon, Edoma)

Age	Keremesit Horizon								Edoma	
Section	16	4	0	16	16	9		16	14	
Species/sample K-	9	4	17	10	11	15	16	13	14	eco
Order Coleoptera										
Family Gyrinidae										
Gyrinus opacus Salb.	–	1	–	–	–	–	–	–	–	**aq**
Family Carabidae										
Subfamily Nebriinae										
Notiophilus aquaticus L.	–	6	–	7	–	1	–	–	2	**xe**
Subfamily Carabinae										
Carabus kolymensis Kryzh. et Bud.	–	2	–	–	–	–	–	–	–	**ms**
C. truncaticollis Esch.	–	1	–	–	–	1	–	–	–	**mt**
Subfamily Elaphrinae										
Blethisa catenaria Brown.	–	1	–	2	–	1	–	–	–	**mt**
Diacheila polita Fald.	–	2	–	3	–	–	–	–	4	**mt**
Elaphrus riparius L.	–	1	–	1	–	–	–	–	–	**ri**
Elaphrus sp.	–	–	–	–	–	–	–	–	1	**ri**
Subfamily Scaritinae										
Dyschiriodes melancholicus Putz.	–	–	–	1	–	–	–	–	–	**ri**
Subfamily Trechinae										
Bembidion (*Asioperyphus*) *umiatense* Lth.	–	2	–	6	–	–	2	–	1	**ri**
B. (*Peryphanes*) *grapii* Gyllenhal	–	1	–	–	–	2	–	–	–	**ri**
B. (*Plataphodes*) *arcticum* L.	–	1	–	–	–	1	–	–	1	**ri**
Subfamily Harpalinae										
Tribe Harpalini										
Dicheirotrichus mannerheimi Sahlb.	–	3	–	5	–	–	–	–	2	**dt**
Harpalus vittatus kiselevi Kat. et Shil.	–	7	–	2	1	5	–	–	–	**ms**
H. cf. *pusillus* Motsch.	–	–	–	1	–	–	–	–	–	**st**
Tribe Lebiini										
Cymindis arctica Kryzh. et Em.	–	–	–	–	–	–	–	–	1	**st**
Tribe Pterostichini										
Poecilus (*Derus*) *nearcticus* Lth.	–	15	11	5	–	7	2	–	7	**dt**
Pterostichus (*Cryobius*) *brevicornis* (Kby.)	–	13	–	15	–	10	2	–	31	**mt**
P. (*Cryobius*) *nigripalpis* Popp.	–	8	2	9	–	38	2	–	1	**dt**
P. (*Cryobius*) *pinguedineus* Esch.	–	17	3	21	–	19	4	–	1	**mt**
P. (*Cryobius*) *ventricosus* Esch.	3	8	2	14	–	7	2	–	2	**mt**
Pterostichus (*Cryobius*) sp.	–	46	4	33	–	63	7	–	51	**mt**
P. (*Lenapterus*) *agonus* Horn.	–	2	1	–	–	6	1	–	–	**mt**
P. (*Lenapterus*) *costatus* Men.	–	–	1	1	–	2	–	–	–	**mt**
P. (*Lenapterus*) *vermiculosus* Men.	–	1	–	–	–	2	–	–	1	**mt**
P. (*Tundraphilus*) *sublaevis* Sahlb.	–	9	–	–	–	1	–	–	–	**dt**
Pterostichus (*Petrophilus*) sp.	–	–	–	–	–	4	–	–	–	**dt**
Stereocerus haematopus (Dej.)	–	10	3	5	–	6	2	–	–	**dt**
Tribe Zabrini										
Amara (*Amarocelia*) *interstitialis* Dej.	–	4	–	1	–	2	–	–	–	**dt**
Curtonotus alpinus Payk.	1	53	11	43	–	53	4	–	11	**dt**
C. bokori Csiki	–	–	–	1	–	–	–	–	–	**dt**
Family Dytiscidae										
Subfamily Agabinae										
Agabus moestus (Curt.)	–	2	–	1	–	1	–	–	–	**aq**
SubfamilyColymbetinae										
Colymbetes dolabratus (Payk.)	–	1	–	–	–	–	–	–	–	**aq**
Subfamily Hydroporinae										
Hydroporus acutangulus Thoms.?	–	7	–	–	–	–	–	–	–	**aq**
Hydroporus sp.	–	–	–	2	–	3	–	–	–	**aq**
Family Hydrophilidae										
Subfamily Helophorinae										
Helophorus splendidus Sahlb.	–	1	–	1	–	–	–	–	–	**aq**

Table 14. (Contd.)

Age	Keremesit Horizon								Edoma	
Section	16	4	0	16	16	9		16	14	
Species/sample K-	9	4	17	10	11	15	16	13	14	eco
Subfamily Hydrophilinae										
Hydrobius fuscipes F.	–	1	–	–	–	–	–	–	–	**aq**
Subfamily Sphaeridiinae										
Cercyon sp.	–	–	–	1	–	1	–	–	1	**ri**
Family Leiodidae										
Subfamily Leiodinae										
Cyrtoplastus irregularis Rtt.?	–	2	–	2	–	–	–	–	5	**pl**
Subfamily Cholevinae										
Cholevinus sibiricus (Jean.)	–	4	–	8	–	–	–	–	3	**mt**
Family Staphylinidae										
Subfamily Omaliinae										
Olophrum consimile Gyll.	–	–	–	–	–	–	–	–	9	**mt**
Subfamily Tachyporinae										
Tachinus arcticus Motsch.	2	2	–	36	–	–	–	–	2	**mt**
Family Byrrhidae										
Subfamily Byrrhinae										
Byrrhus sp.	–	1	–	–	–	–	–	–	–	**me**
Morychus viridis Kuzm. et Korot.	4	199	12	108	11	99	23	1	86	**ss**
Simplocaria arctica Popp.	–	1	–	2	–	–	–	–	–	**dt**
Subfamily Syncalyptinae										
Curimopsis cyclolepidia Muenst.	–	–	–	4	–	1	–	–	–	**dt**
Family Melyridae										
Troglocollops arcticus L. Medv.	–	–	–	–	–	–	–	–	1	**st**
Family Lathridiidae										
Corticaria sp.	–	–	–	1	–	–	–	–	1	**pl**
Family Cerambicidae										
Cerambicidae gen. indet.	–	1	–	–	–	–	–	–	–	**fo**
Family Chrysomelidae										
Subfamily Donaciinae										
Donacia sp.	–	–	–	1	–	–	–	–	–	**ri**
Subfamily Chrysomelinae										
Chrysolina arctica Medv.	–	–	1	–	–	–	–	11	1	**ms**
Ch. brunnicornis bermani Medv.	–	6	–	1	–	4	–	–	–	**st**
Ch. septentrionalis Men.	–	1	3	–	–	1	2	–	–	**mt**
Ch. subsulcata Mnnh.	–	24	–	2	–	–	–	–	–	**tt**
Ch. tolli Jac.	–	2	–	–	–	–	–	–	–	**tt**
Chrysolina sp.	2	–	–	–	–	–	–	–	–	**mt?**
Colaphellus alpinus Gebl.	–	1	–	1	–	–	–	–	–	**ms**
Hydrothassa hannoverana F.	–	–	–	–	–	1	–	–	–	**ri**
Phaedon concinnus Steph.	–	–	–	–	–	–	1	–	–	**me**
Phratora polaris Schn.	–	–	–	–	–	1	–	–	–	**sh**
Family Brentidae										
Subfamily Apioninae										
Hemitrichapion tschernovi T.-M.	–	1	–	4	–	1	1	–	–	**dt**
Pseudoprotapion astragali Payk.	–	3	–	–	–	–	–	–	–	**me**
Family Brachyceridae										
Subfamily Erirhininae										
Notaris bimaculatus F.	–	8	1	6	–	8	1	–	7	**ri**
Grypus equiseti F.	–	1	–	–	–	–	1	–	–	**ri**
Family Curculionidae										
Subfamily Ceutorhynchinae										
Pelenomus sp.	–	1	–	2	–	3	–	–	–	**ri**

Table 14. (Contd.)

Age	Keremesit Horizon								Edoma	
Section	16	4	0	16	16	9		16	14	
Species/sample K-	9	4	17	10	11	15	16	13	14	eco
Subfamily Entiminae										
Tribe Alophinini										
Lepidophorus thulius (Kiss.)	–	2	–	–	–	–	–	–	–	**dt**
Tribe Phyllobini										
Phyllobius kolymensis Kor. et Egorov.	–	18	2	4	–	3	–	–	–	**ms**
Phyllobius sp.	1	–	–	–	–	–	–	–	–	**ms?**
Tribe Sitonini										
Sitona borealis Kor.	–	4	–	1	–	12	–	–	2	**dt**
Subfamily Hyperinae										
Hypera diversipunctata Schrank.	–	4	–	3	–	–	–	–	–	**dt**
H. ornata Cap.	–	9	1	3	–	15	1	–	5	**dt**
Subfamily Lixinae										
Tribe Cleonini										
Coniocleonus astragali T.-M. et Kor.	–	–	–	–	–	–	–	–	1	**ms**
C. cinerascens Hochh.	–	1	–	–	–	3	–	–	–	**ms**
C. ferrugineus Fahr.	–	5	3	–	–	4	–	–	2	**ms**
Coniocleonus sp.	–	–	–	5	–	–	1	–	–	**ms**
Stephanocleonus eruditus Faust	–	–	33	–	–	2	–	–	–	**st**
S. fossulatus F.-W.	–	1	1	–	–	–	–	–	–	**st**
S. incertus Ter-Min.	–	12	1	–	–	6	–	–	–	**st**
S. tricarinatus F.-W.	–	–	–	–	–	–	–	–	5	**st**
Cleonini indet.	1	–	–	–	–	–	–	–	–	**ms?**
Subfamily Molytinae										
Tribe Hylobiini										
Hylobius piceus DeG.	–	–	–	–	–	–	–	–	1	**fo**
Tribe Lepyrini										
Lepyrus nordenskioeldi Faust	–	28	4	3	–	12	2	–	–	**sh**
Tribe Pissodini										
Pissodes insignatus Boh.	–	2	–	–	–	–	–	–	–	**fo**
P. irroratus Reitt.	–	–	–	3	–	3	–	–	–	**fo**
Pissodes sp.	–	–	–	–	–	–	–	–	1	**fo**
Subfamily Curculioninae										
Tribe Elliscini										
Dorytomus sp.	–	1	–	–	–	–	–	–	–	**sh**
Tribe Rhamphini										
Isochnus arcticus Kor.	–	5	–	26	–	–	–	–	–	**tt**
I. flagellum Erics.	–	–	–	–	–	–	–	–	2	**sh**
Order Hymenoptera										
Family Formicidae										
Formica gagatoides Ruzs.	–	–	–	1	–	–	–	–	–	**fo**
Camponotus herculeanus L.	–	4	–	–	–	–	–	–	–	**fo**
Hymenoptera gen. indet	–	3	6	–	–	2	–	–	–	**oth**
Order Megaloptera										
Family Sialidae										
Sialis sp.	–	1	–	–	1	–	–	–	1	**aq**
Order Trichoptera										
Trichoptera gen. indet. (larvae)	–	1	–	–	–	–	–	2	1	**aq**
Sum	14	580	100	408	12	415	61	12	252	

mens of steppe–tundra indicators, *Morychus viridis* and *Harpalus vittatus kiselevi*.

Sample K-15 from the middle part of the Keremesit Superhorizon was taken from sands with plant debris. The assemblage is dominated by the tundra groups; **dt** = 34% (*Poecilus nearcticus, Pterostichus* (*Cryobius*) *nigripalpis*, *P. sublaevis, Stereocerus haematopus, Amara interstitialis, Curtonotus alpinus, Hemitrichapion tschernovi, Sitona borealis, Hypera ornata* and **mt** = 27% (*Pterostichus* (*Cryobius*) *brevicornis, P.* (*Cryobius*) *pinguedineus, P.* (*Cryobius*) *ventricosus*, *P. vermiculosus, P. costatus, P. agonus, Carabus truncaticollis, Blethisa catenaria, Chrysolina septentrionalis*). The steppe–tundra indicators compose one-third of the assemblage, including *Morychus viridis* (24%), **st** group(3%), and **ms** group (4%). The assemblage includes individual forest species, *Pissodes irroratus*. We observe ecological diversity (which has been recorded in many preceding samples in this section) typical for the **S-T/S-T** type.

Sample K-16 from the same unit is characterized by similar but less diverse ecological structure.

The upper part of the Keremesit Superhorizon is represented by poor organic monotonous sand similar to the Maastakh Formation described from the Chukochya and Alazeya rivers. Fossil insects from the units are very similar. In this waste area (about 400 km between the sections), insect samples from the units are surprisingly uniform. Sample K-13 is poor, despite a great screened volume of deposits. It has yielded a few disrupted specimens, one *Morychus viridis* and 11 *Chrysolina arctica*. Such a preservation mode, along with the species composition, suggest that this region developed more or less uniformly during the second part of the Middle Pleistocene. We can reconstruct severe steppe-like environment suitable for species adapted for dry and cold conditions.

The uppermost part of the superhorizon is an ice wedge cast unit. The deposits between Maastakh and top Edoma were similar to that on the Alazeya River (interglacial Kuobakh Beds), but here this unit remains undefined. Despite geological similarity, fossil insects from ice wedge cast in the Keremesit section are not indicative of completely interglacial environment (Fig. 21, Table 14). Sample K-14 from the ice wedge cast only slightly differs from the previous series of samples (except K-13). The assemblage belongs to the **S-T/S-T** type (*Morychus viridis* composes 34%); steppe and meadow–steppe species (forest weevil *Hylobius piceus*) are singular. The difference is manifested in the somewhat higher proportion of the *mt* group (42%) and the number of relatively thermophilous species, such as *Diacheila polita, Elaphrus* sp., *Notaris bimaculatus, Cyrtoplastus irregularis, Olophrum consimile, a*nd *Corticaria* sp., which are more typical for shrub tundra or forest–tundra. We guess that the entire glacial interval is missed in the Keremesit section; the ice wedge cast unit apparently corresponds to the post-interglacial MIS5d stage.

Fossil insects from the Keremesit River have some features in common. Two uncommon species, *Notiophilus aquaticus* and *Notaris bimaculatus,* permanently present throughout the section. In addition, the assemblage contains an unusually high proportion of the xerophilous tundra ground beetle *Poecilus nearcticus,* which probably competes here with the typical dominant of the group, *Curtonotus alpinus*. These features suggest that the local entomofauna remained stable during thousands of years.

Most of assemblages from the Keremesit River belong to the **S-T/S-T** type or closely similar to it. Insect assemblages do not show sharp changes in the ecological structure. Such an ecological continuity may be caused by a northwestern position of the section and the loss of some distinctive events from the section.

3.2b. Yana River

The Paleolithic site on the Yana River is a unique early human settlement dated 28.5–27.0 ka and situated north of the Polar Circle (Pitulko et al., 2004, 2007).

The Yana site is on the left bank of the Yana River (Figs. 1, 2, 11) at an exit from a narrow channel cutting the Kular Ridge to a flat plain. This locality was probably within the route of seasonal migration of grazing mammals. Human tools were discovered in the second (16–18 m high) floodplain terrace on a 7–7.5-m-high elevation. The third floodplain terrace is 40–45 m high; it is composed of the Edoma Formation rich in ice, with large ice wedges. The digger's holes in the ice wedges are presently widely used by local population as food storage. Behavior of ancient humans remains uncertain, but this permafrost feature may help to preserve food hunted during seasonal migrations. Anyway, the settlement was long–lived, maybe because of good location and suitable climate. Radiocarbon dates from bones and tools lie within the interval 28.5–27.0 ka (Pitulko and Pavlova, 2007).

Insect samples (Tables 15, 16) were screened by Pavlova (Pitulko et al., 2007) during a complex archeological study of the site. Thirteen samples come from sandy–silty Pleistocene deposits of the second terrace (including occupation layer), three are from Holocene peat at the top of the terrace, and three small samples come from the third terrace (radiocarbon dates are 37.8–41.5 ka).

The oldest insect assemblage from the site contains mostly wet tundra species (**mt** = 47%), such as *Carabus truncaticollis, Pterostichus (Cryobius) brevicornis, P. (Cryobius) pinguedineus, P. (Cryobius) ventricosus, Cholevinus sibiricus, Tachinus arcticus,* and *Chrysolina septentrionalis*. Arctic species, *Isochnus arcticus, Chrysolina subsulcata,* and *Ch. tolli,* are present here, along with the steppe–tundra indicators *Morychus viridis* and *Stephanocleonus eruditus*. Forest species are absent there. The species composition and ecological

Table 15. Insects from the Yana site (part 1)

Age	Late Pleistocene										
Section	E-135			Tums1							
Species/sample	1	2	3	6	6.5	7	7.5	8	8.5	9	eco
Order Coleoptera											
Family Carabidae											
Subfamily Nebriinae											
Notiophilus aquaticus L.	1	–	–	–	–	–	–	–	–	–	**xe**
Subfamily Carabinae											
Carabus truncaticollis Esch.	1	–	–	–	–	–	–	–	–	–	**mt**
Subfamily Harpalinae											
Tribe Harpalini											
Harpalus vittatus kiselevi Kat. et Shil.	–	–	–	–	–	–	1	1	–	–	**ms**
H. vittatus vittatus Gebl.	–	–	–	2	3	1	1	–	–	–	**ms**
Tribe Pterostichini											
Pterostichus (*Cryobius*) *brevicornis* (Kby.)	1	–	2	1	1	–	–	–	4	–	**mt**
P. (*Cryobius*) *nigripalpis* Popp.	–	–	–	–	–	–	–	1	2	7	**dt**
P. (*Cryobius*) *pinguedineus* Esch.	3	2	–	–	–	–	–	–	1	–	**mt**
P. (*Cryobius*) *ventricosus* Esch.	2	2	–	–	–	–	–	–	–	–	**mt**
Pterostichus (*Cryobius*) sp.	2	–	2	–	–	–	1	1	–	–	**mt**
P. (*Lenapterus*) *vermiculosus* Men.	–	–	1	–	–	–	–	–	–	–	**mt**
P. (*Tundraphilus*) *sublaevis* Sahlb.	1	–	–	–	–	–	–	–	–	–	**dt**
Tribe Zabrini											
Curtonotus alpinus Payk.	1	2	3	2	2	–	3	2	7	2	**dt**
C. bokori Csiki	–	–	–	–	–	–	–	–	–	1	**dt**
Family Dytiscidae											
Subfamily Hydroporinae											
Hydroporus acutangulus Thoms.?	–	–	–	1	–	–	–	–	–	–	**aq**
Family Hydrophilidae											
Subfamily Helophorinae											
Helophorus splendidus Sahlb.	–	–	–	–	–	–	1	–	–	–	**aq**
Subfamily Hydrophilinae											
Hydrobius fuscipes F.	1	–	–	–	–	–	–	–	–	–	**aq**
Family Leiodidae											
Subfamily Cholevinae											
Cholevinus sibiricus (Jean.)	2	–	–	–	–	–	–	1	–	–	**mt**
Family Staphylinidae											
Subfamily Tachyporinae											
Tachinus arcticus Motsch.	2	3	–	–	–	–	–	1	1	–	**mt**
Subfamily Paederinae											
Lathrobium sp.	1	–	–	–	–	–	–	–	–	–	**pl**
Family Scarabaeidae											
Aphodius sp.	–	–	–	1	1	1	4	1	4	3	**xe**
Family Byrrhidae											
Subfamily Byrrhinae											
Morychus viridis Kuzm. et Korot.	5	–	3	30	29	33	138	110	161	222	**ss**
Family Melyridae											
Troglocollops arcticus L. Medv.	–	–	–	–	–	–	6	1	1	1	**ms**
Family Lathridiidae											
Subfamily Corticariinae											
Corticaria sp.	–	–	–	–	–	–	–	–	–	1	**pl**

Table 15. (Contd.)

Age	Late Pleistocene										
Section	E-135			Tums1							eco
Species/sample	1	2	3	6	6.5	7	7.5	8	8.5	9	
Family Chrysomelidae											
Subfamily Chrysomelinae											
Chrysolina arctica Medv.	–	–	–	–	–	–	–	1	–	–	**ms**
Ch. brunnicornis bermani Medv.	–	–	–	–	–	–	2	1	2	2	**st**
Ch. septentrionalis Men.	–	1	–	–	–	1	5	3	7	1	**mt**
Ch. subsulcata Mnnh.	–	1	–	–	–	–	–	–	–	1	**tt**
Ch. tolli Jac.	1	–	–	–	–	–	–	–	–	–	**tt**
Family Brentidae											
Subfamily Apioninae											
Hemitrichapion tschernovi T.-M.	–	–	–	–	3	–	–	–	–	–	**dt**
Pseudoprotapion astragali Payk.?	–	–	–	–	–	1	3	–	4	–	**ms**
Family Brachyceridae											
Subfamily Erirhininae											
Notaris aethiops F.	1	–	–	–	–	–	–	–	–	–	**ri**
Family Curculionidae											
Subfamily Entiminae											
Tribe Phyllobini											
Phyllobius fumigatus Boh.	–	–	–	–	–	–	8	2	3	–	**me**
Phyllobius kolymensis Kor. et Egorov.	–	–	–	–	–	–	–	–	–	7	**ms**
Tribe Sitonini											
Sitona borealis Kor.	1	–	–	–	1	–	1	–	2	1	**dt**
Subfamily Hyperinae											
Hypera sp.	–	–	–	–	–	–	–	–	–	1	**dt**
Subfamily Lixinae											
Tribe Cleonini											
Coniocleonus astragali T.-M. et Kor.	–	–	–	–	1	–	1	–	–	–	**ms**
Stephanocleonus eruditus Faust	1	–	–	6	2	8	5	1	–	13	**st**
Stephanocleonus sp.	–	–	1	–	–	–	–	–	3	–	**st**
Subfamily Molytinae											
Tribe Lepyrini											
Lepyrus nordenskioeldi Faust	–	1	–	–	–	–	–	–	–	–	**sh**
Subfamily Curculioninae											
Tribe Elliscini											
Dorytomus sp.	–	–	1	–	–	–	–	–	–	–	**sh**
Tribe Rhamphini											
Isochnus arcticus Kor.	3	–	–	–	–	–	–	–	–	–	**tt**
Order Hymenoptera											
Hymenoptera gen. indet.	–	–	–	–	–	–	9	–	2	–	**oth**
Order Trichoptera											
Thrichoptera gen. indet. (larvae)	–	–	–	–	–	–	–	–	1	–	**aq**
Order Diptera											
Family Tipulidae											
Tipulidae gen. indet. (larvae)	1	–	–	–	–	–	–	–	–	–	**aq**
Diptera gen. indet (pseudopupia)	–	–	–	–	–	–	–	–	2	–	**oth**
Sum	30	12	13	43	43	45	180	127	202	263	

Table 16. Insects from the Yana site (part 2)

Age	Late Pleistocene						Holocene			
Section	Tums1									
Species/sample	9.5	10	10.5	11	11.5	12	12.5	13	13.5	eco
Order Coleoptera										
Family Carabidae										
Subfamily Carabinae										
Carabus truncaticollis Esch.	1	–	–	–	–	–	–	–	–	**mt**
Subfamily Elaphrinae										
Blethisa sp.	–	–	–	–	–	–	–	1	–	**mt?**
Subfamily Scaritinae										
Dyschiriodes melancholicus Putz.	–	–	–	–	–	–	–	–	1	**ri**
Subfamily Trechinae										
Bembidion (*Asioperyphus*) *umiatense* Lth.	–	–	–	2	–	–	4	4	1	**ri**
B. (*Peryphanes*) *dauricum* Motsch.	–	–	–	1	–	–	1	1	–	**dt**
Subfamily Harpalinae										
Tribe Harpalini										
Dicheirotrichus mannerheimi Sahlb.	–	–	–	–	–	–	2	–	2	**dt**
Harpalus cf. *pusillus* Motsch.	–	–	–	–	1	–	–	2	–	**st**
H. vittatus vittatus Gebl.	–	–	–	1	2	–	2	–	–	**ms**
Tribe Lebiini										
Cymindis arctica Kryzh. et Em.	–	–	–	1	–	–	–	1	–	**st**
C. vaporariorum L.	–	–	–	–	–	–	2	–	–	**dt**
Tribe Pterostichini										
Poecilus (*Derus*) *nearcticus* Lth.	2	–	–	4	1	1	2	3	–	**dt**
Pterostichus (*Cryobius*) *brevicornis* (Kby.)	–	–	–	1	–	–	4	–	4	**mt**
P. (*Cryobius*) *pinguedineus* Esch.	–	–	–	1	–	–	6	5	–	**mt**
P. (*Cryobius*) *ventricosus* Esch.	–	–	–	1	–	–	3	2	1	**mt**
Pterostichus (*Cryobius*) sp.	4	–	–	3	–	1	2	6	4	**mt**
P. (*Lenapterus*) *agonus* Horn.	–	–	–	–	–	–	1	–	–	**mt**
P. (*Lenapterus*) *costatus* Men.	–	–	–	–	–	–	–	–	1	**mt**
P. (*Petrophilus*) *abnormis* Sahlb.	–	–	–	–	–	–	–	2	–	**dt**
P. (*Petrophilus*) *eximius* Mor.	–	–	–	–	1	–	–	–	–	**dt**
P. (*Petrophilus*) *tundrae* Tschitsch.	–	–	–	1	–	–	–	–	2	**dt**
P. (*Tundraphilus*) *sublaevis* Sahlb.	–	–	–	–	1	–	2	1	–	**dt**
Stereocerus haematopus (Dej.)	1	–	–	–	–	–	1	–	1	**dt**
Tribe Zabrini										
Curtonotus alpinus Payk.	2	–	–	7	–	2	10	–	1	**dt**
Family Dytiscidae										
Subfamily Agabinae										
Agabus moestus (Curt.)	–	–	–	–	–	–	–	1	–	**aq**
A. thomsoni (J.Sach.)	–	–	–	–	–	–	–	–	3	**aq**
SubfamilyColymbetinae										
Colymbetes dolabratus (Payk.)	–	–	–	–	–	–	–	–	1	**aq**
Subfamily Hydroporinae										
Hydroporus acutangulus Thoms.?	–	–	–	–	–	–	–	1	2	**aq**
H. punctipennis Sahl.	–	–	–	–	–	–	–	–	1	**aq**
Family Hydrophilidae										
Subfamily Helophorinae										
Helophorus splendidus Sahlb.	–	–	–	4	–	–	1	1	–	**aq**
Subfamily Hydrophilinae										
Hydrobius fuscipes F.	–	–	–	–	–	–	–	–	1	**aq**
Family Hydraenidae										
Ochthebius sp.	–	–	–	–	–	–	–	–	1	**aq**
Family Leiodidae										
Subfamily Leiodinae										
Cyrtoplastus irregularis Rtt.?	–	–	–	–	–	–	1	–	–	**pl**

Table 16. (Contd.)

Age	Late Pleistocene						Holocene			
Section	Tums1									
Species/sample	9.5	10	10.5	11	11.5	12	12.5	13	13.5	eco
Subfamily Cholevinae										
Cholevinus sibiricus (Jean.)	2	–	–	13	–	2	6	7	–	**mt**
Colon sp.	–	–	–	–	–	–	–	1	–	**pl**
Family Silphidae										
Subfamily Silphinae										
Thanatophilus sp.	–	–	–	–	–	–	1	–	–	**oth**
Family Staphylinidae										
Subfamily Omaliinae										
Eucnecosum tenue (LeC.)	–	–	–	–	–	–	2	2	–	**pl**
Subfamily Tachyporinae										
Tachinus arcticus Motsch.	–	–	–	6	–	2	5	13	–	**mt**
Subfamily Paederinae										
Lathrobium sp.	–	–	–	–	–	–	–	–	1	**pl**
Family Scarabaeidae										
Aphodius sp.	–	–	–	9	3	4	7	11	–	**xe**
Family Byrrhidae										
Subfamily Byrrhinae										
Morychus viridis Kuzm. et Korot.	23	4	2	31	13	27	20	37	1	**ss**
Simplocaria semistriata F.	–	–	–	–	–	–	–	–	1	**dt**
Subfamily Syncalyptinae										
Curimopsis cyclolepidia Muenst.	–	–	–	–	–	–	1	1	–	**dt**
Family Bostrichidae										
Stephanopachys substriatus Payk.	–	–	–	–	–	–	1	–	–	**fo**
Family Melyridae										
Troglocollops arcticus L. Medv.	–	–	–	8	–	4	1	–	–	**ms**
Melyridae gen. indet.	–	–	–	–	–	–	1	–	–	**oth**
Family Chrysomelidae										
Subfamily Chrysomelinae										
Chrysolina arctica Medv.	2	–	–	–	–	–	–	–	–	**ms**
Ch. brunnicornis bermani Medv.	1	–	–	–	–	–	–	2	–	**st**
Ch. septentrionalis Men.	–	–	–	–	–	–	1	1	1	**mt**
Ch. rufilabris Fald.	–	–	–	–	–	–	–	1	–	**st**
Chrysolina sp.	–	–	–	1	–	–	–	–	–	**mt?**
Phaedon concinnus Steph.	–	–	–	–	–	–	–	1	–	**me**
Phaedon sp.	–	–	–	–	–	–	1	–	–	**me**
Family Brentidae										
Subfamily Apioninae										
Hemitrichapion tschernovi T.-M.	–	–	–	–	1	2	–	–	–	**dt**
Mesotrichapion wrangelianum Kor.	1	–	–	–	–	–	3	–	–	**dt**
Pseudoprotapion astragali Payk.?	–	–	–	3	–	–	–	10	–	**ms**
Family Brachyceridae										
Subfamily Erirhininae										
Notaris sp.	–	–	–	1	–	–	–	–	–	**ri**
Family Curculionidae										
Subfamily Ceutorhynchinae										
Ceutorhynchus sp.	–	–	–	–	–	–	–	1	–	**dt**
Subfamily Entiminae										
Tribe Phyllobini										
Phyllobius kolymensis Kor. et Egorov.	–	–	–	1	–	1	3	2	–	**ms**
Tribe Sitonini										
Sitona borealis Kor.	1	–	–	3	–	–	2	2	–	**dt**
Subfamily Hyperinae										
Hypera diversipunctata (Schrank.)	–	–	–	–	–	–	2	5	1	**dt**
H. ornata (Cap.)	–	–	–	2	–	–	2	–	–	**dt**

Table 16. (Contd.)

Age	Late Pleistocene						Holocene			
Section	Tums1									
Species/sample	9.5	10	10.5	11	11.5	12	12.5	13	13.5	eco
Subfamily Lixinae										
Tribe Cleonini										
Coniocleonus astragali T.-M.et Kor.	–	–	–	–	–	–	–	1	–	**ms**
C. ferrugineus Fahr.	–	–	–	–	3	–	–	–	2	**ms**
Stephanocleonus eruditus Faust	4	2	1	8	3	2	8	14	–	**st**
S. fossulatus F-W.	–	–	–	–	–	–	2	–	–	**st**
Subfamily Molytinae										
Tribe Lepyrini										
Lepyrus nordenskioeldi Faust	–	–	–	1	–	–	1	3	–	**sh**
Subfamily Curculioninae										
Tribe Rhamphini										
Isochnus arcticus Kor.	1	–	–	3	–	–	–	1	–	**tt**
Order Heteroptera										
Family Corixidae										
Sigara sp.	–	–	–	1	–	–	–	–	–	**aq**
Family Saldidae										
Salda littoralis L.	–	–	–	–	–	4	–	–	–	**ri**
Order Hymenoptera										
Family Formicidae										
Formica gagatoides Ruzs.	–	–	–	1	–	–	–	1	–	**fo**
Hymenoptera gen. indet.	–	–	1	1	–	1	1	–	–	**oth**
Order Megaloptera										
Family Sialidae										
Sialis sp. (larvae)	–	–	–	1	1	1	–	1	–	**aq**
Order Diptera										
Family Chironomidae										
Chironomidae gen. indet. (larvae)	–	–	–	–	–	–	–	1	2	**aq**
Family Tipulidae										
Tipulidae gen. indet. (larvae)	–	–	–	–	–	–	1	–	–	**aq**
Diptera gen. indet. (pseudopupia)	–	–	–	2	1	–	1	–	–	**aq**
Sum	45	6	3	119	29	52	114	148	34	

structure do not give evidence of the “Karginian warming”, but domination of the **mt** group is indicative of attenuation of the moisture-deficit steppe–tundra conditions. The assemblage belongs to the **TU/S-T** type.

The samples from the second terrace are surprisingly uniform. They were taken 1 m below the occupation layer, with a 0.5-m interval. Three samples are poor, but among rich samples, nine of ten belong to the **S-T/SS** type. The proportion of *Morychus vidiris* reaches 85%. Only one sample from 11-m-high elevation (4 m above the occupation layer) belongs to the moderate **S-T/S-T** type, with singular forest species. This material shows very stable existence of a specific kind of the Pleistocene landscape. There was a dry floristically poor low-grass steppe–tundra. The lack of a dense moss cover provides better soil insolation and lower border of the active layer. Dry soil and deep permafrost border prevent thermoerosion caused by intense grazing. Perhaps, this sort of environment was maintained by overgrazing. We have not recorded a long-lived **S-T/SS** entomofauna type in other localities. Unique local conditions of the Pleistocene favorable for large mammals could attract humans to this area.

The environment was established before human activity and remained the same after that. Thus, climatic changes were not a critical factor forcing people to leave the settlement.

Three top samples come from the Lower Holocene (radiocarbon date for the last sample is 8.960 ± 0.08 ka). Two lower samples from the unit are still close to the Pleistocene ones. Both assemblages are dominated by xerophilous species; the role of steppe–tundra indicators is high, the **st**, **ms**, and **ss** group compose in sum 32 and 47%, so that the assemblages belong to the

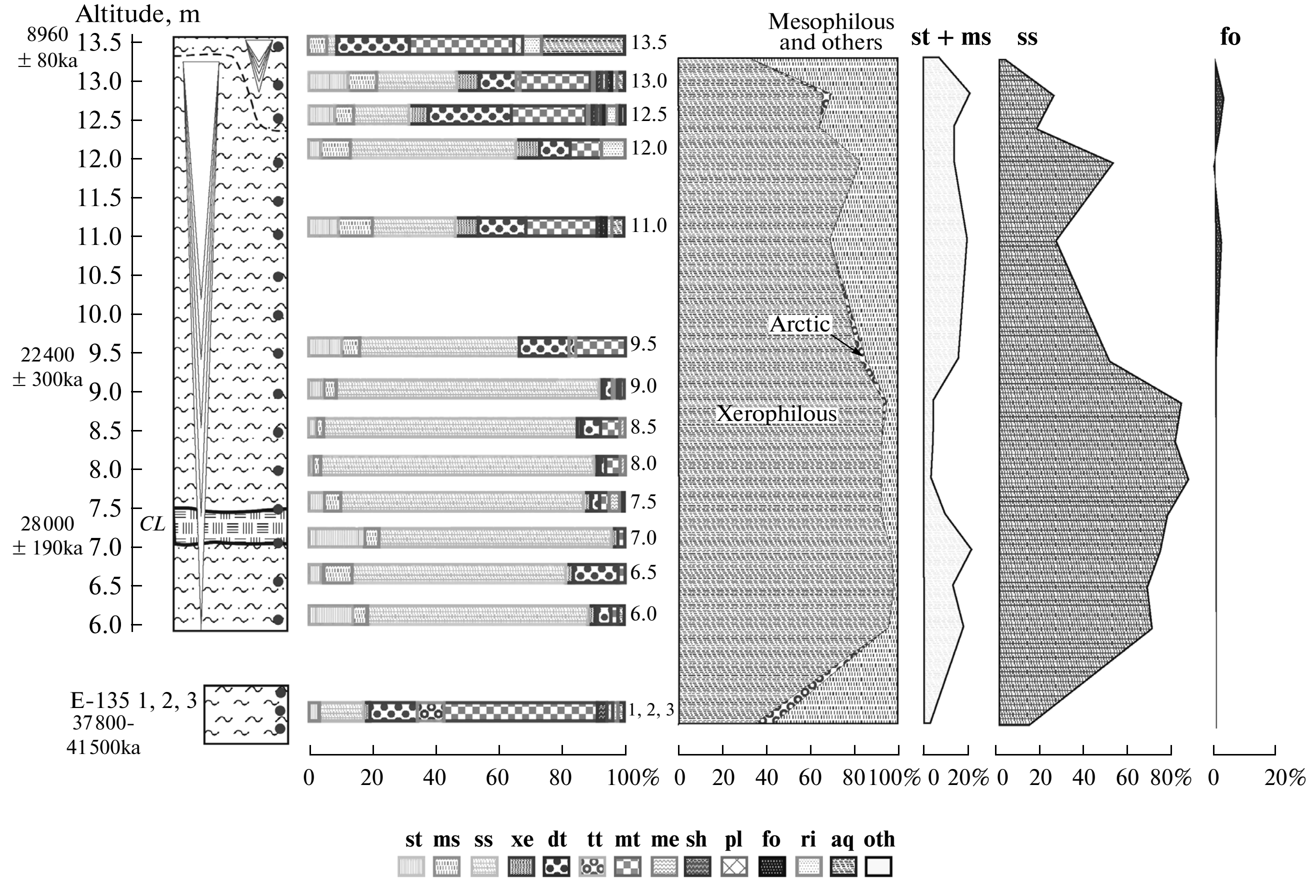


Fig. 22. Stratigraphic scheme and insect assemblages from the Yana site. (*CL*)Culture level. For legend, see Figs. 15 and 16.

S-T/S-T type typical for the Pleistocene. On the other hand, the early Holocene fauna differs from the previous one. Species and ecological diversity of assemblages is much higher. For example, the previous *Morychus*-dominated fauna (sample 7.5) consists of 15 species, with MNI = 180, while in the Holocene fauna (sample 12.5), the MNI is 144, belonging to 36 species. The latter includes rare species, such as the Hydraenid beetle *Ochthebius* sp. This is new a record for the fossil insect list of western Beringia.

The last sample (13.5) has a more familiar Holocene appearance. It is dominated by wet tundra and aquatic species; steppe insects are absent, but some insects from the **ms** and **ss** groups still present. Delay in the steppe–tundra collapse is evident here. A similar situation is observed in the Holocene Alazeya section. Furthermore, the species diversity of steppe and meadow–steppe insects (*Stephanocleonus eruditus*, *S. fossulatus, Chrysolina brunnicornis bermani, Troglocollops arcticus, Phyllobius kolymensis*) became higher in the early Holocene, as compared with poor *Morychus*-dominated Late Pleistocene assemblages.

3.3. Lena Delta and Laptev Sea Coast

3.3a. Bykovsii Peninsula

The Bykovsii Peninsula (Figs. 1, 8) is located in the eastern part of the Lena delta area near the town of Tiksi. This area is well known to paleontologists, because the first complete woolly mammoth corpse (the "Adams' Mammoth") was found here in 1799. A 40-m-high cliff of Mamontovyi Khayata (MKh) is composed of ice saturated silts, sometimes fine silty sands, with a polygonal system of thick syngenetic ice wedges. The section has repeatedly been studied with reference to various, but mostly sedimentary, aspects (Tomirdiaro, 1984; Kunitsky, 1989; Slagoda, 1993). A recent study has been performed under the German–Russian project "The Laptev Sea System 2000" (Andreev et al., 2002; Meyer et al., 2002; Schirrmeister et al., 2002b, 2002c; Siegert et al., 2002; Sher et al., 2005).

Fossil insects (Tables 17–25) were collected during four seasons of field work. The first and basic series was collected in 1998 by me; additional samples from the upper part of the section were collected by A. Sher in 1999; a couple of samples were taken by me during a short visit to the section in 2000; and the final detailed

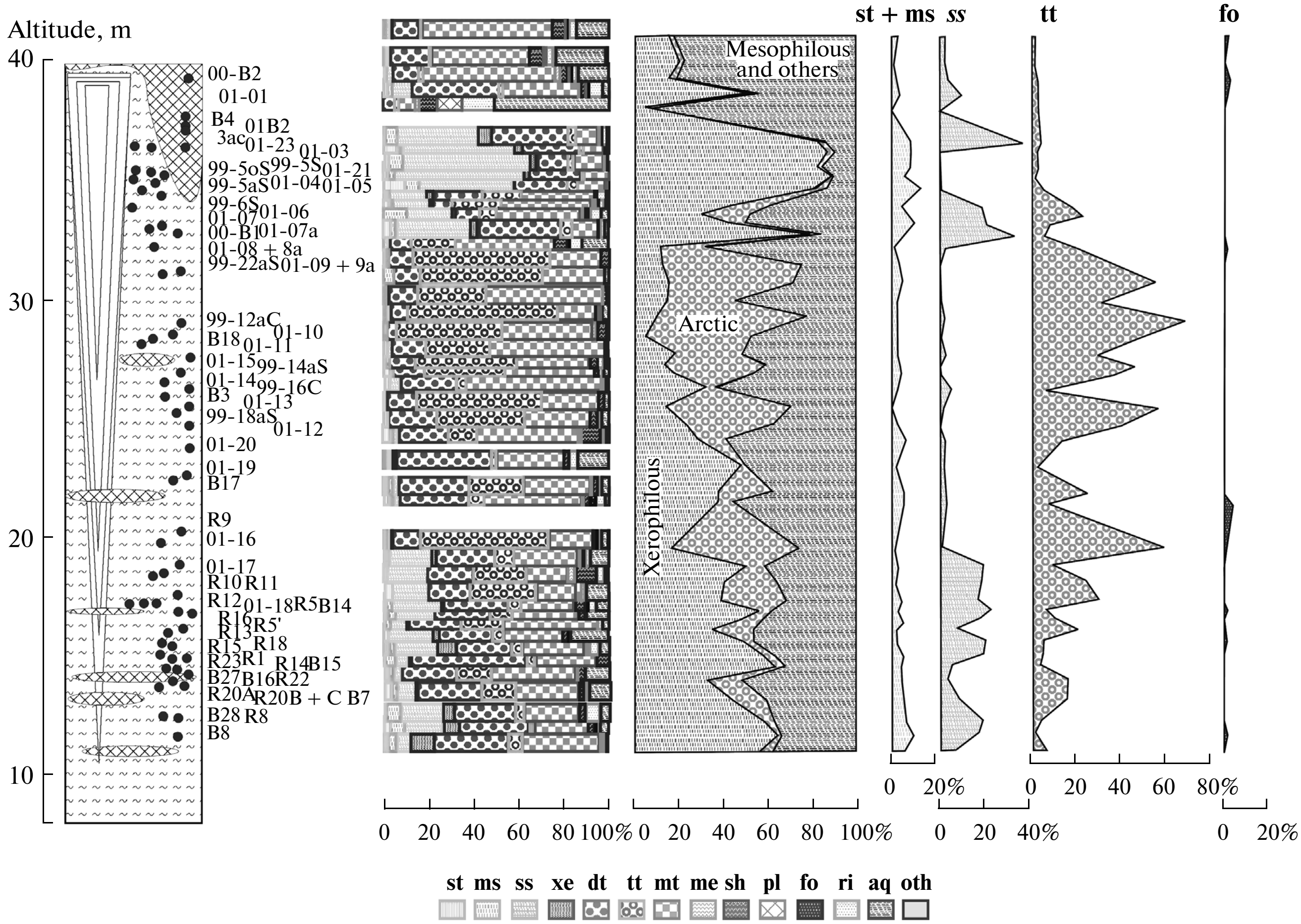


Fig. 23. Stratigraphic scheme and insect assemblages from the Mamontovyi Khayata section, Bykovsii Peninsula. For legend, see Figs. 15 and 16.

series was collected by me and A. Sher in 2002. About 50 samples were screened for insect fossils from the main section (Figs. 23, 25) and a few were from three additional localities (Fig. 25). Altogether, they have yielded nearly 11 000 insect fossils, belonging to at least 5900 individuals. The section became one of the best studied; it provides the most complete record of environmental and climatic history for the last 50000 years in the whole of Arctic Siberia.

The stratigraphy of the section is relatively simple: the bedding is close to horizontal; the sediment is more or less uniform fine-grained sandy silt, with varying organics content, such as fine plant detritus, tiny grass roots, moss peat, and shrub remains. Radiocarbon data suggest that sedimentation was mostly continuous from ca. 48 to 12–12.5 ka. Accumulation of the top peat started about 7.8 ka, so that we have a stratigraphic gap at the Pleistocene–Holocene boundary and missed earliest Holocene stages. This situation is common for most of the western Beringia sections (Kaplina and Lozhkin, 1979).

The lowest samples are B19 and R17 taken from 1 m above sea level. The samples are poor. Most of the remains belong to the mesophilous tundra rove beetle *Tachinus arcticus*. Others are also mostly tundra species (*Pterostichus* (*Cryobius*) *ventricosus, P. costatus, Cholevinus sibiricus*) and xerophilous *Pterostichus tundra* and *Sitona borealis*; the assemblage contains individual *Morychus viridis*.

The next sample (B8) comes from 11.8 m of depth (the lower part of the section is mostly covered). The assemblage is dominated by tundra species; **mt** = 35% (*Pterostichus* (*Cryobius*) *pinguedineus*, *P.* (*Cryobius*) *ventricosus*, *P. costatus, Cholevinus sibiricus, Tachinus arcticus, Chrysolina septentrionalis*) and **dt** = 33% (*Curtonotus alpinus, Poecilus nearcticus, P. tundrae, Simplocaria arctica, Mesotrichapion wrangelianum, Hemitrichapion tschernovi, Sitona borealis, Hypera ornata*). The arctic tundra group is represented by individual *Isochnus arcticus*. The steppe–tundra indicators are represented by abundant (10%) dung beetles of the genus *Aphodius*.

Most of fossil *Aphodius* from the Bykovsii Peninsula belong to *A. pusillus* (identified by V. Martynov). This species is widespread in grazing areas throughout Europe and Siberia, but absent in the modern tundra.

Table 17. Insects from the Mamontovyi Khayata section (part 1)

Age	Late Pleistocene									
Section	MKh									
Species/sample MKh-	B19, R17	B8	B2	R8, B28	B7	B16	B15, R14	R2	R15	eco
Order Coleoptera										
Subfamily Carabinae										
Carabus truncaticollis Esch.	1	1	–	1	–	–	–	–	–	**mt**
Subfamily Trechinae										
Bembidion (*Asioperyphus*) *umiatense* Lth.	–	–	–	–	4	–	–	–	–	**ri**
Subfamily Harpalinae										
Tribe Harpalini										
Harpalus vittatus kiselevi Kat. et Shil.	–	–	–	2	4	–	–	–	–	**ms**
H. vittatus vittatus Gebl.	–	–	–	1	–	–	2	–	–	**ms**
Harpalus sp.	–	–	1	4	–	–	–	–	–	**ms**
Tribe Pterostichini										
Poecilus (*Derus*) *nearcticus* Lth.	–	2	–	1	2	–	–	–	–	**dt**
Pterostichus (*Cryobius*) *brevicornis* (Kby)	–	–	–	–	2	–	5	–	3	**mt**
P. (*Cryobius*) *nigripalpis* Popp.	–	–	–	–	–	–	2	–	1	**dt**
P. (*Cryobius*) *pinguedineus* Esch.	–	1	3	3	7	–	1	1	3	**mt**
P. (*Cryobius*) *ventricosus* Esch.	3	1	3	3	–	2	1	–	–	**mt**
Pterostichus (*Cryobius*) sp.	–	1	3	9	2	3	10	3	–	**mt**
P. (*Lenapterus*) *costatus* Men.	2	2	–	2	1	–	2	1	1	**mt**
P. (*Petrophilus*) *abnormis* Sahlb.	–	–	4	4	1	–	3	2	–	**dt**
P. (*Petrophilus*) *magus* Mnnh.	–	–	1	1	–	–	–	–	–	**fo**
P. (*Petrophilus*) *montanus* (Motsch.)	–	–	4	4	–	–	–	–	–	**dt**
P. (*Petrophilus*) *tundrae* Tschitsch.	1	1	–	2	1	–	–	–	1	**dt**
P. (*Tundraphilus*) *sublaevis* Sahlb.	–	–	1	1	–	1	–	1	2	**dt**
Stereocerus haematopus (Dej.)	–	–	–	1	–	–	–	–	–	**dt**
Tribe Zabrini										
Curtonotus alpinus Payk.	1	5	7	29	11	4	19	6	5	**dt**
Family Dytiscidae										
Subfamily Agabinae										
Agabus moestus (Curt.)	–	–	4	5	1	–	7	–	1	**aq**
Subfamily Hydroporinae										
Hydroporus acutangulus Thoms.?	–	–	–	–	2	–	7	–	–	**aq**
Hydroporus sp.	–	–	1	2	–	–	–	1	–	**aq**
Family Hydrophilidae										
Subfamily Helophorinae										
Helophorus splendidus Sahlb.	1	1	1	1	2	–	4	–	5	**aq**
Family Leiodidae										
Subfamily Cholevinae										
Cholevinus sibiricus (Jean.)	3	4	3	3	5	1	4	–	2	**mt**
Family Staphylinidae										
Subfamily Tachyporinae										
Tachinus arcticus Motsch.	13	5	9	17	8	6	23	1	11	**mt**
Family Scarabaeidae										
Aphodius sp.	–	5	5	13	5	–	1	–	–	**xe**
Family Byrrhidae										
Subfamily Byrrhinae										
Morychus viridis Kuzm. et Korot.	1	3	3	30	20	2	14	1	2	**ss**
Simplocaria arctica Popp.	–	1	–	–	–	–	–	–	–	**dt**
Subfamily Syncalyptinae										
Curimopsis cyclolepidia Muenst.	–	–	–	1	1	–	3	–	–	**dt**
Family Chrysomelidae										
Subfamily Chrysomelinae										
Chrysolina arctica Medv.	–	2	–	1	–	–	1	–	–	**ms**
Ch. brunnicornis bermani Medv.	–	–	–	–	–	1	1	–	–	**st**
Ch. purpurata Fald. ?	–	–	–	1	–	–	–	–	–	**st**
Ch. septentrionalis Men.	–	2	–	3	1	–	1	–	–	**mt**
Ch. subsulcata Mnnh.	–	–	–	–	–	2	2	–	1	**tt**

Table 17. (Contd.)

Age	Late Pleistocene									
Section	MKh									
Species/sample MKh-	B19, R17	B8	B2	R8, B28	B7	B16	B15, R14	R2	R15	eco
Ch. tolli Jac.	–	–	–	–	–	1	–	–	–	**tt**
Chrysolina sp.	–	–	2	2	–	1	–	–	–	**mt?**
Hydrothassa hannoverana F.	–	1	–	–	3	–	–	–	–	**ri**
Phaedon armoraciae L.	–	–	–	–	–	–	–	–	1	**me**
Phratora polaris Schn.	–	–	–	1	–	–	–	–	–	**sh**
Subfamily Galerucinae										
Galeruca interrupta circumdata Duft.	–	–	1	1	–	–	1	–	1	**st**
Family Brentidae										
Subfamily Apioninae										
Hemitrichapion tschernovi T.-M.	–	4	3	3	2	2	4	–	–	**dt**
Mesotrichapion wrangelianum Kor.	–	1	1	2	4	5	4	–	1	**dt**
Family Brachyceridae										
Subfamily Erirhininae										
Erirhinus aethiops (F.)	–	–	–	–	–	–	1	–	–	**ri**
Notaris bimaculatus F.	–	–	–	–	–	–	1	–	–	**ri**
Family Curculionidae										
Subfamily Entiminae										
Tribe Phyllobini										
Phyllobius kolymensis Kor. et Egorov.	–	–	–	–	1	–	–	–	–	**ms**
Tribe Sitonini										
Sitona borealis Kor.	2	1	–	1	3	2	2	–	–	**dt**
Subfamily Hyperinae										
Hypera diversipunctata Schrank.	–	–	2	2	–	1	4	–	–	**dt**
H. ornata Cap.	–	1	1	5	4	–	7	2	3	**dt**
Subfamily Lixinae										
Tribe Cleonini										
Coniocleonus ferrugineus Fahr.	–	–	2	2	–	–	–	–	–	**ms**
Coniocleonus sp.	–	–	–	–	2	–	1	–	1	**ms**
Stephanocleonus eruditus Faust	–	1	2	4	–	–	2	1	–	**st**
S. paradoxus Fahr.	–	–	–	1	–	–	–	–	–	**st**
Stephanocleonus sp.	–	–	–	–	1	–	1	–	–	**st**
Subfamily Molytinae										
Tribe Lepyrini										
Lepyrus nordenskioeldi Faust	1	–	4	5	3	3	3	1	1	**sh**
Subfamily Curculioninae										
Tribe Rhamphini										
Isochnus arcticus Kor.	–	3	1	3	4	2	24	1	7	**tt**
Order Heteroptera										
Family Corixidae										
Sigara sp.	–	–	–	–	–	1	–	–	–	**aq**
Family Saldidae										
Salda littoralis L	–	–	1	1	–	–	1	–	–	**ri**
Order Hymenoptera										
Hymenoptera gen. indet.	3	2	–	4	3	3	1	–	–	**oth**
Order Megaloptera										
Family Sialidae										
Sialis sp.	1	–	–	–	–	–	1	–	–	**aq**
Order Trichoptera										
Trichoptera gen. indet. (larvae)	–	2	–	–	2	2	1	–	–	**aq**
Order Diptera										
Family Chironomidae										
Chironomidae gen. indet.	1	1	–	1	–	1	–	–	–	**aq**
Family Tipulidae										
Tipulidae gen. indet.	–	–	–	–	–	4	–	–	–	**oth**
Diptera fam. indet. (puparia)	–	–	–	–	1	–	–	–	–	**oth**
Sum	29	49	73	178	87	40	169	22	53	

Table 18. Insects from the Mamontovyi Khayata section (part 2)

Age	Late Pleistocene										
Section	MKh										
Species/sample MKh-	R18	R13	R5'	1B18	R16	B14	R5	R12	R11	R10	eco
Order Coleoptera											
Family Carabidae											
Subfamily Trechinae											
Bembidion (*Asioperyphus*) *umiatense* Lth.	–	–	–	1	–	–	–	1	–	–	**ri**
B. (*Peryphanes*) *dauricum* Motsch.	–	1	–	–	–	–	2	–	–	–	**dt**
Bembidion (*Peryphus*) sp.	–	1	–	–	–	–	4	–	1	–	**ri**
B. (*Plataphus*) *hyperboraeorum* Munst.	–	–	–	1	–	–	–	–	–	–	**ri**
Subfamily Harpalinae											
Tribe Harpalini											
Harpalus vittatus alaskensis Lth.	–	–	–	2	–	–	–	–	–	–	**ms**
Harpalus sp.	–	–	–	–	–	–	–	–	–	–	**ms**
Tribe Pterostichini											
Poecilus (*Derus*) *nearcticus* Lth.	1	–	1	–	–	–	2	–	–	–	**dt**
Pterostichus (*Cryobius*) *brevicornis* (Kby.)	2	–	–	3	1	2	2	1	–	–	**mt**
P. (*Cryobius*) *nigripalpis* Popp.	–	–	–	–	–	–	6	–	–	–	**dt**
P. (*Cryobius*) *pinguedineus* Esch.	2	8	–	1	–	1	–	2	3	–	**mt**
P. (*Cryobius*) *ventricosus* Esch.	4	–	–	1	–	–	3	–	–	–	**mt**
Pterostichus (*Cryobius*) sp.	8		8	5	5	4	12	1	1	2	**mt**
P. (*Lenapterus*) *costatus* Men.	3	2	2	1	–	3	4	–	1	–	**mt**
P. (*Petrophilus*) *abnormis* Sahlb.	3	1	2	–	–	–	1	–	–	–	**dt**
P. (*Petrophilus) magus* Mnnh.	–	–	1	–	–	–	1	–	–	–	**fo**
P. (*Petrophilus*) *montanus* (Motsch.)	–	–	–	–	–	–	3	–	–	–	**dt**
P. (*Petrophilus*) *tundrae* Tschitsch.	–	–	–	–	–	–	4	–	1	1	**dt**
P. (*Tundraphilus*) *sublaevis* Sahlb.	3	2	1	1	–	2	1	–	1	–	**dt**
Stereocerus haematopus (Dej.)	–	–	–	–	–	–	–	1	1	–	**dt**
Tribe Zabrini											
Amara glacialis Mnnh.	–	–	–	1	–	–	–	–	–	–	**dt**
Curtonotus alpinus Payk.	27	3	11	11	10	11	19	5	2	5	**dt**
C. bokori Csiki	–	–	–	1	–	1	–	–	–	–	**dt**
Family Dytiscidae											
Subfamily Agabinae											
Agabus moestus (Curt.)	–	2	2	–	–	–	5	1	1	–	**aq**
Agabus sp.	–	–	–	1	–	–	–	–	–	–	**aq**
Subfamily Dytiscinae											
Dytiscus sp.	–	–	1	–	–	–	–	–	–	–	**aq**
Subfamily Hydroporinae											
Hydroporus acutangulus Thoms.?	–	–	–	–	–	–	3	4	–	–	**aq**
H. ex gr. *fuscipennis* Schaum.	–	–	9	–	–	–	–	–	–	–	**aq**
Hydroporus sp.	–	1	–	1	–	3	–	–	–	1	**aq**
Family Hydrophilidae											
Subfamily Helophorinae											
Helophorus sibiricus Motsch.	–	–	–	–	1	–	–	–	–	–	**aq**
H. splendidus Sahlb.	–	–	2	1	4	4	5	1	–	–	**aq**
Family Leiodidae											
Subfamily Cholevinae											
Cholevinus sibiricus (Jean.)	3	2	2	–	2	1	1	2	2	–	**mt**
Family Staphylinidae											
Subfamily Tachyporinae											
Tachinus arcticus Motsch.	5	5	7	29	1	8	14	3	3	3	**mt**
Family Scarabaeidae											
Aphodius sp.	2	5	2	1	–	–	2	–	–	2	**xe**
Family Byrrhidae											
Subfamily Byrrhinae											
Morychus viridis Kuzm. et Korot.	5	13	16	7	1	12	40	9	10	3	**ss**
Subfamily Syncalyptinae											
Curimopsis cyclolepidia Muenst.	1	5	–	–	–	–	–	–	–	–	**dt**

Table 18. (Contd.)

Age	Late Pleistocene										
Section	MKh										
Species/sample MKh-	R18	R13	R5'	1B18	R16	B14	R5	R12	R11	R10	eco
Family Chrysomelidae											
Subfamily Chrysomelinae											
Chrysolina arctica Medv.	–	–	–	–	–	1	–	–	–	–	**ms**
Ch. brunnicornis bermani Medv.	–	–	–	–	–	–	–	1	–	–	**st**
Ch. bungei Jac.	–	–	–	–	–	–	1	1	1	–	**tt**
Ch. purpurata Fald.?	–	–	1	–	–	–	–	1	–	–	**st**
Ch. septentrionalis Men.	1	–	2	1	–	2	6	–	–	–	**mt**
Ch. subsulcata Mnnh.	–	–	–	–	3	–	1	–	–	–	**tt**
Ch. tolli Jac.	–	–	1	–	–	–	–	–	–	–	**tt**
Hydrothassa hannoverana F.	–	2	–	–	–	–	1	–	–	–	**ri**
H. glabra Hbst.	–	–	–	–	–	–	1	–	–	–	**ri**
Phaedon armoraciae L.	–	–	–	–	–	–	–	–	2	–	**me**
Ph. concinnus Steph.	–	1	–	–	–	–	–	1	–	–	**me**
Phratora polaris Schn.	2	–	–	–	–	–	–	–	–	–	**sh**
Subfamily Galerucinae											
Galeruca interrupta circumdata Duft.	–	–	–	–	–	1	–	–	–	–	**st**
Family Brentidae											
Subfamily Apioninae											
Hemitrichapion tschernovi T.-M.	–	–	–	1	–	–	1	–	–	–	**dt**
Mesotrichapion wrangelianum Kor.	–	–	–	4	3	2	3	1	1	2	**dt**
Family Curculionidae											
Subfamily Entiminae											
Tribe Phyllobini											
Phyllobius kolymensis Kor. et Egor.	–	–	–	–	–	–	1	–	–	–	**ms**
Tribe Sitonini											
Sitona borealis Kor.	–	–	2	1	1	–	6	2	1	–	**dt**
Subfamily Hyperinae											
Hypera diversipunctata Schrank.	1	–	–	3	–	–	2	1	–	1	**dt**
H. ornata Cap.	18	3	2	–	3	1	2	–	4	–	**dt**
Subfamily Lixinae											
Tribe Cleonini											
Coniocleous cinerascens Hochh.	–	1	–	–	–	–	–	–	–	–	**ms**
C. ferrugineus Fahr.	3	–	–	–	1	–	4	–	–	–	**ms**
Coniocleonus sp.	2	–	–	–	–	2	–	–	–	–	**ms**
Stephanocleonus eruditus Faust	1	–	1	1	–	–	2	–	–	–	**st**
S. fossulatus F.-W.	–	–	–	–	2	–	–	–	–	1	**st**
Stephanocleonus sp.	–	1	–	–	–	–	1	–	1	–	**st**
Subfamily Molytinae											
Tribe Lepyrini											
Lepyrus nordenskioeldi Faust	4	–	2	–	–	2	9	–	5	–	**sh**
Subfamily Curculioninae											
Tribe Rhamphini											
Isochnus arcticus Kor.	5	3	3	18	2	7	8	16	12	1	**tt**
Order Heteroptera											
Family Saldidae											
Salda littoralis L	–	–	–	–	–	–	–	–	1	–	**ri**
Order Megaloptera											
Family Sialidae											
Sialis sp.	1	–	–	2	–	1	2	–	–	–	**aq**
Order Hymenoptera											
Hymenoptera gen. indet.	1	–	–	1	3	4	1	2	1	–	**oth**
Order Diptera											
Diptera fam. indet. (puparia)	–	–	–	–	–	–	2	–	–	–	**oth**
Crustacea, order Cladocera											
Daphnia sp.	–	–	–	–	–	–	1	–	–	–	**aq**
Sum	106	52	81	98	40	70	183	55	55	22	

Table 19. Insects from the Mamontovyi Khayata section (part 3)

Age	Late Pleistocene										
Species/sample MKh-	1B17	1B16	R9	B17	01B19	01B20	01B12	18as	01B13	01B14	eco
Order Coleoptera											
Subfamily Carabinae											
Carabus truncaticollis Esch.	–	1	–	–	–	–	–	–	–	–	**mt**
Subfamily Trechinae											
Bembidion (*Asioperyphus*) *umiatense* Lth.	3	–	–	–	–	1	–	–	–	–	**ri**
Bembidion (*Peryphus*) sp.	–	–	1	1	–	–	–	–	–	1	**ri**
Bembidion (*Plataphus*) sp.	–	–	1	–	–	–	–	–	–	–	**ri**
Subfamily Harpalinae											
Tribe Harpalini											
Harpalus vittatus vittatus Gebl.	1	–	–	–	–	–	–	–	–	–	**ms**
Harpalus sp.	–	–	1	–	–	–	–	–	–	–	**ms**
Tribe Pterostichini											
Poecilus (*Derus*) *nearcticus* Lth.	2	1	–	–	–	–	–	–	–	–	**dt**
Pterostichus (*Cryobius*) *brevicornis* (Kby.)	3	2	–	3	2	1	1	–	1	–	**mt**
P. (*Cryobius*) *nigripalpis* Popp.	–	–	–	4	1	–	1	–	4	–	**dt**
P. (*Cryobius*) *pinguedineus* Esch.	1	2	1	2	8	–	6	2	3	3	**mt**
P. (*Cryobius*) *ventricosus* Esch.	–	–	1	2	–	–	1	–	–	1	**mt**
Pterostichus (*Cryobius*) sp.	19	14	3	1	2	8	3	4	2	9	**mt**
P. (*Lenapterus*) *agonus* Horn.	–	–	–	2	–	–	–	–	–	–	**mt**
P. (*Lenapterus*) *costatus* Men.	2	1	–	5	–	1	–	–	–	–	**mt**
P. (*Petrophilus*) *abnormis* Sahlb.	2	–	–	1	–	–	–	–	–	1	**dt**
P. (*Petrophilus*) *eximius* Mor.	–	–	–	3	–	–	–	–	–	–	**dt**
P. (*Petrophilus*) *magus* Mnnh.	–	–	–	1	–	–	–	–	–	–	**fo**
P. (*Petrophilus*) *tundrae* Tschitsch.	1	3	–	–	–	–	2	–	–	–	**dt**
P. (*Tundraphilus*) *sublaevis* Sahlb.	2	–	–	2	3	–	–	–	2	1	**dt**
Stereocerus haematopus Dej.	1	–	–	–	2	–	–	–	1	–	**dt**
Tribe Zabrini											
Amara interstitialis Dej.	–	–	–	–	–	–	–	–	–	1	**dt**
Curtonotus alpinus Payk.	20	8	10	9	12	6	9	3	9	6	**dt**
Family Dytiscidae											
Subfamily Agabinae											
Agabus moestus (Curt.)	3	–	–	–	1	1	1	–	2	–	**aq**
Agabus sp.	–	1	–	–	–	4	–	–	–	1	**aq**
Subfamily Hydroporinae											
Hydroporus acutangulus Thoms.?	4	3	–	–	–	2	–	–	2	–	**aq**
Hydroporus sp.	–	–	–	1	1	–	1	2	–	–	**aq**
Family Hydrophilidae											
Subfamily Helophorinae											
Helophorus splendidus Sahlb.	6	6	1	–	1	–	–	–	–	–	**aq**
Family Leiodidae											
Subfamily Cholevinae											
Cholevinus sibiricus (Jean.)	4	2	–	5	5	3	6	2	6	8	**mt**
Family Silphidae											
Thanatophilus lapponicus Hbst.?	–	1	–	–	–	–	–	–	–	–	**oth**
Family Staphylinidae											
Subfamily Tachyporinae											
Tachinus arcticus Motsch.	11	35	5	17	9	1	15	5	16	4	**mt**
Family Scarabaeidae											
Aphodius sp.	3	1	–	–	–	1	–	–	–	–	**xe**
Family Byrrhidae											
Subfamily Byrrhinae											
Morychus viridis Kuzm. et Korot.	29	3	1	2	2	1	1	1	–	2	**ss**

Table 19. (Contd.)

Age	Late Pleistocene										
Species/sample MKh-	1B17	1B16	R9	B17	01B19	01B20	01B12	18as	01B13	01B14	eco
Subfamily Syncalyptinae											
Curimopsis cyclolepidia Muenst.	–	–	1	–	–	–	–	–	–	–	**dt**
Family Chrysomelidae											
Subfamily Chrysomelinae											
Chrysolina arctica Medv.	–	–	–	–	1	1	–	1	–	–	**ms**
Ch. brunnicornis bermani Medv.	–	–	–	2	2	–	–	–	–	–	**st**
Ch. bungei Jac.	–	–	–	–	–	–	1	–	2	–	**st**
Ch. septentrionalis Men.	4	6	–	1	1	1	–	3	–	3	**mt**
Ch. subsulcata Mnnh.	2	6	–	–	1	1	2	–	2	–	**tt**
Ch. tolli Jac.	–	3	–	–	1	–	3	–	2	–	**tt**
Chrysolina sp.	–	–	–	–	–	–	1	–	–	–	**mt?**
Hydrothassa hannoverana F.	–	3	1	2	1	–	1	–	1	–	**ri**
Phaedon armoraciae L.	–	–	–	1	–	–	1	–	–	–	**me**
Ph. concinnus Steph.	2	–	–	–	–	–	–	–	–	–	**me**
Phaedon sp.	–	–	–	–	1	–	–	–	–	–	**me**
Family Brentidae											
Subfamily Apioninae											
Hemitrichapion tschernovi T.-M.	–	21	7	5	–	–	3	2	1	–	**dt**
Mesotrichapion wrangelianum Kor.	1	–	2	–	7	–	–	–	–	1	**dt**
Pseudoprotapion astragali Payk.?	–	–	–	–	–	–	–	–	–	–	**ms**
Family Curculionidae											
Subfamily Ceutorhynchinae											
Ceutorhynchus sp.	–	1	–	–	–	–	–	–	–	–	**dt**
Pelenomus sp.	–	1	–	–	–	–	–	–	–	–	**ri**
Subfamily Entiminae											
Tribe Sitonini											
Sitona borealis Kor.	2	5	1	1	4	2	2	–	1	–	**dt**
S. lineellus Bonsd.	–	–	–	–	–	–	1	–	–	–	**me**
Subfamily Hyperinae											
Hypera diversipunctata Schrank.	6	2	–	1	–	12	–	–	3	2	**dt**
H. ornata Cap.	3	3	2	1	–	1	–	–	–	–	**dt**
Subfamily Lixinae											
Tribe Cleonini											
Coniocleonus sp.	–	2	–	1	1	–	1	–	–	–	**ms**
Stephanocleonus eruditus Faust	2	–	–	1	–	–	1	–	–	–	**st**
S. fossulatus F.-W.	1	–	–	–	–	–	1	–	–	1	**st**
Stephanocleonus sp.	–	2	–	–	–	–	–	–	–	–	**st**
Subfamily Molytinae											
Tribe Lepyrini											
Lepyrus nordenskioeldi Faust	–	3	2	2	3	1	6	1	3	–	**sh**
Lepyrus sp.	3	–	–	–	–	–	–	–	–	–	**sh**
Subfamily Curculioninae											
Tribe Rhamphini											
Isochnus arcticus Kor.	11	166	3	6	20	–	5	5	34	2	**tt**
I. flagellum Erics.	–	–	–	1	–	–	–	–	–	–	**sh**
Order Heteroptera											
Family Corixidae											
Sigara sp.	–	–	–	1	–	–	–	–	–	–	**aq**
Family Saldidae											
Salda littoralis L.	–	–	–	–	–	1	–	–	–	–	**ri**

Table 19. (Contd.)

Age	Late Pleistocene										
Species/sample MKh-	1B17	1B16	R9	B17	01B19	01B20	01B12	18as	01B13	01B14	eco
Order Hymenoptera											
Family Formicidae											
Leptothorax acervorum F.	–	1	–	1	–	–	–	–	–	–	**fo**
Hymenoptera gen. indet.	–	14	2	6	12	–	23	1	8	4	**oth**
Order Megaloptera											
Family Sialidae											
Sialis sp.	4	22	1	4	–	6	5	1	–	1	**aq**
Order Trichoptera											
Trichoptera gen. indet. (larvae)	6	2	–	2	–	2	8	1	2	2	**aq**
Order Diptera											
Family Chironomidae											
Chironomidae gen. indet.	–	3	–	–	1	–	2	3	–	–	**aq**
Family Tipulidae											
Tipulidae gen. indet.	2	3	–	–	1	–	–	–	1	–	**oth**
Diptera fam. indet. (puparia)	–	4	–	–	1	3	4	–	5	11	**oth**
Crustacea, order Cladocera											
Daphnia sp.	–	53	–	–	2	–	–	–	1	1	**aq**
Sum	154	309	44	88	92	50	76	31	97	47	

The beetle feeds on dung of large mammals; it was probably an important member of steppe–tundra ecosystem.

The assemblage contains steppe and meadow–steppe species: *Stephanocleonus eruditus, Chrysolina arctica* (6% in sum), and *Morychus viridis* (6%). The fauna is tentatively correlated with **TU/S-T**, which is close to the **TU/XE** type.

Two samples (B28 and R8) were taken from the same 12.5-m-high elevation, but a different part of the section. Assemblage B28 is close to the previous one (B8). It is dominated by tundra species; the proportions of the **st**, **ms**, and **ss** groups are low, but the role of *Aphodius* sp. is relatively high, 7%. This fauna contains some thermophilous species, such as *Pterostichus abnormis, P. montanus,* and *P. magus,* which are probably indicative of environments close to forest–tundra.

Assemblage R8 significantly differs in ecological structure from B28, the sample was probably taken stratigraphically higher. Assemblage R8 is dominated by xerophilous species, including steppe–tundra indicators. Steppe and meadow–steppe insects are more frequent: **st** (4%) comprises *Chrysolina purpurata?, Stephanocleonus paradoxus,* and *S. eruditus*; **ms** (9%) is represented by *Harpalus vittatus kiselevi, H. vittatus vittatus, Chrysolina arctica,* and *Coniocleonus ferrugineus;* the group **ss** (*Morychus viridis*) is 28%, *Aphodius* sp., 8%. The assemblage belongs to the **S-T/S-T** type. This is the first occurrence of a true steppe–tundra assemblage in the Bykovsii fossil record.

Sample B7 from 13.8 m shows a less evident influence of xerophilous species. The frequency of the steppe group is low, only 1% (*Stephanocleonus* sp.); **ms** = 6% (*Harpalus vittatus kiselevi, Phyllobius kolymensis, Coniocleonus* sp.); and **ss** = 19%. The proportions of the tundra groups **dt** and **mt** are almost equal, about 25% each. This assemblage belongs to a less prominent xerophilous type **TU/S-T**.

All assemblages from the lower part of the section, which is correlated with the 45–42 ka time interval, is indicative of mild steppe–tundra environment. The role of steppe species varies, but always remains relatively high for this northern site. Assemblages contain thermophilous species and the proportion of the arctic group is low, less than 4%. Thus, a relatively dry and warm climate is reconstructed.

Sample B16 comes from elevation of 14.7 m. The assemblage contains mostly tundra species: **dt** = 37%, **mt** = 34%, and **tt** = 12%. Arctic insects are more diverse here, including not only the common weevil *Isochnus arcticus*, but also the high arctic leaf beetles *Chrysolina subsulcata* and *Ch. tolli*. The steppe tundra indicators are represented by rare *Chrysolina brunnicornis bermani* and *Morychus viridis*. This fauna is indicative of quite severe tundra environment, with restricted steppe–tundra areas of the **TU/S-T** type.

Two samples (B15 and R14) were taken from different parts of the section at elevation of 15- m. Assemblages are close to each other and similar to the previous one. The fauna is dominated by tundra species; the arctic group (*Isochnus arcticus, Chrysolina subsulcata*) composes 15%; the proportion of the steppe groups is low: **st** = 3%, **ms** = 2%, and **ss** = 8%.

Table 20. Insects from the Mamontovyi Khayata section (part 4)

Age	Late Pleistocene										
Species/sample MKh-	01B15	01B11	B3	16c	14as	B18	01B10	99-12c	22as	01B9	eco
Order Coleoptera											
Subfamily Carabinae											
Carabus truncaticollis Esch.	1	–	–	–	–	–	–	–	–	–	**mt**
Subfamily Harpalinae											
Tribe Pterostichini											
Poecilus (*Derus*) *nearcticus* Lth.	1	–	–	–	–	–	–	–	–	–	**dt**
Pterostichus (*Cryobius*) *brevicornis* (Kby.)	–	2	–	–	–	–	–	–	–	–	**mt**
P. (*Cryobius*) *nigripalpis* Popp.	–	–	1	–	–	–	–	–	–	2	**dt**
P. (*Cryobius*) *pinguedineus* Esch.	6	6	–	–	–	–	5	–	–	1	**mt**
P. (*Cryobius*) *ventricosus* Esch.	–	1	–	–	–	–	1	–	–	–	**mt**
Pterostichus (*Cryobius*) sp.	3	–	2	2	3	5	1	–	1	7	**mt**
P. (*Lenapterus*) *costatus* Men.	3	3	–	–	–	2	1	–	–	–	**mt**
P. (*Petrophilus*) *eximius* Mor.	–	–	–	–	–	1	–	–	–	–	**dt**
P. (*Petrophilus*) *tundrae* Tschitsch.	3	–	–	–	–	–	–	–	–	–	**dt**
P. (*Tundraphilus*) *sublaevis* Sahlb.	–	2	–	–	–	–	1	–	–	4	**dt**
Pterostichus sp.	–	–	1	–	–	1	–	–	–	–	**dt?**
Tribe Zabrini											
Curtonotus alpinus Payk.	7	6	3	3	1	6	2	3	4	5	**dt**
C. bokori Csiki	1	1	–	–	–	–	–	–	1	–	**dt**
Family Dytiscidae											
Subfamily Agabinae											
Agabus moestus (Curt.)	–	–	–	–	–	–	–	–	1	–	**aq**
Agabus sp.	1	1	–	–	1	–	1	–	–	1	**aq**
Subfamily Hydroporinae											
Hydroporus acutangulus Thoms.?	1	–	–	–	–	1	–	–	2	–	**aq**
H. lapponicus (Gyll.)	1	–	–	–	–	–	–	–	–	–	**aq**
Hydroporus sp.	–	1	–	–	–	–	–	–	–	–	**aq**
Family Leiodidae											
Subfamily Cholevinae											
Cholevinus sibiricus (Jean.)	16	6	3	–	–	6	7	–	2	20	**mt**
Family Staphylinidae											
Subfamily Tachyporinae											
Tachinus arcticus Motsch.	12	10	4	5	–	12	12	2	10	20	**mt**
Staphilinidae gen. indet.	–	–	–	–	–	–	–	–	2	–	**pl**
Family Scarabaeidae											
Aphodius sp.	–	–	–	–	–	–	–	–	–	1	**xe**
Family Byrrhidae											
Subfamily Byrrhinae											
Morychus viridis Kuzm. et Korot.	–	1	1	–	1	1	–	1	1	–	**ss**
Family Chrysomelidae											
Subfamily Chrysomelinae											
Chrysolina arctica Medv.	2	–	–	–	–	–	–	–	–	2	**ms**
Ch. bungei Jac.	3	–	–	–	–	–	–	–	–	–	**st**
Ch. septentrionalis Men.	1	3	1	–	–	2	1	–	–	–	**mt**
Ch. subsulcata Mnnh.	2	–	2	–	–	–	2	–	–	4	**tt**
Ch. tolli Jac.	–	2	–	4	–	–	1	–	–	–	**tt**
Chrysolina sp.	–	–	–	–	–	–	–	–	1	1	**mt?**
Hydrothassa hannoverana F.	1	2	1	1	–	–	–	–	–	–	**ri**
Phaedon armoraciae L.	–	–	–	–	–	–	–	–	–	1	**me**
Phaedon sp.	–	–	–	–	–	–	1	–	–	–	**me**

Table 20. (Contd.)

Age	Late Pleistocene										
Species/sample MKh-	01B15	01B11	B3	16c	14as	B18	01B10	99-12c	22as	01B9	eco
Family Brentidae											
Subfamily Apioninae											
Hemitrichapion tschernovi T.-M.	–	–	–	–	–	–	–	–	1	1	**dt**
Family Curculionidae											
Subfamily Ceutorhynchinae											
Ceutorhynchus sp.	1	–	–	–	–	–	–	–	–	–	**dt**
Subfamily Entiminae											
Tribe Sitonini											
Sitona borealis Kor.	1	2	1	–	–	–	–	1	1	–	**dt**
Subfamily Hyperinae											
Hypera diversipunctata Schrank.	–	–	–	–	–	–	–	–	–	1	**dt**
Subfamily Lixinae											
Tribe Cleonini											
Coniocleonus sp.	–	1	–	–	–	–	–	–	1	–	**ms**
Cleonini gen. indet.	–	–	–	–	–	–	1	–	–	–	**ms**
Subfamily Molytinae											
Tribe Lepyrini											
Lepyrus nordenskioeldi Faust	2	3	–	1	–	1	1	–	1	2	**sh**
Lepyrus sp.	–	–	–	–	1	–	–	–	–	–	**sh**
Subfamily Curculioninae											
Tribe Rhamphini											
Isochnus arcticus Kor.	36	41	22	9	2	15	30	5	59	25	**tt**
I. flagellum Erics.	–	–	–	–	–	–	2	–	–	–	**sh**
Order Heteroptera											
Family Saldidae											
Salda littoralis L.	1	1	–	–	–	–	–	–	–	–	**ri**
Order Hymenoptera											
Hymenoptera gen. indet.	5	2	1	–	2	–	–	1	1	8	**oth**
Order Megaloptera											
Family Sialidae											
Sialis sp.	–	5	–	–	–	–	–	–	–	–	**aq**
Order Trichoptera											
Trichoptera gen. indet. (larvae)	1	–	4	–	2	5	–	–	1	3	**aq**
Order Diptera											
Family Chironomidae											
Chironomidae gen. indet.	–	–	1	1	6	–	–	4	–	–	**aq**
Family Tipulidae											
Tipulidae gen. indet.	1	–	1	–	–	–	–	–	–	–	**oth**
Diptera fam. indet. (puparia)	2	3	–	–	–	–	–	–	–	3	**oth**
Crustacea, order Cladocera											
Daphnia sp.	1	2	–	–	–	–	–	–	–	–	**aq**
Sum	106	95	42	25	9	53	70	12	88	98	

Two samples from elevation of 15.5–15.7 m (R2 and R15) are small, but we can recognize certain difference. The group **mt** is more frequent, up to 40%. The arctic and steppe groups remain the same contribution.

Sample R18 from elevation of 16.3 m is rather large. The xerophilous tundra group prevails again (51%), including abundant *Hypera ornata,* which is more common for steppe–tundra communities. Steppe, meadow–steppe, and *Morychus viridis* taken together compose only 10% of the assemblage.

The species listed were taken at elevation from 14.7 to 16.3 m (time interval from 39 to 36 ka). All of them have share certain features. Tundra species dominate

Table 21. Insects from the Mamontovyi Khayata section (part 5)

Age	Late Pleistocene										
Species/sample MKh-	01B8	01B7a	01B7	01B6	00B1	6s	01B4	5s	01B5	01B22	eco
Order Coleoptera											
Subfamily Carabinae											
Carabus odoratus Motsch.?	–	–	–	–	1	–	–	–	–	–	**dt**
Subfamily Elaphrinae											
Blethisa catenaria Brown	–	–	1	–	–	–	–	–	–	–	**ri**
Diacheila polita Fald.	–	–	1	–	–	–	–	–	–	–	**mt**
Elaphrus riparius L.	–	–	1	–	–	–	–	–	–	–	**ri**
Subfamily Trechinae											
Bembidion (*Asioperyphus*) *umiatense* Lth.	–	–	3	–	3	2	3	–	1	–	**ri**
Subfamily Harpalinae											
Tribe Harpalini											
Dicheirotrichus mannerheimi Sahlb.	–	–	1	–	–	–	–	–	–	–	**dt**
Harpalus vittatus alaskensis Lth.	–	–	–	–	–	–	–	2	–	2	**ms**
H. vittatus vittatus Gebl.	–	–	–	–	2	–	–	–	–	–	**ms**
Harpalus sp.											
Tribe Platynini											
Agonum quinquepunctatum Motsch.	–	–	1	–	–	–	–	–	–	–	**ri**
A. fuliginosum Panz.	–	–	1	–	–	–	–	–	–	–	**ri**
Tribe Pterostichini											
Poecilus (*Derus*) *nearcticus* Lth.	–	–	1	–	4	–	1	–	1	3	**dt**
Pterostichus (*Cryobius*) *brevicornis* (Kby.)	1	–	51	1	2	–	10	1	1	3	**mt**
P. (*Cryobius*) *nigripalpis* Popp.	–	–	–	–	–	–	–	–	–	2	**dt**
P. (*Cryobius*) *pinguedineus* Esch.	–	–	3	1	2	5	–	–	–	1	**mt**
P. (*Cryobius*) *ventricosus* Esch.	–	–	4	–	–	–	–	–	1	–	**mt**
Pterostichus (*Cryobius*) sp.	3	2	4	4	24	1	3	3	8	2	**mt**
P. (*Lenapterus*) *agonus* Horn.	–	–	–	–	–	–	–	1	–	–	**mt**
P. (*Lenapterus*) *costatus* Men.	1	–	–	–	1	–	1	–	1	1	**mt**
P. (*Lenapterus*) *vermiculosus* Men.	–	–	3	–	–	–	–	–	–	–	**mt**
P. (*Petrophilus*) *abnormis* Sahlb.	–	–	1	–	3		1	–	–	2	**dt**
P. (*Petrophilus*) *montanus* (Motsch.)	–	–	1	–	–	–	–	–	–	–	**fo**
P. (*Tundraphilus*) *sublaevis* Sahlb.	1	1	1	2	3	–	1	2	3	1	**dt**
Stereocerus haematopus (Dej.)	–	–	2	–	–	–	–	–	–	–	**dt**
Tribe Zabrini											
Curtonotus alpinus Payk.	7	2	12	10	24	5	7	11	8	17	**dt**
Family Dytiscidae											
Subfamily Agabinae											
Agabus moestus (Curt.)	–	–	7	–	–	1	–	–	–	–	**aq**
A. thomsoni (J. Sach.)	–	–	7	–	–	–	–	–	–	–	**aq**
SubfamilyColymbetinae											
Colymbetes dolabratus (Payk.)	–	–	–	–	1	–	–	–	–	–	**aq**
Subfamily Hydroporinae											
Hydroporus acutangulus Thoms.?	–	–	10	–	1	1	–	–	–	–	**aq**
H. lapponicus (Gyll.)	1	–	–	–	–	–	–	–	–	–	**aq**
Hydroporus sp.	–	–	–	–	–	–	–	–	1	–	**aq**
Family Hydrophilidae											
Subfamily Helophorinae											
Helophorus splendidus Sahlb.	–	–	2	–	2	–	2	–	–	–	**aq**
H. sibiricus Motsch.	–	–	1	–	–	–	–	–	–	–	
Subfamily Hydrophilinae											
Hydrobius fuscipes F.	–	–	1	–	–	–	–	–	–	–	**aq**
Subfamily Sphaeridiinae											
Cercyon sp.	–	–	1	–	–	–	–	–	–	–	**ri**

Table 21. (Contd.)

Age	Late Pleistocene										eco
Species/sample MKh-	01B8	01B7a	01B7	01B6	00B1	6s	01B4	5s	01B5	01B22	
Family Leiodidae											
Subfamily Cholevinae											
Cholevinus sibiricus (Jean.)	5	1	1	6	6	7	22	–	11	2	**mt**
Family Staphylinidae											
Subfamily Tachyporinae											
Subfamily Omaliinae											
Olophrum consimile Gyll.	–	–	14	–	–	–	–	–	–	–	**mt**
Tachinus arcticus Motsch.	3	2	6	8	7	6	6	3	4	5	**mt**
T. brevipennis Sahlb.	1	–	–	–	–	–	–	–	–	–	**mt**
Tachyporus sp.	–	–	–	–	–	–	–	1	–	–	**pl**
Family Scarabaeidae											
Aphodius sp.	–	–	–	–	11	1	2	1	3	5	**xe**
Family Byrrhidae											
Subfamily Byrrhinae											
Morychus viridis Kuzm. et Korot.	–	–	3	–	102	11	19	54	15	98	**ss**
Family Melyridae											
Troglocollops arcticus L. Medv.	–	–	–	–	1	–	–	–	–	1	**ms**
Family Chrysomelidae											
Subfamily Chrysomelinae											
Chrysolina arctica Medv.	4	–	–	2	0	–	–	2	–	1	**ms**
Ch. brunnicornis bermani Medv.	–	–	–	1	2	–	–	7	–	2	**st**
Ch. septentrionalis Men.	–	–	1	3	0	2	6	4	2	3	**mt**
Ch. subsulcata Mnnh.	2	1	1	4	0	–	–	4	–	2	**tt**
Ch. tolli Jac.	–	1	–	–	–	–	–	–	–	–	**tt**
Chrysolina sp.	–	–	–	–	–	–	–	2	–	–	**mt?**
Chrysomela blaisdelli Van Dyke	–	–	1	–	–	–	–	–	–	–	**sh**
Hydrothassa hannoverana F.	–	–	–	–	–	–	–	–	2	–	**ri**
Phaedon armoraciae L.	–	–	–	–	–	1	–	–	–	–	**me**
Ph. concinnus Steph.	–	–	–	–	2	–	2	–	–	–	**me**
Phratora polaris Schn.	–	–	3	–	–	–	–	–	–	–	**sh**
Family Brentidae											
Subfamily Apioninae											
Hemitrichapion tschernovi T.-M.	–	–	–	–	44	1	–	10	–	2	**dt**
Mesotrichapion wrangelianum Kor.	–	–	1	–	22	–	–	2	5	7	**dt**
Pseudoprotapion astragali Payk.?	–	–	–	–	3	4	–	–	–	–	**ms**
Family Brachyceridae											
Subfamily Erirhininae											
Notaris ochoticus Kor.	–	–	2	–	–	–	–	–	–	–	**ri**
Family Curculionidae											
Subfamily Ceutorhynchinae											
Ceutorhynchus sp.	–	–	1	–	–	–	–	–	–	–	**dt**
Subfamily Entiminae											
Tribe Sitonini											
Sitona borealis Kor.	1	2	1	–	8	–	–	5	1	3	**dt**
Subfamily Hyperinae											
Hypera diversipunctata Schrank.	1	–	–	–	2	–	–	–	1	2	**dt**
H. ornata Cap.	–	–	1	–	–	–	–	–	–	–	**dt**
Subfamily Lixinae											
Tribe Cleonini											
Coniocleonus cinerascens Hochh.	–	–	–	–	2	–	2	–	1	–	**ms**
C. ferrugineus Fahr.	–	–	–	–	1	–	–	3	–	–	**ms**
Coniocleonus sp.	–	1	1	–	–	2	–	–	–	–	**ms**

Table 21. (Contd.)

Age	Late Pleistocene										eco
Species/sample MKh-	01B8	01B7a	01B7	01B6	00B1	6s	01B4	5s	01B5	01B22	
Stephanocleonus eruditus Faust	–	–	–	–	6	–	3	6	–	3	**st**
S. fossulatus F.-W.	–	–	–	–	2	–	–	–	1	–	**st**
Stephanocleonus sp.	–	–	–	–	–	–	1	–	–	–	**st**
Subfamily Molytinae											
Tribe Lepyrini											
Lepyrus nordenskioeldi Faust	6	3	5	4	–	1	1	2	1	2	**sh**
Tribe Pissodini											
Pissodes sp.	–	–	–	–	–	–	–	1	–	–	**fo**
Subfamily Curculioninae											
Tribe Elliscini											
Dorytomus imbecillus Faust	–	–	2	–	–	–	–	–	–	–	**sh**
Tribe Rhamphini											
Isochnus arcticus Kor.	43	23	39	62	15	4	27	2	15	–	**tt**
I. flagellum Erics.	2	–	–	2	–	–	–	–	–	–	**sh**
Order Heteroptera											
Family Corixidae											
Sigara sp.	1	–	–	–	–	–	–	–	–	–	**aq**
Family Saldidae											
Salda littoralis L	–	–	–	–	1	1	1	–	1	–	**ri**
Order Hymenoptera											
Family Formicidae											
Hymenoptera gen. indet.	13	6	7	4	2	2	4	1	5	1	**oth**
Order Megaloptera											
Family Sialidae											
Sialis sp.	–	1	2	1	1	2	5	1	2	–	**aq**
Order Trichoptera											
Trichoptera gen. indet. (larvae)	2	–	3	2	2	1	3	3	2	–	**aq**
Order Diptera											
Family Chironomidae											
Chironomidae gen. indet.	2	–	–	1	–	–	–	2	–	–	**aq**
Family Tipulidae											
Tipulidae gen. indet.	1	–	–	–	–	–	–	–	–	–	**oth**
Diptera fam. indet. (puparia)	3	1	1	1	–	2	–	1	–	1	**oth**
Sum	83	39	204	110	310	56	121	129	88	172	

the assemblages, the arctic group plays an important role, steppe insects are present, but infrequent, and thermophilous species are almost absent. Thus, a cold and dry climate is reconstructed. Steppe–tundra vegetation occupied only the most appropriate areas, such as south faced slopes. We can notice gradually increasing aridity and temperature.

Sample R13 from elevation of 16.4 m is richer in steppe insects; it includes individual steppe weevil *Stephanocleonus* sp. and meadow–steppe *Coniocleonus cinerascens* and abundant (20%) *Morychus viridis*. The assemblage contains the arctic group (6%). Some members of the community are cold resistant (*Pterostichus costatus, Tachinus arcticus, Isochnus arcticus*), while others are more or less thermophilous (*Pterostichus abnormis, Hydrothassa hannoverana, Phaedon concinnus*).

The next assemblage (R5', elevation of 17.2 m) is similar in ecological structure. It also includes a number of thermophilous species, such as *Pterostichus magus* and *Dytiscus* sp. Several small samples from elevation of 17.3–17.5 m are close to the previous two. The proportion of the steppe group is slightly greater, the last assemblage (R5) includes 22% of the **ss** group.

These samples from the 16.4–17.5 m interval (35–36 ka) includes almost one-third of steppe insects, about 5% of arctic species, and a number of thermophilous insects, which are probably indicative of mild environment close to shrub tundra or forest–tundra. A significant part of landscapes was occupied by low grass–sedge steppes.

Table 22. Insects from the Mamontovyi Khayata section (part 6)

Age	Late Pleistocene			Holocene					
Species/sample MKh-	01B21	01B3	01B23	B4	01B2	01B1	3ac	00B2	
Order Coleoptera									
Family Carabidae									
Subfamily Nebriinae									
Nebria frigida Sahlb.	–	–	–	–	1	–	–	–	**ri**
Nebria sp.	–	–	–	–	1	–	–	–	**ri**
Pelophila borealis Payk.	–	–	1	–	–	–	–	–	**ri**
Subfamily Carabinae									
Carabus truncaticollis Esch.	–	–	–	–	1	1	–	2	**mt**
Subfamily Elaphrinae									
Blethisa catenaria Brown.	–	–	–	–	2	–	–	–	**mt**
Diacheila polita Fald.	–	–	–	–	1	–	–	–	**mt**
Elaphrus lapponicus Gyll.	–	–	1	–	–	–	–	–	**ri**
Elaphrus sp.	–	–	–	1	1	–	–	–	**ri**
Subfamily Trechinae									
Bembidion (*Asioperyphus*) *umiatense* Lth.	–	–	2	1	5	–	–	2	**ri**
B. (*Peryphanes*) *dauricum* Motsch.	–	1	–	–	2	–	–	1	**dt**
Bembidion (*Peryphus*) sp.	1	–	–	–	–	–	–	–	**ri**
Subfamily Scaritinae									
Dyschiriodes melancholicus Putz.	–	–	–	–	–	–	–	1	**ri**
Subfamily Harpalinae									
Tribe Harpalini									
Dicheirotrichus mannerheimi Sahlb.	–	–	–	–	1	1	–	4	**dt**
Harpalus vittatus kiselevi Kat. et Shil.	1	1	1	–	–	–	–	–	**ms**
Harpalus sp.	–	–	1	1	–	–	–	–	**ms**
Tribe Platynini									
Agonum quinqueounctatum Motsch.	–	–	–	–	–	1	2	–	**ri**
A. fuliginosum Panz.	–	–	–	–	–	1	–	–	**ri**
Agonum sp.	–	–	–	–	2	–	–	–	**ri**
Tribe Pterostichini									
Poecilus (*Derus*) *nearcticus* Lth.	2	–	4	–	–	2	–	–	**dt**
Pterostichus (*Cryobius*) *brevicornis* (Kby.)	3	1	6	6	179	63	–	64	**mt**
P. (*Cryobius*) *pinguedineus* Esch.	–	1	3	4	–	2	–	–	**mt**
P. (*Cryobius*) *ventricosus* Esch.	3	–	–	2	–	1	–	–	**mt**
Pterostichus (*Cryobius*) sp.	7	15	8	19	8	13	2	4	**mt**
P. (*Lenapterus*) *agonus* Horn.	–	–	–	–	–	2	–	1	**mt**
P. (*Lenapterus*) *costatus* Men.	–	1	–	6	6	3	1	2	**mt**
P. (*Lenapterus*) *vermiculosus* Men.	–	–	–	1	7	2	–	2	**mt**
P. (*Petrophilus*) *abnormis* Sahlb.	–	2	–	–	3	–	–	–	**dt**
P. (*Petrophilus*) *magus* Mnnh.	–	–	–	1	–	–	–	–	**fo**
P. (*Petrophilus*) *montanus* (Motsch.)	–	–	–	1	6	–	–	–	**dt**
P. (*Petrophilus*) *tundrae* Tschitsch.	–	–	–	–	–	1	–	–	**dt**
P. (*Tundraphilus*) *sublaevis* Sahlb.	1	1	1	7	3	–	–	4	**dt**
Stereocerus haematopus (Dej.)	–	–	–	1	4	3	–	4	**dt**
Tribe Zabrini									
Amara interstitialis Dej.	–	–	–	–	–	2	–	–	**dt**
Curtonotus alpinus Payk.	9	6	12	18	24	6	1	12	**dt**
Family Dytiscidae									
Subfamily Agabinae									
Agabus moestus (Curt.)	1	–	–	2	13	15	–	5	**aq**
A. thomsoni (J. Sach.)?	–	–	–	–	14	–	2	–	**aq**
Agabus sp.	1	1	1	–	–	1	–	–	**aq**
Subfamily Hydroporinae									
Hydroporus acutangulus Thoms.?	–	2	1	3	17	–	13	28	**aq**
H. lapponicus (Gyll.)	–	–	–	–	2	–	–	–	**aq**
H. ex gr. *fuscipennis* Schaum.	–	–	–	–	–	–	4	–	**aq**
Hydroporus sp.	–	–	–	–	–	6	–	–	**aq**

Table 22. (Contd.)

Age	Late Pleistocene			Holocene					
Species/sample MKh-	01B21	01B3	01B23	B4	01B2	01B1	3ac	00B2	
Family Hydrophilidae									
Subfamily Helophorinae									
Helophorus splendidus Sahlb.	–	–	1	–	7	1	3	5	**aq**
Subfamily Hydrophilinae									
Hydrobius fuscipes F.	–	–	–	–	5	2	–	3	**aq**
Laccobius sp.	–	–	–	–	1	–	–	–	**aq**
Subfamily Sphaeridiinae									
Cercyon sp.	1	–	1	–	1	–	–	–	**ri**
Hydrophilidae gen. indet.	–	–	–	–	–	–	–	1	**aq**
Family Leiodidae									
Subfamily Leiodinae									
Cyrtoplastus irregularis Rtt.?	–	–	–	1	–	1	1	2	**pl**
Subfamily Cholevinae									
Cholevinus sibiricus (Jean.)	2	2	3	2	–	2	–	–	**mt**
Family Silphidae									
Subfamily Silphinae									
Aclypea opaca (L.)	–	–	–	–	1	–	–	2	**oth**
Phosphuga atrata L.	–	–	–	–	–	1	–	–	**fo**
Family Staphylinidae									
Subfamily Omaliinae									
Olophrum consimile Gyll.	2	–	–	2	31	6	–	–	**mt**
Subfamily Tachyporinae									
Tachinus arcticus Motsch.	1	2	7	3	2	–	–	–	**mt**
Tachyporus sp.	–	–	–	–	–	–	–	–	**pl**
Subfamily Steninae									
Stenus sensu stricto sp.	–	–	–	–	–	–	1	–	**ri**
Subfamily Paederinae									
Lathrobium sp.	–	–	–	–	–	–	1	–	**pl**
Subfamily Staphylininae									
Philonthus sp.	–	–	–	–	1	–	2	–	**pl**
Staphilinidae gen. indet.	–	–	–	–	–	–	1	–	**pl**
Family Scarabaeidae									
Aphodius sp.	5	8	14	–	1	–	–	–	**xe**
Family Byrrhidae									
Subfamily Byrrhinae									
Byrrhus sp.	–	–	–	–	–	1	–	–	**me**
Morychus viridis Kuzm. et Korot.	104	116	90	13	5	4	–	2	**ss**
Simplocaria arctica Popp.	–	–	–	–	4	–	–	2	**dt**
Subfamily Syncalyptinae									
Curimopsis cyclolepidia Muenst.	–	–	–	–	1	–	–	2	**dt**
Family Cucujidae									
Pediacus fuscus Er.	–	–	–	–	1	–	–	–	**fo**
Family Lathridiidae									
Corticaria sp.	–	–	–	–	1	–	–	–	**pl**
Family Chrysomelidae									
Subfamily Chrysomelinae									
Chrysolina arctica Medv.	1	1	–	1	–	–	–	–	**ms**
Ch. brunnicornis bermani Medv.	–	9	–	–	–	–	–	–	**st**
Ch. septentrionalis Men.	5	–	–	1	–	–	–	–	**mt**
Ch. subsulcata Mnnh.	1	2	–	–	1	1	–	–	**tt**
Ch. tolli Jac.	3	–	–	–	–	2	–	–	**tt**
Chrysomela blaisdelli Van Dyke	–	–	–	1	5	–	–	–	**sh**
Gonioctena affinis Gyll.	–	–	–	–	–	–	–	1	**sh**
Prasocuris phellandrii L.	–	–	–	–	–	–	–	1	**ri**
Phaedon armoraciae L.	–	–	–	2	–	2	–	–	**me**
Ph. concinnus Steph.	–	–	1	–	–	–	1	–	**me**
Phratora polaris Schn.	–	–	–	–	7	2	2	–	**sh**
Ph. vulgatissima L.	–	–	–	–	–	–	–	3	**sh**

Table 22. (Contd.)

Age	Late Pleistocene			Holocene					
Species/sample MKh-	01B21	01B3	01B23	B4	01B2	01B1	3ac	00B2	
Subfamily Galerucinae									
Galerucella grisescens Joann.	–	–	–	–	–	–	2	–	**ri**
Family Brentidae									
Subfamily Apioninae									
Hemitrichapion tschernovi T.-M.	7	28	55	11	1	–	–	2	**dt**
Mesotrichapion wrangelianum Kor.	5	12	8	6	–	–	–	2	**dt**
Pseudoprotapion astragali Payk.	–	–	3	–	3	–	–	–	**ms**
Family Brachyceridae									
Subfamily Erirhininae									
Notaris bimaculatus F.	–	–	–	5	4	1	–	–	**ri**
Family Curculionidae									
Subfamily Ceutorhynchinae									
Pelenomus quadrituberculatus F.	–	–	–	–	–	–	–	1	**ri**
Pelenomus sp.	–	–	–	–	1	–	–	–	**ri**
Subfamily Entiminae									
Tribe Sitonini									
Sitona borealis Kor.	1	3	1	–	1	2	–	1	**dt**
S. lineellus Bonsd.	–	–	–	–	–	1	–	–	**me**
Subfamily Hyperinae									
Hypera diversipunctata Schrank.	–	4	4	3	1	2	1	–	**dt**
H. ornata Cap.	–	–	–	8	3	–	–	–	**dt**
Subfamily Lixinae									
Tribe Cleonini									
Coniocleonus astragali T.-M.et Kor.	3	1	6	–	–	–	–	–	**ms**
C. cinerascens Hochh.	–	–	1	–	–	–	–	–	**ms**
C. ferrugineus Fahr.	–	–	–	–	–	–	–	1	**ms**
Coniocleonus sp.	–	–	2	–	2	1	–	–	**ms**
Stephanocleonus eruditus Faust	3	6	2	2	–	1	–	–	**st**
S. fossulatus F.-W.	2	–	–	1	–	1	–	–	**st**
Subfamily Molytinae									
Tribe Lepyrini									
Lepyrus nordenskioeldi Faust	–	1	1	2	–	2	1	1	**sh**
Subfamily Curculioninae									
Tribe Elliscini									
Dorytomus imbecillus Fst.	1	–	1	–	10	–	–	–	**sh**
Dorytomus sp.	–	–	–	–	–	1	–	6	**sh**
Tribe Rhamphini									
Isochnus arcticus Kor.	–	3	9	3	1	–	1	1	**tt**
Order Heteroptera									
Family Saldidae									
Salda littoralis L.	–	–	–	2	–	–	1	–	**ri**
Order Hymenoptera									
Family Formicidae									
Camponotus herculeanus L.	–	–	–	–	1	–	–	–	**fo**
Hymenoptera gen. indet.	13	3	9	–	3	–	6	–	**oth**
Order Homoptera									
Family Cicadellidae									
Cicadellidae gen. indet.	–	–	–	–	1	–	–	–	**me**
Order Megaloptera									
Family Sialidae									
Sialis sp.	–	–	4	–	–	3	3	2	**aq**
Order Trichoptera									
Trichoptera gen. indet. (larvae)	2	–	2	–	–	–	–	–	**aq**
Order Diptera									
Family Chironomidae									
Chironomidae gen. indet.	2	–	–	–	–	–	1	1	**aq**
Family Tipulidae									
Tipulidae gen. indet.	1	–	–	–	–	–	1	–	**oth**
Diptera fam. indet. (puparia)	3	1	5	–	–	–	3	–	**oth**
Sum	176	230	252	143	406	163	43	175	

Table 23. Insects from the Holocene sections, Bykovsii Peninsula, alas 1, log

Age	Holocene								
Section	alas1			log					eco
Species/sample MKh-	B11	B10	B9	R20,BC	R20A	R22	B27	R23	
Order Coleoptera									
Family Carabidae									
Subfamily Nebriinae									
Nebria frigida Sahlb.	–	–	–	–	–	–	–	1	**ri**
Notiophilus aquaticus L.	–	–	–	–	1	–	–	1	**xe**
Subfamily Scaritinae									
Dyschiriodes melancholicus Putz.	–	–	1	–	–	–	–	–	**ri**
Subfamily Harpalinae									
Tribe Harpalini									
Harpalus vittatus kiselevi Kat. et Shil.	1	–	–	–	–	–	–	–	**ms**
Tribe Pterostichini									
Poecilus (*Derus*) *nearcticus* Lth.	1	–	–	–	–	–	–	–	**dt**
Pterostichus (*Cryobius*) *brevicornis* (Kby.)	1	1	2	9	6	–	–	9	**mt**
P. (*Cryobius*) *pinguedineus* Esch.	–	–	–	3	3	–	–	1	**mt**
P. (*Cryobius*) *ventricosus* Esch.	–	–	–	3	1	–	–	2	**mt**
Pterostichus (*Cryobius*) sp.	2	2	6	3	4	1	4	–	**mt**
P. (*Lenapterus*) *agonus* Horn.	1	–	–	–	–	–	–	1	**mt**
P. (*Lenapterus*) *costatus* Men.	3	–	–	–	1	–	–	–	**mt**
P. (*Lenapterus*) *vermiculosus* Men.	–	–	–	–	–	–	–	1	**mt**
P. (*Petrophilus*) *tundrae* Tschitsch.	1	–	–	–	1	–	–	–	**dt**
P. (*Petrophilus*) *uralensis* Motsch.									
P. (*Tundraphilus*) *sublaevis* Sahlb.	–	1	–	1	2	–	–	–	**dt**
Stereocerus haematopus (Dej.)	–	–	1	–	–	–	–	–	**dt**
Tribe Zabrini									
Curtonotus alpinus Payk.	3	2	2	1	6	2	3	3	**dt**
Family Dytiscidae									
Subfamily Agabinae									
Agabus moestus (Curt.)	1	–	–	–	–	–	–	–	**aq**
Subfamily Hydroporinae									
Hydroporus acutangulus Thoms.?	1	–	–	–	–	–	–	–	**aq**
Family Hydrophilidae									
Subfamily Helophorinae									
Helophorus splendidus Sahlb.	–	–	–	–	1	1	–	1	**aq**
Family Leiodidae									
Subfamily Cholevinae									
Cholevinus sibiricus (Jean.)	–	–	1	4	5	–	1	–	**mt**
Family Staphylinidae									
Subfamily Omaliinae									
Olophrum consimile Gyll.	–	–	1	1	–	–	–	–	**mt**
Subfamily Tachyporinae									
Tachinus arcticus Motsch.?	1	3	12	3	4	3	7	4	**mt**
Tachyporus sp.	–	–	–	–	–	1	–	–	**pl**
Subfamily Paederinae									
Lathrobium sp.	–	–	1	4	–	–	–	–	**pl**
Subfamily Staphylininae									
Staphilininae gen. indet.	–	–	–	–	–	–	1	–	**pl**
Family Byrrhidae									
Subfamily Byrrhinae									
Morychus viridis Kuzm. et Korot.	4	2	–	3	4	2	1	3	**ss**
Subfamily Syncalyptinae									
Curimopsis cyclolepidia Muenst.	–	1	–	–	–	–	–	–	**dt**

Table 23. (Contd.)

Age	Holocene								
Section	alas1			log					eco
Species/sample MKh-	B11	B10	B9	R20,BC	R20A	R22	B27	R23	
Family Chrysomelidae									
Subfamily Chrysomelinae									
Chrysolina subsulcata Mnnh.	–	–	–	–	–	–	1	2	**tt**
Chrysolina sp.	–	–	–	–	2	–	–	–	**mt?**
Family Brentidae									
Subfamily Apioninae									
Hemitrichapion tschernovi T.-M.	1	–	–	1	1	–	–	–	**dt**
Mesotrichapion wrangelianum Kor.	–	–	–	–	2	–	–	1	**dt**
Apioninae gen. indet.	–	–	–	–	–	–	–	1	**dt?**
Family Brachyceridae									
Subfamily Erirhininae									
Notaris bimaculatus F.	–	–	–	1	1	1	–	–	**ri**
Family Curculionidae									
Subfamily Ceutorhynchinae									
Ceutorhynchus sp.	–	–	–	–	–	–	1	–	**dt**
Pelenomus velaris Gyll.	–	–	–	–	–	–	–	1	**ri**
Subfamily Entiminae									
Tribe Sitonini									
Sitona borealis Kor.	–	–	–	1	1	–	–	–	**dt**
Subfamily Hyperinae									
Hypera diversipunctata Schrank.	–	–	–	2	–	–	–	–	**dt**
H. ornata Cap.	1	–	–	1	–	–	–	–	**dt**
Subfamily Lixinae									
Tribe Cleonini									
Coniocleonus ferrugineus Fahr.	–	–	–	–	1	–	–	–	**ms**
Coniocleonus sp.	1	–	–	–	–	1	1	–	**ms**
Stephanocleonus sp.	1	–	–	–	–	–	–	–	**st**
Subfamily Molytinae									
Tribe Lepyrini									
Lepyrus nordenskioeldi Faust	–	1	–	1	1	–	1	3	**sh**
Tribe Pissodini									
Pissodes sp.	–	–	1	–	–	–	–	–	**fo**
Subfamily Curculioninae									
Tribe Rhamphini									
Isochnus arcticus Kor.	–	1	2	5	4	3	1	2	**tt**
Order Hymenoptera									
Hymenoptera gen. indet.	–	1	2	1	–	–	–	–	**oth**
Order Megaloptera									
Family Sialidae									
Sialis sp.	–	–	2	1	–	–	1	–	**aq**
Order Trichoptera									
Trichoptera gen. indet. (larvae)	–	–	–	–	–	–	–	1	**aq**
Order Diptera									
Family Tipulidae									
Tipulidae gen. indet.	–	–	–	–	–	–	–	1	**oth**
Diptera fam. indet. (puparia)	–	–	–	–	1	1	–	–	**oth**
Sum	24	14	30	47	52	15	22	37	

Table 24. Insects from Mamontovyi Bysagasa and alas 3, Bykovsii Peninsula

Age	Late Pleistocene			Holocene					
Section	alas 2 (Mamontovyi Bysagasa)							alas3	
Species/sample MKh-	B25, 26	B24	B23	B22	B21	B20	R21	B29	eco
Order Coleoptera									
Family Carabidae									
Subfamily Nebriinae									
Nebria frigida Sahlb.	–	–	–	–	1	2	–	–	**ri**
Notiophilus aquaticus L.	–	–	–	–	–	1	–	–	**xe**
Subfamily Carabinae									
Carabus odoratus Motsch.	1	–	–	–	–	–	–	–	**dt**
C. truncaticollis Esch.	–	–	1	1	–	–	–	–	**mt**
C. vietinghoffi Ad.	–	–	–	–	1	–	–	–	**fo**
Subfamily Elaphrinae									
Blethisa catenaria Brown.	–	–	–	–	–	–	–	1	**mt**
Diacheila polita Fald.	–	–	–	–	1	1	–	–	**mt**
Elaphrus sp.	–	–	–	–	–	–	–	1	**ri**
Loricera pilicornis L.	–	–	–	–	1	–	–	–	**fo**
Subfamily Scaritinae									
Dyschiriodes melancholicus Putz.	–	–	–	–	–	1	–	–	**ri**
Subfamily Trechinae									
Bembidion (*Peryphanes*) *dauricum* Motsch.	–	1	–	–	–	–	–	–	**dt**
Bembidion (*Peryphus*) sp.	–	–	–	1	1	3	2	–	**ri**
Bembidion (*Plataphus*) sp.	–	–	–	1	–	–	–	–	**ri**
Subfamily Harpalinae									
Tribe Harpalini									
Dicheirotrichus mannerheimi Sahlb.	–	–	–	1	–	2	–	–	**dt**
Tribe Pterostichini									
Poecilus (*Derus*) *nearcticus* Lth.	–	–	–	–	1	–	1	–	**dt**
Pterostichus (*Cryobius*) *brevicornis* (Kby.)	–	2	2	5	39	44	4	1	**mt**
P. (*Cryobius*) *pinguedineus* Esch.	1	1	2	–	1	–	2	4	**mt**
P. (*Cryobius*) *ventricosus* Esch.	3	3	–	2	6	–	–	–	**mt**
Pterostichus (*Cryobius*) sp.	4	2	1	–	4	–	1	–	**mt**
P. (*Lenapterus*) *costatus* Men.	–	2	1	1	–	–	2	–	**mt**
P. (*Lenapterus*) *vermiculosus* Men.	–	–	–	–	1	–	–	–	**mt**
P. (*Petrophilus*) *abnormis* Sahlb.	1	–	–	–	–	–	–	–	**dt**
P. (*Petrophilus*) *eximius* Mor.	–	–	–	–	1	–	–	–	**dt**
P. (*Petrophilus*) *magus* Mnnh.	–	–	–	–	–	–	–	1	**fo**
P. (*Petrophilus*) *montanus* (Motsch.)	–	–	–	–	–	1	–	1	**dt**
P. (*Petrophilus*) *uralensis* Motsch.	–	–	–	1	–	–	–	–	**fo**
Pterostichus (*Petrophilus*) sp.	2	1	–	–	–	–	–	–	**dt?**
P. (*Tundraphilus*) *sublaevis* Sahlb.	2	3	2	–	2	–	–	–	**dt**
Stereocerus haematopus (Dej.)	–	–	–	1	2	–	1	–	**dt**
Tribe Zabrini									
Amara interstitialis Dej.	–	–	–	–	–	–	2	–	**dt**
Curtonotus alpinus Payk.	5	8	4	2	4	3	7	6	**dt**
Family Dytiscidae									
Subfamily Agabinae									
Agabus moestus (Curt.)	–	–	–	2	1	1	–	1	**aq**
Subfamily Hydroporinae									
Hydroporus acutangulus Thoms.?	–	–	–	–	1	–	–	1	**aq**
Hydroporus sp.	–	–	–	–	–	1	–	–	**aq**
Dytiscidae gen. indet.	–	–	–	–	–	1	–	–	**aq**

Table 24. (Contd.)

Age	Late Pleistocene		Holocene						
Section	alas 2 (Mamontovyi Bysagasa)							alas3	
Species/sample MKh-	B25, 26	B24	B23	B22	B21	B20	R21	B29	eco
Family Hydrophilidae									
Subfamily Helophorinae									
Helophorus splendidus Sahlb.	–	1	–	–	–	1	–	–	**aq**
Subfamily Hydrophilinae									
Hydrobius fuscipes F.	–	–	–	–	1	–	1	–	**aq**
Family Leiodidae									
Subfamily Leiodinae									
Cyrtoplastus irregularis Rtt.?	–	–	–	–	2	2	–	1	**pl**
Subfamily Cholevinae									
Cholevinus sibiricus (Jean.)	2	2	2	1	1	2	2	2	**mt**
Family Silphidae									
Subfamily Silphinae									
Aclypea opaca (L.)	–	1	–	–	–	–	–	–	**oth**
Family Staphylinidae									
Subfamily Omaliinae									
Olophrum consimile Gyll.	–	–	1	–	4	–	1	–	**mt**
O. latum Maekl.	4	–	–	–	–	–	–	–	**mt**
Eucnecosum tenue (LeC.)	–	–	1	1	–	4	–	–	**pl**
Subfamily Tachyporinae									
Tachinus arcticus Motsch.?	5	18	5	9	9	9	2	3	**mt**
Tachyporus sp.	–	–	–	–	1	1	–	–	**pl**
Subfamily Steninae									
Stenus sensu stricto sp.	–	–	–	–	1	–	–	–	**ri**
Subfamily Paederinae									
Lathrobium sp.	–	–	–	1	2	1	–	–	**pl**
Subfamily Staphylininae									
Philonthus sp.	–	–	–	3	2	1	–	–	**pl**
Staphylininae gen. indet.	–	–	–	–	–	2	–	–	**pl**
Family Scarabaeidae									
Aphodius sp.	–	1	1	–	–	1	–	–	**st?**
Family Byrrhidae									
Subfamily Byrrhinae									
Morychus viridis Kuzm. et Korot.	4	2	1	5	6	3	3	3	**ss**
Simplocaria arctica Popp.	–	–	1	–	–	–	1	–	**dt**
Simplocaria sp.	–	–	–	–	–	1	–	–	**dt**
Subfamily Syncalyptinae									
Curimopsis cyclolepidia Muenst.	–	1	–	–	–	1	–	–	**dt**
Family Elateridae									
Subfamily Dendrometrinae									
Denticollis varians Germ.	–	–	–	–	–	1	–	–	**fo**
Family Melyridae									
Troglocollops arcticus L. Medv.	–	–	–	1	1	–	–	–	**ms**
Family Coccinelidae									
Scymnus sp.	–	–	–	–	–	1	–	–	**ri**
Family Lathridiidae									
Corticaria sp.	–	–	–	–	2	3	–	–	**pl**
Family Chrysomelidae									
Subfamily Chrysomelinae									
Chrysolina septentrionalis Men.	3	3	2	–	–	1	–	–	**mt**
Ch. subsulcata Mnnh.	–	4	1	–	1	–	–	–	**tt**

Table 24. (Contd.)

Age	Late Pleistocene			Holocene					
Section	alas 2 (Mamontovyi Bysagasa)							alas3	
Species/sample MKh-	B25, 26	B24	B23	B22	B21	B20	R21	B29	eco
Hydrothassa hannoverana F.	1	3	–	–	1	–	–	–	**ri**
Phaedon armoraciae L.	–	–	2	–	–	1	–	–	**me**
Ph. vulgatissima L.	–	–	–	–	1	–	–	–	**sh**
Subfamily Galerucinae									
Galeruca interrupta circumdata Duft.	–	–	–	–	1	–	–	–	**st**
Family Brentidae									
Subfamily Apioninae									
Hemitrichapion tschernovi T.-M.	2	2	1	4	–	1	–	–	**dt**
Mesotrichapion wrangelianum Kor.	5	6	2	6	1	–	–	–	**dt**
Family Brachyceridae									
Subfamily Erirhininae									
Notaris bimaculatus F.	–	–	–	–	–	1	–	–	**ri**
Family Curculionidae									
Subfamily Ceutorhynchinae									
Pelenomus sp.	–	–	–	–	–	1	–	–	**ri**
Subfamily Entiminae									
Tribe Sitonini									
Sitona borealis Kor.	–	2	2	1	–	–	1	–	**dt**
Subfamily Hyperinae									
Hypera diversipunctata Schrank.	–	–	–	–	–	–	1	1	**dt**
H. ornata Cap.	2	1	1	–	1	1	–	–	**dt**
Subfamily Lixinae									
Tribe Cleonini									
Coniocleonus ferrugineus Fahr.	–	–	–	1	–	–	–	–	**ms**
Coniocleonus sp.	–	1	–	–	–	–	–	–	**ms**
Stephanocleonus eruditus Faust	–	–	–	–	1	–	–	–	**st**
Stephanocleonus sp.	–	–	–	–	–	–	1	2	**st**
Subfamily Molytinae									
Tribe Lepyrini									
Lepyrus nordenskioeldi Faust	1	1	–	3	2	1	–	–	**sh**
Lepyrus sp.	–	–	–	–	–	–	2	–	**sh**
Subfamily Curculioninae									
Tribe Rhamphini									
Isochnus arcticus Kor.	8	9	3	7	5	4	–	2	**tt**
Order Heteroptera									
Family Saldidae									
Salda sp.	–	1	–	–	–	–	–	–	**ri**
Family Pentatomidae									
Aelia frigida Kir.	–	–	–	1	–	–	–	–	**ms**
Order Hymenoptera									
Family Formicidae									
Leptothorax acervorum F.	–	–	–	–	2	–	–	–	**fo**
Hymenoptera gen. indet.	–	1	2	–	3	–	–	–	**oth**
Order Megaloptera									
Family Sialidae									
Sialis sp.	1	2	2	–	–	1	1	2	**aq**
Order Trichoptera									
Trichoptera gen. indet. (larvae)	–	–	1	–	–	1	–	–	**aq**
Order Diptera									
Family Chironomidae									
Chironomidae gen. indet.	–	1	1	1	2	3	–	–	**aq**
Diptera fam. indet. (puparia)	–	1	1	–	11	9	–	–	
Sum	56	82	39	62	116	106	37	31	

Table 25. Insects from the Bolshoi Lyakhovskii site (part 1)

Age	Yukogir Formation						
Section L-	R14		R17				eco
Species/sample	R5	R6	R4	B2	R3	R2	
Order Coleoptera							
Family Carabidae							
Subfamily Harpalinae							
Tribe Pterostichini							
Poecilus (*Derus*) *nearcticus* Lth.	1	2	1	–	–	1	**dt**
Pterostichus (*Cryobius*) *brevicornis* (Kby.)	26	5	3	4	–	–	**mt**
P. (*Cryobius*) *nigripalpis* Popp.	–	–	–	–	1	–	**dt**
P. (*Cryobius*) *pinguedineus* Esch.	–	–	–	2	–	–	**mt**
P. (*Cryobius*) *ventricosus* Esch.	–	1	–	–	–	–	**mt**
Pterostichus (*Cryobius*) sp.	2	–	3	1	3	1	**mt**
P. (*Lenapterus*) *agonus* Horn.	1	1	–	1	–	–	**mt**
P. (*Lenapterus*) *costatus* Men.	1	–	1	–	–	–	**mt**
P. (*Petrophilus*) *abnormis* Sahlb.?	–	1	–	–	–	–	**dt**
P. (*Tundraphilus*) *sublaevis* Sahlb.	2	–	–	–	–	2	**dt**
Tribe Zabrini							
Curtonotus alpinus Payk.	11	2	–	5	6	2	**dt**
Family Dytiscidae							
Subfamily Agabinae							
Agabus moestus (Curt.)	1	–	–	–	–	1	**aq**
Subfamily Hydroporinae							
Hydroporus sp.	–	1	–	1	–	–	**aq**
Family Hydrophilidae							
Subfamily Helophorinae							
Helophorus splendidus Sahlb.	1	–	–	1	–	–	**aq**
Family Staphylinidae							
Subfamily Tachyporinae							
Tachinus arcticus Motsch.	17	3	1	13	3	1	**mt**
Family Byrrhidae							
Subfamily Byrrhinae							
Morychus viridis Kuzm. et Korot.	–	–	1	1	5	2	**ss**
Family Chrysomelidae							
Subfamily Chrysomelinae							
Chrysolina bungei Jac.	–	–	–	–	–	1	**tt**
Ch. magniceps (Sahlb)	4	4	1	6	–	1	**tt**
Ch. septentrionalis Men.	–	–	1	1	–	–	**mt**
Ch. subsulcata Mnnh.	9	2	8	–	3	3	**tt**
Ch. tolli Jac.	3	1	–	2	–	–	**tt**
Hydrothassa hannoverana F.	1	–	–	1	–	–	**ri**

Table 25. (Contd.)

Age	Yukogir Formation						
Section L-	R14		R17				eco
Species/sample	R5	R6	R4	B2	R3	R2	
Family Curculionidae							
Subfamily Entiminae							
Tribe Sitonini							
Sitona borealis Kor.	–	–	–	–	1	1	**dt**
Subfamily Hyperinae							
Hypera ornata Cap.	–	–	–	–	1	2	**dt**
Subfamily Lixinae							
Tribe Cleonini							
Coniocleonus sp.	–	1	–	1	–	–	**ms**
Subfamily Molytinae							
Tribe Lepyrini							
Lepyrus nordenskioeldi Faust	1	1	–	–	1	2	**sh**
Subfamily Curculioninae							
Tribe Rhamphini							
Isochnus arcticus Kor.	3	1	–	3	1	–	**tt**
Order Hymenoptera							
Hymenoptera gen. indet.	1	–	–	1	–	–	**oth**
Order Megaloptera							
Family Sialidae							
Sialis sp.	–	1	–	–	–	–	**aq**
Sum	84	26	20	43	25	20	

Sample B18 taken in different years is consider to be from this interval, but the ecological structure of the assemblage is more similar to the next group of samples, so that we suggested incorrect assignment to particular level.

Samples from a neighboring part of the section is indicative of cooling. Assemblage R12 (elevation of 17.7 m) is dominated by the arctic group (30%). The group includes a high arctic leaf beetle, *Chrysolina bungei,* and the weevil *Isochnus arcticus* typical for the Bykovsii record. Species diversity of other insects is not great: *Pterostichus* (*Cryobius*) *spp., P. costatus, Cholevinus sibiricus, Tachinus arcticus* from the **mt** group; *Curtonotus alpinus, Pterostichus haematopus, Mesotrichapion wrangelianum, Sitona borealis, Hypera diversipunctata* from the **dt** group, one meadow leaf beetle, *Phaedon concinnus,* rare steppe leaf beetle *Chrysolina brunnicornis bermani,* and a surprisingly high number of *Morychus viridis* (16%).

Sample R11 from elevation of 18.4 m shows a similar complicated structure: **tt** = 24%, individual steppe weevil *Stephanocleonus* sp., and 18% of *Morychus viridis.*

This interval of 17.7–18.4 m (35–34 ka) is apparently correlated with a short cold event. The environment was close to modern one, but included remains of steppe vegetation in local refuges and significant areas of low grass–sedge steppes.

The succeeding assemblage shows a very unstable situation, with a reduced proportion of the arctic group in assemblage 01-17 at elevation of 19 m and, after that, a dramatic increase in the proportion of **tt** up to 57% in sample 01-16 from elevation of 20 m. This sudden fluctuation was rapidly restored, so that sample R9 from 20.2 m displays a normal ecological structure close to 01-17. It is hard to explain such a strange feature. Sample 01-16, with an enormous abundance of the arctic weevil *Isochnus arcticus,* comes from a bed with shrub remains. The species composition is mixed, the assemblage contains a number of cold resistant species (*Pterostichus costatus, Tachinus arcticus, Chrysolina subsulcata, Ch. tolli*) and individual specimens of thermophilous species (*Hydrothassa hannoverana, Leptothorax acervorum*). The short cooling episode was probably about 33.5 ka, but in connection with a great volume of screened sediment, the insect method preclude the possibility to trace it accurately. We can have undesirable impurity in the sample which requires at least a 10-cm-thick layer of sediment.

Sample B17 from elevation of 22.5 m (about 33 ka) is dominated by wet tundra insects (48%) (*Pterostichus* (*Cryobius*) *brevicornis, P.* (*Cryobius*) *pinguedineus, P.* (*Cryobius*) *ventricosus*, *P. costatus, P. agonus, Tachinus arcticus*, *Chrysolina septentrionalis*); some of these species are cold resistant. The dry tundra group composes 31% of individuals (*Curtonotus alpinus, P. sublaevis*, *Hemitrichapion tschernovi, Sitona borealis, Hypera ornata, H. diversipunctata*). The assemblage contains the arctic group –(7%) and, on the other hand, a number of thermophilous insects, such as *Pterostichus abnormis, P. eximius, P. magus, Hydrothassa hannoverana, Leptothorax acervorum*. These species are indicative of a warmer climate than at the present time. The steppe–tundra indicators in the samples from 01-16 to B17 are infrequent. The environment was tundra-like, the temperature varied from cold to warm, but humidity remained relatively high.

The next sample (99-18c) from elevation of 25.4 m is small; it contains tundra and individual steppe species; the arctic group composes 17%. The assemblage corresponds to climatic trend towards cooling (with fluctuations).

Two neighboring samples from elevation of 26–26.2 m are similar to each other. They are dominated by arctic insects (57%); most of specimens belong to *Isochnus arcticus* and a few are *Chrysolina subsulcata* and *Ch. tolli*. Species diversity of other groups is low; only one specimen belongs to *Morychus viridis*.

The proportion of arctic insects remains high, but declined in sample B18 from elevation of 28.5 m. This assemblage is dominated by wet tundra species, such as *Pterostichus* (*Cryobius*) spp., *Cholevinus sibiricus*, *Tachinus arcticus*, and *Chrysolina septentrionalis*; the **tt** and **dt** groups compose 28 and 15%, respectively. The steppe groups are only represented by individual *Morychus viridis*.

The arctic group returned to the dominant position in sample 99-22ac from elevation of 31.3 m (**tt** = 67%); species diversity of the fauna is low, all species are cold resistant, but some are more typical for steppe–tundra communities (*Sitona borealis, Morychus viridis, Coniocleonus* sp.). A number of samples collected in this part of the section in different years show permanent participation of the arctic group. The proportion of **tt** varies from 20 to 67% (on average 44%), but anyway, the arctic group plays an unusually significant role, compared with other Pleistocene assemblages.

All assemblages taken from the 26–31.5 m interval (24–19 ka) are indicative of cold tundra environments. The proportion of the arctic group varies widely, but usually it is high; the role of steppe–tundra indicators is permanently low. True steppe insects, which require relatively warm summer, are absent here, but infrequent indicators of the low grass–sedge steppe occur in each sample. The climate was cold; the environment was tundra-like, with restricted refuges of steppe–tundra habitants.

The ecological structure of insect assemblages changes dramatically, beginning from sample 00-B1 from elevation of 33 m. The arctic group decreases to 5% and various steppe–tundra indicators become notable. There are *Aphodius* sp., (4%); the **st** group composes 3% (*Chrysolina brunnicornis bermani*, *Stephanocleonus eruditus, S. fossulatus*); **ms** = 3% (*Troglocollops arcticus, Harpalus vittatus vittatus, Pseudoprotapion astragali, Coniocleonus ferrugineus, C. cinerascens*); and 33% are *Morychus viridis*. Among tundra species, xerophilous insects are more numerous and diverse **dt** = 36% (*Curtonotus alpinus*, *Carabus odoratus*, *Poecilus nearcticus*, *Pterostichus abnormis*, *P. sublaevis*, *Mesotrichapion wrangelianum, Hemitrichapion tschernovi, Sitona borealis*, *Hypera diversipunctata*). The assemblage contains thermophilous species, such as *Pterostichus abnormis*, *Colymbetes dolabratus*, and *Phaedon concinnus*.

This assemblage belongs to the **S-T/S-T** type, which is common in the southern and eastern regions of western Beringia, but rare in the Laptev Sea area.

The next sample (99-6s) from elevation of 34.1 m contains a smaller proportion of the steppe group (only 20%, *Morychus viridis*), but a number of samples upward in the section from elevation of 34.8–35.2 m are dominated by the steppe groups again: **st** = 10% (*Chrysolina brunnicornis bermani*, *Stephanocleonus eruditus*), **ms** = 7% (*Chrysolina arctica*), and 43% are *Morychus viridis*. We can see a mixture of cold resistant (*Tachinus arcticus, Pterostichus agonus, Chrysolina subsulcata, Isochnus arcticus*) and thermophilous species, such as the forest weevil *Pissodes* sp., which is indicative of the presence of coniferous trees.

The 33–35.2 m interval (17–14 ka) is characterized by the highest proportion in the section of xerophilous steppe insects. There was evident prosperity of the steppe–tundra biome during that time, which contrasts with tundra-like and arctic environment commonly widespread in this northern area. Low grass–sedge steppe, a typical part of the mosaic steppe–tundra environment, was established here.

Fossil insects in combination with other methods (Sher et al., 2005) allow the recognition of four zones in the Pleistocene part of the MKh section. The first (IFZ 1) reflects the time interval from 44.6 to 34 ka, which is the early part of the Middle Weichselian (MIS3). The compositions of insects and plants are indicative of mosaic biotopes, with a high proportion of dry grassland vegetation.

Caryophyllaceae and *Artemisia* pollen reach the highest values throughout the section. Some plants, such as *Carex duriuscula* and *Linum perenne,* are more common in steppe or meadow–steppe habitats, but most of plant macrofossils are indicative of dry tundra. We can see some variations inside the zone. The pollen spectrum shows an increase in the hygrophilous species in the peat beds; this may result from local conditions. The insect curve is also uneven. There are three peaks of xeric insects at the elevations of 13, 16.5, and 19 m, separated by assemblages dominated by wet tundra and arctic species. The highest peak is the first. We can see a trend of decreasing xerophilous component and probably decreasing summer temperature.

IFZ 2 (about 34–24 ka, Middle Weichselian II) corresponds to the later part of MIS3. It is marked by a sharp decrease in true xerophilous insects, primarily *Morychus viridis*. The percentage of arctic tundra insects (mostly *Isochnus arcticus*) varies, but is on average much higher than in Zone 1. Regarding the pollen record, the upper half of Zone 2 shows rather homogeneous spectra essentially similar to that of Zone 1. *Artemisia* becomes less abundant, while the Cichoriaceae and Asteraceae show higher values; *Selaginella rupestris* increases its role up to 12% in some samples.

At first glance, paleoecological evidence from Zone 2 is contradictory; insect data are indicative of a sharp reduction of the steppe and dry tundra groups, but plant macrofossils show a high percentage of xerophilous tundra species. This could have been caused by a decrease in the summer temperature. More sensitive insects survived only in the warmest spots with open soil.

IFZ 3 (from 24 to about 15 ka) corresponds to most of the Late Weichselian (MIS2). All insect samples are characterized by the lowest values of the **ms** and **ss** groups, the role of **st** is extremely low; this group is absent in some samples. The main feature is dominance, up to 67%, of the arctic group. Plant macrofossil assemblages contain abundant willow remains; this is correlated with a rise in the proportion of *Salix* pollen and dominance of the dwarf willow weevil *Isochnus arcticus*. Thus, the coldest time in the section is reconstructed here.

IFZ 4 (15–12.5 ka) corresponds to the second part of the Late Weichselian, or late MIS2. Regarding insects, this zone demonstrates the highest values of xerophilous species in general and steppe species in particular. The proportion of thermophilous insects also increases. Insect and plant fossils are well correlated here; mesophilous sedges have not been found; only xerophilous sedges, such as *Carex duriuscula,* show the highest proportion in the section. *Selaginella* spores are absent in the assemblage.

The latest Pleistocene date in this area of the section is 12.79 ± 0.06 ka. The dates from the lower part of the Holocene sediment cover are around 8 ka and the supposed gap in the fossil record is about 4000 years. This gap in the main Bykovsii section does not allow us to reconstruct the very important transitional period between the Pleistocene and Holocene.

3.3a1. Bykovsii, Holocene

The Holocene part of the main cliff Mamontovyi Khayata is a number of thick peat bodies at the top of the section (Fig. 24f). The Holocene deposits begin from brown silt with small peat lenses; a massive peat layer from 0.5 to 2 m lies above the silt; and gray stratified silt terminates the section. Five insect samples were taken from different parts of the section in different years.

The lowest Holocene sample is probably 3ac (Table 22). This small sample comes from brown silt with peat lenses at elevation of 36.7 m and reflects local boggy environment. The assemblage is dominated by aquatic (51%) and riparian (14%) species. The fauna contains species rare for the Pleistocene, such as *Agonum quinqueounctatum, Agabus thomsoni, Hydroporus fuscipennis,* and *Galerucella grisescens*. The age of the sediment is 7.79 ± 0.05 ka.

Sample B4 was taken from gray silt under the peat bed in the baidzherakh, which is positioned separately from the wall. The elevation is 37.4 m, but it is difficult to correlate different parts of the top Holocene unit affected by melting and compression of deposits. Stratigraphically, the silt bed is the lower unit in the Holocene sequence. This is probably an older bed than brown silt, where sample 3ac comes from, because the top thin peat layer is older, dated 8.23 ± 0.05 and 8.050 ± 0.187 ka. This assemblage is dominated by tundra insects: **dt** = 38% and **mt** = 32%; arctic species are almost absent; the proportion of steppe groups is low: **st** = 2%, **ms** = 1%, and **ss** = 9%. The assemblage contains thermophilous species, such as rare for the Pleistocene shrub leaf beetle *Chrysomela blaisdelli*, meadow *Phaedon armoraciae*, and riparian weevil *Notaris bimaculatus*. This assemblage is most xerophilous among Holocene samples, but anyway, its species composition fits the Holocene well. The sharp difference from sample 3ac is probably attributable to taphonomic factors.

Three other samples, 01-B2, 01-01, and 00-B2, are similar to each other. All three assemblages are dominated by the **mt** group (43–58%); the most popular species is *Pterostichus* (*Cryobius*) *brevicornis*. The steppe–tundra indicators are represented by individual specimens of *Morychus viridis, Coniocleonus* sp., *Stephanocleonus eruditus*, and *S. fossulatus*. There are forest species, such as *Phosphuga atrata*, *Pediacus fuscus, Camponotus herculeanus*, and a number of thermophilous species from other groups: *Dyschiriodes melancholicus*, *Agonum quinqueounctatum*, *A. fuliginosum*, *Agabus thomsoni*, *Hydrobius fuscipes*, *Cyrtoplastus irregularis*, *Aclypea opaca*, *Olophrum consimile*, *Lathrobium* sp., *Philonthus* sp., *Chrysomela blaisdelli, Gonioctena affinis*, *Prasocuris phellandrii*, *Phaedon*

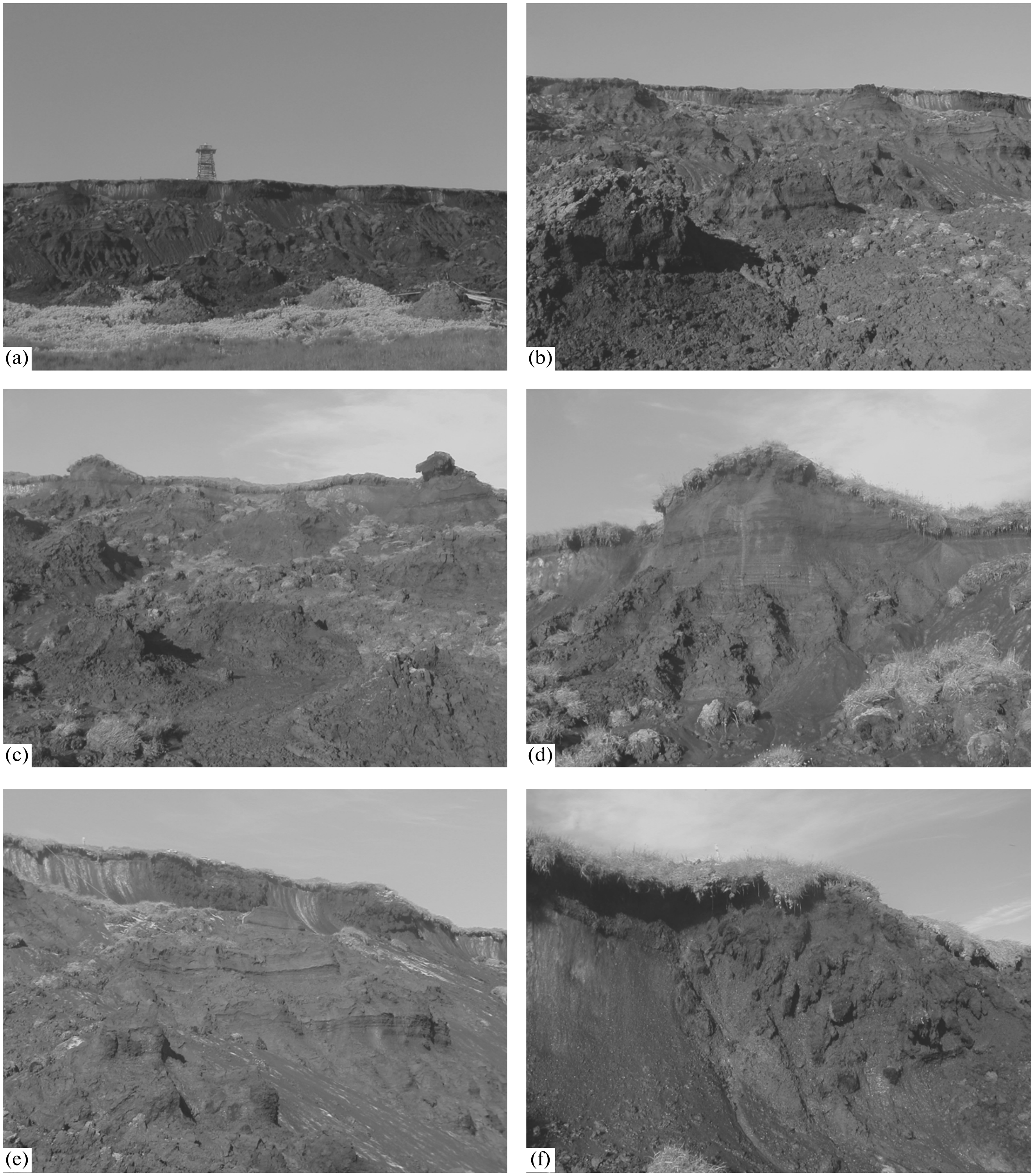


Fig. 24. Photograph of the Mamontovyi Khayata section, Bykovsii Peninsula: (a) general view, (b) lower peat, (c) middle part, (d) upper sandy unit, (e) ice wedges and Holocene peat inclusions in the upper part, (f) Holocene peat at the top of the section.

armoraciae, *Phratora polaris*, *Ph. vulgatissima*, *Notaris bimaculatus*, *Pelenomus quadrituberculatus*, and *Dorytomus imbecillus*. The number of thermophilous species is greater than in warm Pleistocene assemblages; some of these species are very rare in the fossil record (*Chrysomela blaisdelli, Gonioctena affinis*, *Prasocuris phellandrii*) and only recorded in the Holocene. These typical Holocene features, i.e., a wide species diver-

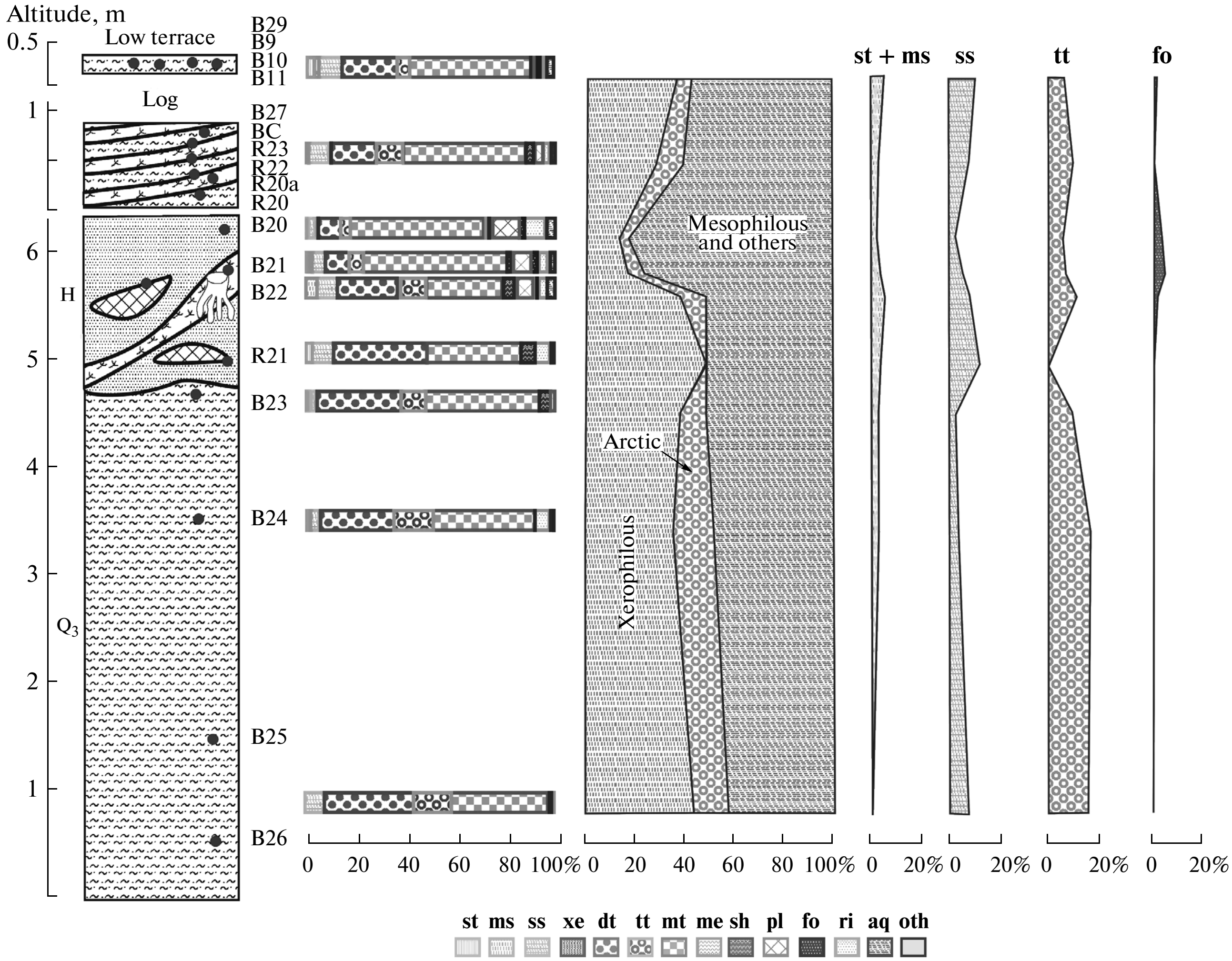


Fig. 25. Stratigraphic scheme and insect assemblages from the Holocene sections, Bykovsii Peninsula. For legend, see Figs. 15 and 16.

sity; rare species; a greater role of small ecological groups, such as plant litter, meadow, and shrub inhabitants, comes in conflict with the existence of typical Pleistocene steppe insects. Two steppe weevils species which cannot live in the modern tundra (*Stephanocleonus eruditus, S. fossulatus*) have been found here in the Holocene. We still do not have certain opinion about such finds. On the one hand, the possibility of reworking is rather high in the lower Holocene units. Radiocarbon dating has shown that the latest stage of the Pleistocene is absent in the section, probably the deposits were eroded during the early Holocene and fossils from the melted sediment were redeposited in the Holocene thermokarst lakes. On the other hand, such an impurity is typical for most of the early Holocene insect assemblages across Beringia (Kiselev, 1981; Nelson and Carter, 1987; Matthews and Telka, 1997; Kuzmina and Sher, 2006; Kiselev and Nazarov, 2009). Perhaps, some steppe fossils are actually Pleistocene reworked material, although it is also possible that some elements of the former ecosystem survived during this transitional time.

In addition to the main section, the Holocene was tested in several small sections (Fig. 25). The first is the "log" section, i.e., small stream valley deposits cut into the Pleistocene surface. The sediment is silt with peat lenses and abundant steams and roots of large grasses. We took six insect samples from here, but all of them are poor. The fossil fauna is clearly mixed due to a high possibility of reworking in this dynamic environment. The fauna is dominated by wet tundra species, but the percent of the arctic group and xerophilous insects is higher than in other Holocene samples.

Three small samples were taken from a low thermokarst lake terrace located close to the main section. These samples are also affected by reworking; *Morychus viridis*, *Stephanocleonus*, and *Coniocleonus* are common here; the preservation of fossils is not good.

An interesting section is Mamontovyi Bysagasa, a 7-m-high sea cliff 2 km apart from the main section (Fig. 25, Table 24). The section is composed of silt and sand without ice wedges; the upper part is a bed overfull with shrub twigs and roots and with a medium-sized tree stump. Wood remains from the bed have provided two radiocarbon dates: 8.997 ± 0.251 and 8.326 ± 0.236 ka (Kuznetsova et al., 1999).

The cliff attracts attention due to abundant fossil bones found on the beach under the section. The youngest bone is dated 28.80 ± 0.18 ka.

A detailed study has shown that the section consists of two different units. The lower unit (from 0 to 5.5 m above sea level) is solid silt with tiny layers of plant debris and fine-grained sand. The upper unit is more complex. It consists of the lower yellow coarse-grained sand bed, with plant debris and freshwater mollusk shells, the middle shrub bed, and the upper gray sand bed. The upper unit is probably lacustrine in origin; it was formed in a Holocene thermokarst lake, so that the lower unit should be melted and compressed Pleistocene sediment under the lake.

We took four samples from the lower unit and four from the upper unit.

The four lower samples are similar to each other. They are dominated by the tundra groups (**dt** and **mt**); arctic insects are rather common, but the steppe–tundra indicators are singular. The deposits of the Pleistocene part of the section may have Late Karginian–Early Sartanian age; cooling affected the environment.

Samples from the upper part of the section are various. The first sample (R21) is similar to the Pleistocene ones, but does not include the arctic group. The possibility of reworking is high here, so that we believe that the insect assemblage from the thermokarst unit base just above the melted and compressed Pleistocene sediment cannot give correct environmental information.

Other three Holocene samples were also probably affected by reworking, but some features are indicative of a Holocene environment. The xerophilous part of insect assemblages gradually decreased; forest and plant litter insects appeared. The forest group includes *Carabus vietinghoffi, Loricera pilicornis, Pterostichus uralensis, Denticollis varians,* and *Leptothorax acervorum*. Plant litter (*Cyrtoplastus irregularis, Eucnecosum tenue*, *Tachyporus* sp., *Lathrobium* sp., *Philonthus* sp., *Corticaria* sp.), shrub (*Phratora vulgatissima*), and meadow (*Phaedon armoraciae*) insects, along with forest species suggest that the climate was warmer than at present. The tundra ground beetle *Pterostichus (Cryobius) brevicornis* became the dominant of assemblages (in the Pleistocene part, the rove beetle *Tachinus arcticus* is most abundant in the **mt** group). Thus, despite the possibility of reworking, early Holocene insect assemblages are clearly indicative of changes in the environment from the steppe–tundra to tall shrub tundra or forest–tundra type.

3.3b. Bolshoi Lyakhovskii Island

The insect fauna (Fig. 26, Tables 25–28) from Bolshoi Lyakhovskii Island (Figs. 1, 6) is most complete compared to the others in this region. This is the southern island of the Novosibirskie Islands Archipelago. Modern environment is transitional between typical and arctic tundra; open ground spots are frequent, but plant diversity is relatively poor. The modern beetle fauna is also impoverished, while the number of beetles is large. A significant part of the modern insect collection is represented by species adapted to cold conditions, primarily arctic *Chrysolina: Ch. tolli, Ch. bungei, Ch. subsulcata,* and *Ch. magniceps.* These species presently live here and are recorded in the Pleistocene. The site is interesting primarily in its northern position. Insect faunas show not only temporal environmental changes, but also natural zones of the past.

Quaternary history of Bolshoi Lyakhovskii Island has been discussed in a number of papers (Romanovskii, 1958a, 1958b; Vol'nov, 1975; Trufanov et al., 1979; Alekseev, 1989; Arkhangelov et al., 1996). Fossil insects from the New Siberian Islands (Faddeevsky and Bolshoi Lyakhovskii) were collected by A.A. Archangelov and studied by Kiselev (Kiselev and Nazarov, 2009). These samples are small, but important as rare information on a hard-to-rich region. Special samples of fossil insects were collected by me during a Russian–German expedition in 1999.

The site tested (Figs. 26, 27a) is a more than 10-km-long sea cliff on both sides of the Zimov'e River mouth. This area was visited by Arkhangelov. According to his unpublished research (Arkhangelov, personal communication), the oldest ice wedges are probably discovered there. He tested the basal unit of the section using the paleomagnetic and thermoluminescence methods and got applicable results: the dates 950 ± 250 and 980 ± 250 ka and reversed magnetics. One task of the expedition was reexamination of the oldest deposits and screening rodent bones for the biostratigraphic age determination.

The study of the section was complicated by a lack of unfrozen sediment; it was impossible to pick up large samples for screening. The samples were sufficient for fossil insects, but too small for rodents. Uranium–thorium sample from the cover peat has given the date 201 ± 3 ka (Schirrmeister et al., 2002a), which is close to the limiting case of the method.

A new stratigraphic scheme was proposed by Tumskoi (2012). He considers that the lower sediment with ice wedge (Fig. 27b) is the Middle Pleistocene Yukagir Formation (Table 2), which is correlated with early stages of the Keremesit Superhorizon. The unit is 1–3.5 up to 6-m-thick ice-rich silty sediment with small lenses of peat and inclusion of clastic bedrock. The unit is terminated by reddish residual soil of the Yukagir–Zimov'ie beds and, in places, by peat of the Zimov'e beds (Tumskoi, 2012).

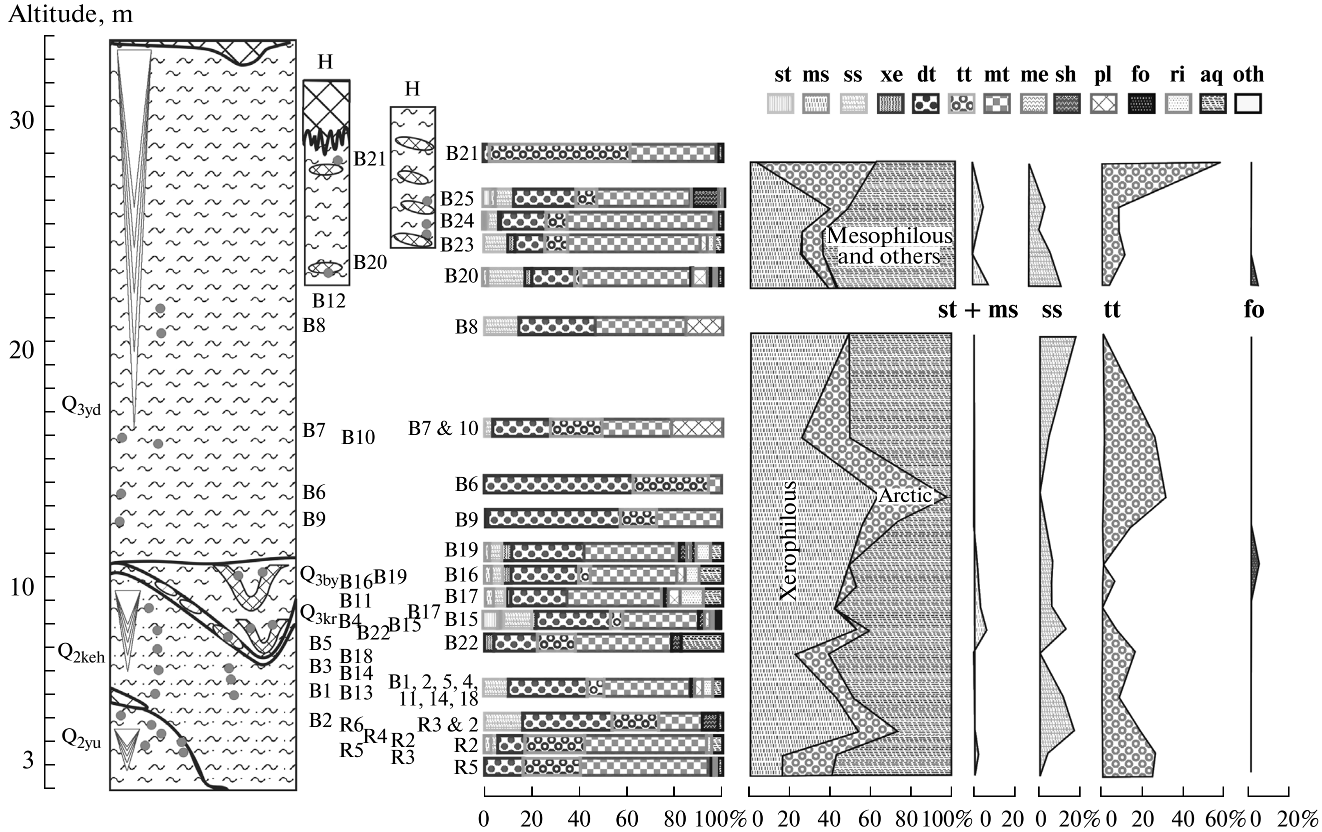


Fig. 26. Stratigraphic scheme and insect assemblages from the Bolshoi Lyakhovskii sites. For legend, see Figs. 15 and 16.

The next unit is the Middle Pleistocene Kuchchugui Formation (Figs. 27c–27f). It is up to 15 m thick and very distinct in the section. Originally, the formation was divided into two facies, subaerial and subaquatic Kuchchugui (Andreev et al., 2004). Both facies are ice poor. The first consists of gray silt with ground wedges and rare ice wedges; the second is a blue uniform silt bed (Fig. 27e). Tumskoi (2012) considers that both facies are aerial in origin; the difference is caused by the geological position of the deposits: the blue unit was located under thermokarst lakes and affected by melting and compression. Both are characterized by a poor organic content, but for tiny grass roots (Fig. 27f).

The Kuchchugui Formation is overlain in places by ice-rich silt with peat layers. This unit was described as the Bychchagy Formation (Tumskoi and Basilyan, 2009). It is represented only locally; the thickness is 5–8 m, but sometimes it is reduced to a single peat bed or absent. The age of the unit is uncertain; we have poor evidence of the paleoenvironment; the high ice content and presence of ice wedges is apparently indicative of rather cool conditions.

The last interglacial deposits are represented by a 10–12-m-thick gray silt unit with two ice wedge cast layers, the Krest-Yuryakh Formation (Ivanov, 1972; Andreev et al., 2004; Tumskoi, 2012). The ice wedge casts are filled with plant debris, including pieces of large shrubs, freshwater mollusk shells, and abundant fossil insects (Figs. 28a, 28b).

The Late Pleistocene is represented by a remarkable ice complex typical for high Arctic (Figs. 28d, 28e). The section looks as a wall of ice, with rare sediment inclusions. Such a subvertical surface provides difficulties in sampling, especially in the case of large volume screening; thus, insect samples were collected only in accessible places, mostly in the lower part of the unit. According to Tumskoi (2012), this unit belongs to the Edoma Superhorizon and includes two formations. The most of the sediment belongs to the Oiagoss Formation, which is the oldest for Edoma. Radiocarbon dating show variation from 40–30 ka to over limit value (Andereev et al., 2009). The youngest date was 28.71 ± 0.82 ka (Nagaoka et al., 1995). Recent investigations have shown that the last glacial deposits are also present in the section. Tumskoi (2012) believes that the top unit (Yana Formation) fills an erosive depression in Oiagoss deposits. This statement is supported by dating 22.32 ± 0.24 and 23.92 ± 0.18 ka (Wetterich et al., 2011).

The Holocene of Bolshoi Lyakhovskii is represented by different types, including low river flood-

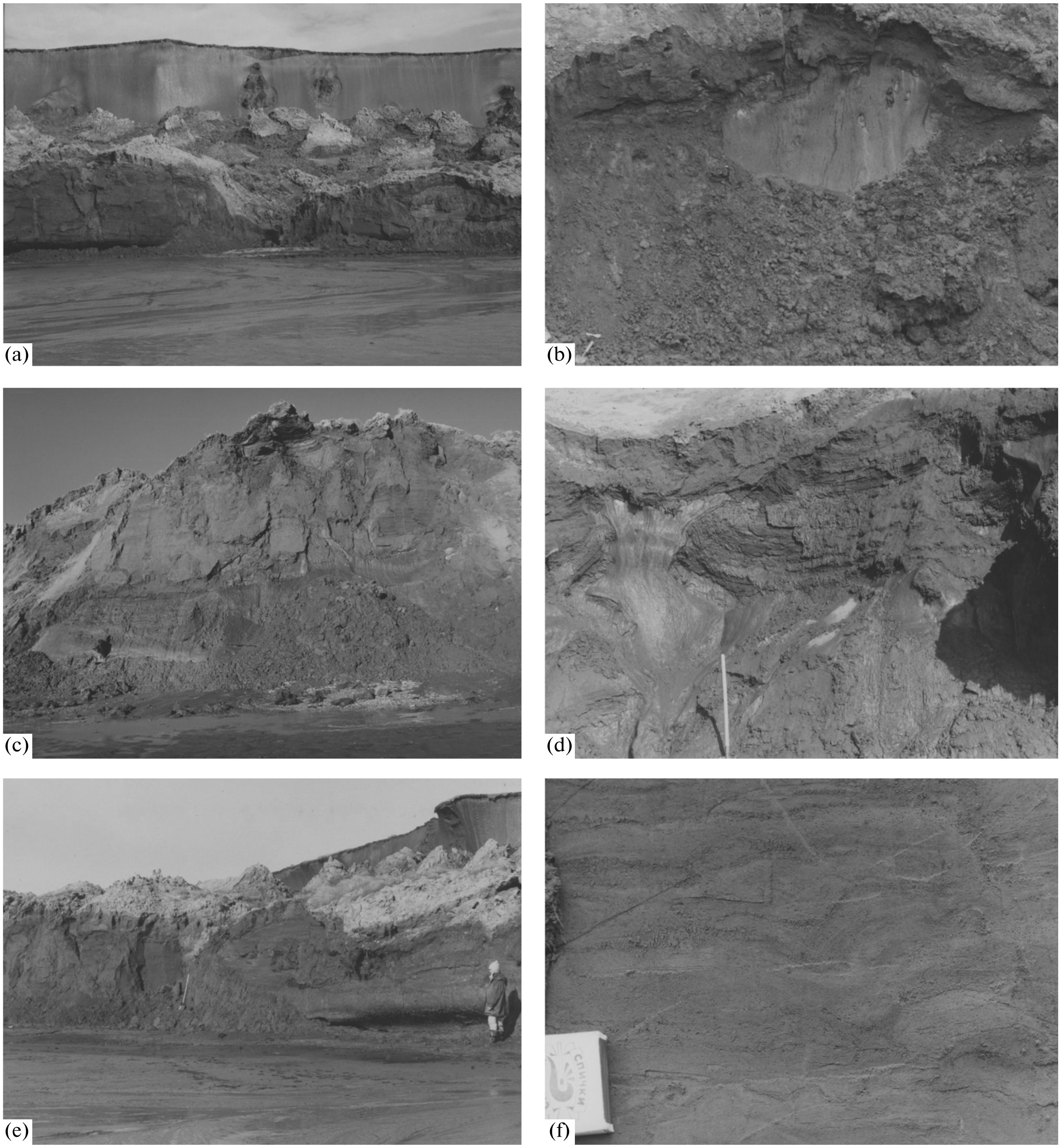


Fig. 27. Photograph of the Bolshoi Lyakhovskii sections (Middle Pleistocene): (a) Lyakhovskii section, general view, (b) Yukagir Formation with ice wedge, (c) contact between Yukagir and Kuchchugui formations, (d) Kuchchugui Formation with ice wedge, (e) yellow–gray and blue sands of the Kuchchugui Formation, (f) ground vein in Kuchchugui Formation.

plain terraces and alas complexes. Small lenses of the Holocene alases could be observed at the top of the Late Pleistocene Ice Complex. There are brown-gray silt bodies with peat and abundant remains of tall shrubs. The deposits are hard to reach, but melted sediment with peat and shrubs fell down from the ice wall, allowing the recognition of some features. Tall shrub from the Holocene bodies is well preserved shrub alder (*Duschekia* sp.). Vegetation of this sort strongly differs from the modern arctic tundra; this is a clear indicator

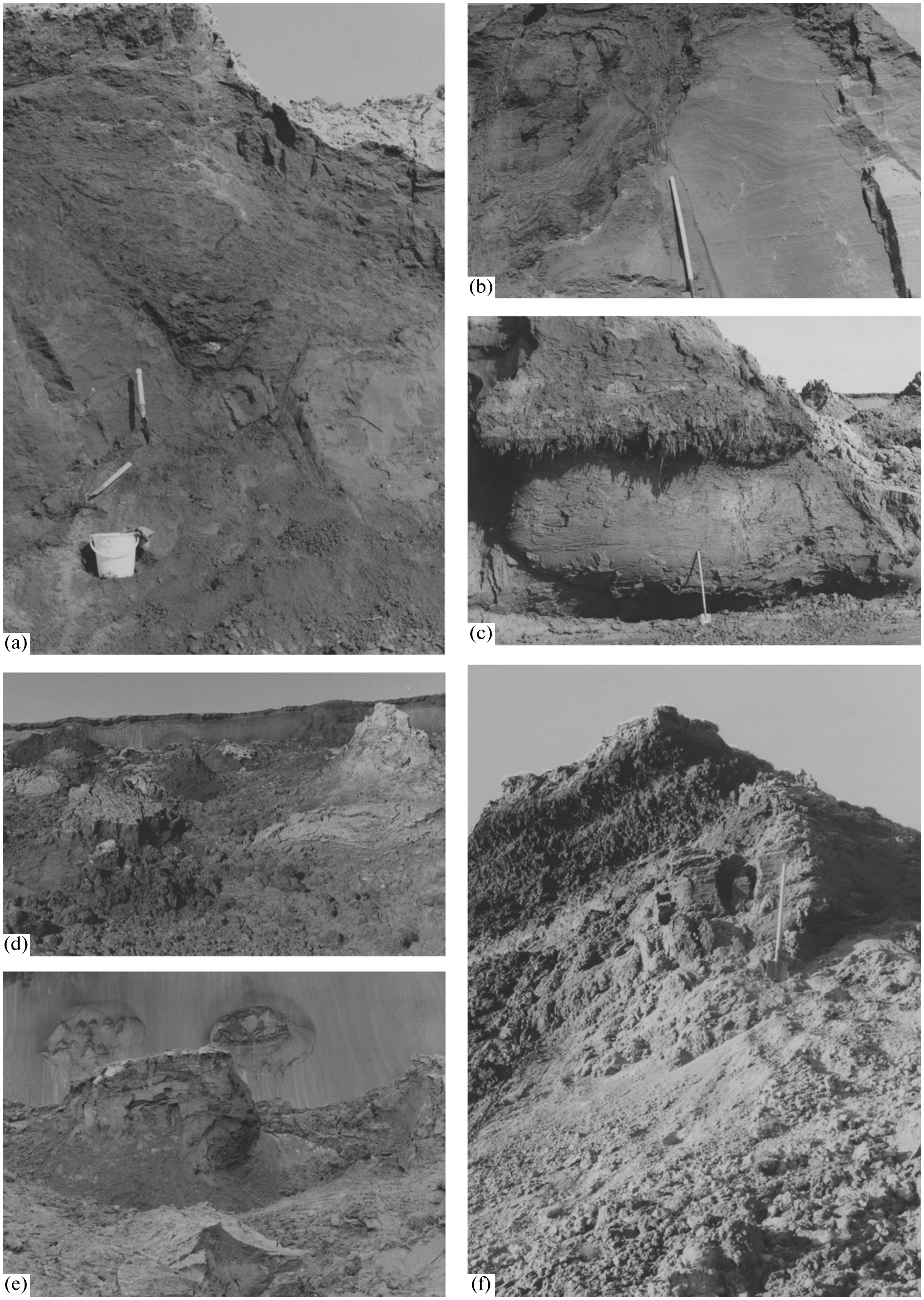


Fig. 28. Photograph of the Bolshoi Lyakhovskii sections (Late Pleistocene and Holocene): (a) Krest-Yuryakh ice wedge casts filled by clay, (b) Krest-Yuryakh ice wedge cast filled by plant debris, (c) contact of the Kuchchugui and Krest-Yuryakh formations, (d, e) Edoma Formation, (f) Holocene thermokarst lake deposits.

Table 26. Insects from the Bolshoi Lyakhovskii site (part 2)

Age	Kuchchugui Formation								Bychchytyy Suite	
Section L-	R17	R6			R18	R22		L11	L17	
Species/sample	B1	B3	B5	B4	B11	B13	B14	B18	B22	eco
Order Coleoptera										
Family Carabidae										
Subfamily Nebriinae										
Notiophilus aquaticus L.	–	–	–	–	–	–	–	–	1	**xe**
Subfamily Trechinae										
Bembidion (*Asioperyphus*) *umiatense* Lth.	–	–	–	–	–	–	–	1	–	**ri**
Subfamily Harpalinae										
Tribe Harpalini										
Dicheirotrichus mannerheimi Sahlb.	–	–	–	–	–	–	–	–	1	**dt**
Tribe Pterostichini										
Poecilus (*Derus*) *nearcticus* Lth.	–	–	–	1	–	–	–	–	1	**dt**
Pterostichus (*Cryobius*) *brevicornis* (Kby.)	–	–	–	1	–	–	–	1	2	**mt**
P. (*Cryobius*) *pinguedineus* Esch.	–	–	–	–	–	–	–	–	2	**mt**
P. (*Cryobius*) *ventricosus* Esch.	–	–	–	2	–	–	–	–	–	**mt**
Pterostichus (*Cryobius*) sp.	–	1	–	–	–	–	1	–	1	**mt**
Tribe Zabrini										
Amara interstitialis Dej.	–	–	–	–	–	–	1	–	–	**dt**
Curtonotus alpinus Payk.	1	1	3	4	1	1	2	1	4	**dt**
Family Dytiscidae										
Subfamily Agabinae										
Agabus lapponicus (Thoms.)?	–	–	–	–	–	–	–	–	1	**aq**
A. moestus (Curt.)	–	–	–	1	–	1	–	–	–	**aq**
Subfamily Hydroporinae										
Hydroporus acutangulus Thoms.?	–	–	–	–	–	–	–	–	2	**aq**
H. ex gr. *fuscipennis* Schaum.	–	–	–	–	–	–	–	–	3	**aq**
Family Leiodidae										
Subfamily Cholevinae										
Cholevinus sibiricus (Jean.)	–	1	–	–	–	–	–	–	–	**mt**
Family Staphylinidae										
Subfamily Omaliinae										
Eucnecosum tenue LeC.	–	–	–	–	–	1	–	1	–	**pl**
Subfamily Tachyporinae										
Tachinus arcticus Motsch.	–	1	3	2	–	–	3	–	8	**mt**
Family Byrrhidae										
Subfamily Byrrhinae										
Morychus viridis Kuzm. et Korot.	–	–	–	2	–	–	1	1	–	**ss**
Family Chrysomelidae										
Subfamily Chrysomelinae										
Chrysolina bungei Jac.	–	–	–	–	–	–	–	–	2	**tt**
Ch. magniceps (Sahlb.)	1	–	–	1	–	–	–	–	–	**mt**
Ch. subsulcata Mnnh.	–	1	1	–	–	–	–	–	3	**tt**

Table 26. (Contd.)

Age	Kuchchugui Formation								Bychchytyy Suite	
Section L-	R17	R6			R18	R22		L11	L17	eco
Species/sample	B1	B3	B5	B4	B11	B13	B14	B18	B22	
Hydrothassa hannoverana F.	–	–	–	–	–	–	–	1	–	**ri**
Family Curculionidae										
Subfamily Hyperinae										
Hypera diversipunctata Schrank.	–	–	–	1	–	–	–	–	–	**dt**
Subfamily Molytinae										
Tribe Lepyrini										
Lepyrus sp.	–	–	–	–	–	–	–	1	1	**sh**
Subfamily Curculioninae										
Tribe Rhamphini										
Isochnus arcticus Kor.	–	–	–	1	–	–	1	–	–	**tt**
Order Hymenoptera										
Hymenoptera gen. indet.	19	1	3	8	5	5	8	2	1	**oth**
Order Trichoptera										
Trichoptera gen. indet. (larvae)	–	–	–	–	5	4	2	1	1	**aq**
Order Diptera										
Family Chironomidae										
Chironomidae gen. indet.	–	–	–	–	–	–	2	2	–	**aq**
Family Tipulidae										
Tipulidae gen. indet. (larvae)	–	–	–	1	–	–	–	–	–	**oth**
Sum	2	5	7	16	1	3	9	7	32	

of a much warmer climate. The radiocarbon date of 7.37 ± 0.82 ka (Nagaoka et al., 1995) suggests the early Holocene age of the deposits.

Another type of alas deposits was observed at the top of the Krest-Yuryakh Formation. These structures are located in a long-lived depression. Ice Complex sediment was melted and compressed under great thermokarst lakes, so that the volume of underlying sediment decreased dramatically. The Holocene alas section starts from sandy deposits with plant debris and tall shrub remains; it gradually transforms into silty sediment with individual peat lenses; the section is terminated by a moss peat body up to 2–3 m thick. Radiocarbon data from the section show that the alas developed for at least several thousand years. The lower dates are 8.35 ± 0.05 and 8.865 ± 0.05 ka, the date from the top peat is 6.456 ± 0.174 ka (Andreev et al., 2009; Shirrmeister, personal communication), and one date from the lower lake sediment is 7.993 ± 0.183 ka (Kunitsky, 1998).

The insect samples were taken from each accessible unit (Tables 25–28). We collected 25 insect samples and six rodent samples (screened in sieves with 1 mm mesh), which contain fossil insects. The number of specimens varies widely, despite the equal volume of the screened sediment. Interglacial units: the Krest-Yuryakh Formation and early Holocene alas deposits are very rich in fossils; the Yukagir Formation and Edoma include a moderate number of fossil insects and Kuchchugui deposits are the poorest.

One insect and five rodent samples from several Yukagir Formation exposures were screened. The lowest sample (LR-17-R1) lacks insects. The next sample (LR-14-R5) was taken at elevation of 4 m above sea level. The assemblage is dominated by the mesophilous tundra group (57%), most of the specimens belong to a common tundra species, *Pterostichus* (*Cryobius*) *brevicornis* other specimens are *P.* (*Cryobius*) spp., *P.* (*Lenapterus*) *costatus*, *P.* (*Lenapterus*) *agonus*, and *Tachinus arcticus*. The second most frequent group is arctic insects (22%), including *Chrysolina tolli, Ch. subsulcata, Ch. magniceps,* and *Isochnus arcticus*. Xerophilous species play a minor role; only a few dry tundra species have been found here (**dt** = 16%). Steppe–tundra indicators are absent. This is a typical tundra assemblage. Only one exotic species, *Poecilus nearcticus,* is a distinction from the modern tundra entomofauna. Most of the species are cold resistant

Table 27. Insects from the Bolshoi Lyakhovskii site (part 3)

Age	Krest-Yuryakh				Edoma Formation						
Section L-	R22		L11		R18	R5		R18	R4	R10	
Species/sample	B15	B16	B17	B19	B9	B6	B7	B10	B8	B12	eco
Order Coleoptera											
Family Gyrinidae											
Gyrinus opacus Salb.	–	–	1	–	–	–	–	–	–	–	**aq**
Family Carabidae											
Subfamily Nebriinae											
Nebria frigida Sahlb.	–	–	2	–	–	–	–	–	–	–	**ri**
Notiophilus aquaticus L.	2	1	2	2	1	–	–	–	–	–	**xe**
Pelophila borealis Payk.	–	–	1	–	–	–	–	–	–	–	**mt**
Subfamily Carabinae											
Carabus kolymensis Kryzh. et Bud.	–	–	–	1	–	–	–	–	–	–	**ms**
C. shilenkovi O. Berlov	1	1	3	–	–	–	–	–	–	–	**dt**
Subfamily Elaphrinae											
Blethisa catenaria Brown	–	–	–	1	–	–	–	–	–	–	**mt**
Diacheila polita Fald.	2	2	3	–	–	–	–	–	–	–	**mt**
Elaphrus lapponicus Gyll.	–	–	–	1	–	–	–	–	–	–	**ri**
E. riparius L.	–	–	1	–	–	–	–	–	–	–	**ri**
Subfamily Trechinae											
Bembidion (*Asioperyphus*) *umiatense* Lth.	–	2	6	2	–	–	–	–	–	–	**ri**
B. (*Peryphanes*) *grapii* Gyll.	1	–	2	1	–	–	–	–	–	–	**dt**
B. (*Plataphus*) *hyperboraeorum* Munch	–	–	–	1	–	–	–	–	–	–	**ri**
Subfamily Harpalinae											
Tribe Harpalini											
Dicheirotrichus mannerheimi Sahlb.	2	2	1	–	–	–	–	–	–	–	**dt**
Harpalus vittatus kiselevi Kat. et Shil.	–	1	2	–	–	–	–	–	–	–	**ms**
H. vittatus vittatus Gebl.	–	–	2	–	–	–	–	–	–	–	**ms**
Tribe Lebiini											
Cymindis arctica Kryzh. et Em.	3	–	–	–	–	–	–	–	–	–	**st**
Tribe Platynini											
Agonum impressum Panz.	1	–	2	–	–	–	–	–	–	–	**ri**
Sericoda quadripunctata (DeG)	1	–	–	–	–	–	–	–	–	–	**ri**
Tribe Pterostichini											
Poecilus (*Derus*) *nearcticus* Lth.	2	–	3	–	2	–	–	–	–	–	**dt**
Pterostichus (*Cryobius*) *brevicornis* (Kby.)	20	4	24	8	–	1	–	–	–	–	**mt**
P. (*Cryobius*) *nigripalpis* Popp.	3	2	2	1	10	–	–	–	–	–	**dt**
P. (*Cryobius*) *pinguedineus* Esch.	5	–	6	2	3	–	–	–	2	–	**mt**
P. (*Cryobius*) *ventricosus* Esch.	2	4	2	2	–	–	–	–	–	–	**mt**
Pterostichus (*Cryobius*) sp.	3	4	14	5	16	–	–	–	2	–	**mt**
P. (*Lenapterus*) *agonus* Horn.	3	–	–	–	–	–	–	–	–	–	**mt**
P. (*Lenapterus*) *costatus* Men.	–	1	2	–	–	–	–	–	1	–	**mt**
P. (*Lenapterus*) *vermiculosus* Men.	–	–	4	1	–	–	–	–	–	–	**mt**
P. (*Tundraphilus*) *sublaevis* Sahlb.	–	2	3	2	–	–	–	–	1	–	**dt**
Stereocerus haematopus (Dej.)	3	–	3	1	–	–	–	–	1	–	**dt**

Table 27. (Contd.)

Age	Krest-Yuryakh				Edoma Formation						
Section L-	R22		L11		R18	R5		R18	R4	R10	
Species/sample	B15	B16	B17	B19	B9	B6	B7	B10	B8	B12	eco
P. (*Petrophilus*) *abnormis* Sahlb.	–	–	–	–	1	–	–	–	–	–	**dt**
P. (*Petrophilus*) *magus* Mnnh.	–	–	–	1	–	–	–	–	–	–	**fo**
P. (*Petrophilus*) *montanus* (Motsch.)	–	–	–	1	–	–	–	–	–	–	**dt**
P. (*Petrophilus*) *tundrae* Tschitsch.	–	–	–	1	–	–	–	–	–	–	**dt**
P. (*Petrophilus*) *eximius* Mor.	1	–	–	–	–	–	–	–	–	–	**dt**
Tribe Zabrini											
Amara interstitialis Dej.	1	–	–	1	–	–	–	–	–	–	**dt**
Curtonotus alpinus Payk.	46	11	23	8	44	19	8	1	15	7	**dt**
Family Dytiscidae											
Subfamily Agabinae											
Agabus moestus (Curt.)	–	1	–	2	–	–	–	–	–	–	**aq**
A. thomsoni (J.Sach.)	–	–	7	–	–	–	–	–	–	–	**aq**
SubfamilyColymbetinae											
Colymbetes dolabratus (Payk.)	2	1	2	1	–	–	–	–	–	–	**aq**
Subfamily Hydroporinae											
Hydroporus acutangulus Thoms.?	–	2	–	–	–	–	–	–	–	–	**aq**
H. ex gr. *fuscipennis* Schaum.	–	–	6	–	–	–	–	–	–	–	**aq**
Family Hydrophilidae											
Subfamily Helophorinae											
Helophorus sibiricus Motsch.	–	1	–	–	–	–	–	–	–	–	**aq**
H. splendidus Sahlb.	2	3	1	–	–	–	–	–	–	–	**aq**
Subfamily Hydrophilinae											
Berosus sp.	–	1	–	–	–	–	–	–	–	–	**aq**
Hydrobius fuscipes F.	–	–	1	1	–	–	–	–	–	–	**aq**
Subfamily Sphaeridiinae											
Cercyon sp.	–	–	6	–	–	–	–	–	–	–	**ri**
Family Leiodidae											
Subfamily Leiodinae											
Cyrtoplastus irregularis Rtt.?	–	–	2	–	–	–	–	–	–	–	**pl**
Subfamily Coloninae											
Colon sp.	–	–	1	–	–	–	–	–	–	–	**pl**
Subfamily Cholevinae											
Cholevinus sibiricus (Jean.)	4	4	5	1	1	–	8	–	9	–	**mt**
Family Staphylinidae											
Subfamily Omaliinae											
Eucnecosum tenue (LeC.)	1	1	3	–	–	–	8	–	9	–	**pl**
Micralymma brevilingue Schtd.	–	–	–	–	–	1	–	–	–	–	**dt**
Olophrum consimile Gyll.	3	4	16	6	–	–	–	–	–	–	**mt**
Subfamily Tachyporinae											
Tachinus arcticus Motsch.	24	9	10	1	7	1	3	–	8	4	**mt**
Tachyporus sp.	1	–	–	–	–	–	–	–	–	–	**pl**

Table 27. (Contd.)

Age	Krest-Yuryakh				Edoma Formation						
Section L-	R22		L11		R18	R5		R18	R4	R10	
Species/sample	B15	B16	B17	B19	B9	B6	B7	B10	B8	B12	eco
Subfamily Steninae											
Stenus sp.	–	–	1	–	–	–	–	–	–	–	**ri**
Subfamily Paederinae											
Lathrobium sp.	1	–	2	–	–	–	–	–	–	–	**pl**
Subfamily Staphylininae											
Philonthus sp.	–	–	1	1	–	–	–	–	–	–	**pl**
Quedius sp.	–	–	1	–	–	–	–	–	–	–	**pl**
Staphylininae gen. indet.	–	1	–	–	–	–	–	–	–	–	**pl**
Family Scarabaeidae											
Aegalia kamtschatica Motsch.	1	1	1	–	–	–	–	–	–	–	**ri**
Aphodius sp.	–	3	2	1	–	–	–	–	–	–	**xe**
Family Byrrhidae											
Subfamily Byrrhinae											
Morychus viridis Kuzm. et Korot.	29	4	12	4	–	–	–	1	8	–	**ss**
Simplocaria arctica Popp.	1	5	7	2	–	–	–	–	–	–	**dt**
S. semistriata F.	–	–	–	1	–	–	–	–	–	–	**dt**
Subfamily Syncalyptinae											
C*urimopsis cyclolepidia* Muenst.	1	–	1	–	–	–	–	–	–	–	**dt**
Family Melyridae											
Troglocollops arcticus L. Medv.	–	–	2	–	–	–	–	–	–	–	**ms**
Family Coccinellidae											
Subfamily Coccinellinae											
Scymnus sp.	1	–	–	–	–	–	–	–	–	–	**ri**
Coccinelinae gen. Indet	1	–	–	–	–	–	–	–	–	–	**oth**
Family Lathridiidae											
Corticaria sp.	2	1	1	–	–	–	–	–	–	–	**pl**
Family Chrysomelidae											
Subfamily Chrysomelinae											
Chrysolina brunnicornis bermani Medv.	3	–	–	–	–	–	–	–	–	–	**st**
Ch. bungei Jac.	1	1	–	–	–	–	–	–	–	1	**tt**
Ch. septentrionalis Men.	1	2	–	1	2	–	–	–	–	–	**mt**
Ch. subsulcata Mnnh.	6	2	–	–	–	10	8	1	–	3	**tt**
Chrysolina tolli Jac.	4	–	–	–	4	–	–	–	–	–	**tt**
Hydrothassa glabra Hbst	–	–	1	–	–	–	–	–	–	–	**ri**
H. hannoverana F.	–	1	–	1	–	–	–	–	–	–	**ri**
Phaedon concinnus Steph.	–	–	–	1	–	–	–	–	–	–	**me**
Phratora sp.	–	–	1	–	–	–	–	–	–	–	**sh**
Subfamily Eumolpinae											
Bromius obscurus L.	–	–	1	–	–	–	–	–	–	–	**me**
Family Brentidae											
Subfamily Apioninae											
Hemitrichapion tschernovi T.-M.	–	1	–	1	–	–	–	–	–	–	**dt**

Table 27. (Contd.)

Age	Krest-Yuryakh				Edoma Formation						
Section L-	R22		L11		R18	R5		R18	R4	R10	
Species/sample	B15	B16	B17	B19	B9	B6	B7	B10	B8	B12	eco
Family Brachyceridae											
Subfamily Erirhininae											
Notaris bimaculatus F.	1	1	1	–	–	–	–	–	–	–	**ri**
Family Curculionidae											
Subfamily Ceutorhynchinae											
Pelenomus sp.	–	–	1	–	–	–	–	–	–	–	**ri**
Tribe Sitonini											
Sitona borealis Kor.	2	–	1	–	–	–	–	–	–	–	**dt**
Subfamily Hyperinae											
Hypera diversipunctata Schrank.	2	1	–	2	–	–	–	–	–	–	**dt**
H. ornata Cap.	1	1	3	–	–	–	–	–	–	–	**dt**
Hypera sp.	–	–	–	–	–	–	–	–	1	–	**dt**
Subfamily Lixinae											
Tribe Cleonini											
Coniocleonus sp.	2	1	1	–	–	–	–	–	–	–	**ms**
Stephanocleonus eruditus Faust	4	–	–	–	–	–	–	–	–	–	**st**
S. fossulatus F.-W.	1	–	–	–	–	–	–	–	–	–	**st**
Subfamily Molytinae											
Tribe Lepyrini											
Lepyrus nordenskioeldi Faust	2	–	1	2	–	–	–	–	–	–	**sh**
Subfamily Curculioninae											
Tribe Elliscini											
Dorytomus imbecillus Fst.	1	–	1	–	–	–	–	–	–	–	**sh**
Tribe Rhamphini											
Isochnus arcticus Kor.	–	1	–	–	11	–	–	–	–	–	**tt**
I. flagellum Erics.	–	–	1	–	–	–	–	–	–	–	**sh**
Order Heteroptera											
Family Corixidae											
Sigara sp.	–	–	–	–	–	–	–	–	–	1	**aq**
Family Saldidae											
Salda sp.	–	1	–	–	–	–	–	–	–	–	**ri**
Order Hymenoptera											
Hymenoptera gen. indet.	8	9	2	1	3	5	8	2	14	6	**oth**
Order Megaloptera											
Family Sialidae											
Sialis sp. (larvae)	1	–	–	–	–	–	–	–	–	–	**ri**
Order Trichoptera											
Trichoptera gen. indet. (larvae)	2	–	–	–	–	6	7	–	–	8	**aq**
Order Diptera											
Family Chironomidae											
Chironomidae gen. indet. (larvae)	2	–	1	–	–	4	2	–	1	3	**aq**
Family Tipulidae											
Tipulidae gen. indet. (larvae)	–	–	–	–	3	–	–	–	–	–	**oth**
Diptera fam. indet. (puparia)	–	–	1	–	1	1	2	–	1	–	**oth**
Sum	207	92	218	72	102	32	35	3	57	16	

Table 28. Insects from the Bolshoi Lyakhovskii site, Holocene

Age	Holocene					
Section L-	L17		L1			eco
Species/sample	B20	B21	B23	B24	B25	
Order Coleoptera						
Family Carabidae						
Subfamily Nebriinae						
Nebria frigida Sahlb.	4	–	–	–	–	**ri**
Notiophilus aquaticus L.	5	–	1	1	–	**xe**
Subfamily Carabinae						
Carabus shilenkovi O. Berlov	1	–	–	–	–	**dt**
Subfamily Elaphrinae						
Diacheila polita Fald.	1	–	–	1	–	**mt**
Elaphrus riparius L.	–	–	1	–	–	**ri**
Subfamily Scaritinae						
Dyschiriodes melancholicus Putz.	1	–	–	–	–	**ri**
Subfamily Trechinae						
Bembidion (*Asioperyphus*) *umiatense* Lth.	2	–	–	–	1	**ri**
B. (*Peryphanes*) *dauricum* Motsch.	2	–	–	2	1	**dt**
Subfamily Harpalinae						
Tribe Harpalini						
Harpalus vittatus kiselevi Kat. et Shil.	–	–	–	2	–	**ms**
Tribe Pterostichini						
Poecilus (*Derus*) *nearcticus* Lth.	3	–	–	2	1	**dt**
Pterostichus (*Cryobius*) *brevicornis* (Kby.)	58	–	3	35	13	**mt**
P. (*Cryobius*) *nigripalpis* Popp.	–	–	–	6	2	**dt**
P. (*Cryobius*) *pinguedineus* Esch.	9	4	2	7	7	**mt**
P. (*Cryobius*) *ventricosus* Esch.	7	–	2	4	2	**mt**
Pterostichus (*Cryobius)* sp.	40	–	2	15	47	**mt**
P. (*Lenapterus*) *agonus* Horn.	–	3	–	2	1	**mt**
P. (*Lenapterus*) *costatus* Men.	1	–	–	–	2	**mt**
P. (*Lenapterus*) *vermiculosus* Men.	3	–	–	–	–	**mt**
P. (*Tundraphilus*) *sublaevis* Sahlb.	2	–	–	1	7	**dt**
Stereocerus haematopus (Dej.)	4	–	1	–	3	**dt**
P. (*Petrophilus*) *abnormis* Sahlb.	–	–	–	–	1	**dt**
P. (*Petrophilus*) *montanus* (Motsch.)	1	–	–	–	1	**dt**
Tribe Zabrini						
Amara interstitialis Dej.	–	–	–	–	1	**dt**
Curtonotus alpinus Payk.	30	1	3	17	32	**dt**
C. bokori Csiki	–	–	–	1	–	**dt**
Family Dytiscidae						
Subfamily Agabinae						
Agabus moestus (Curt.)	3	–	–	1	1	**aq**
Subfamily Hydroporinae						
Hydroporus acutangulus Thoms.?	1	–	–	–	–	**aq**
Hydroporus sp.	–	1	1	1	–	**aq**

Table 28. (Contd.)

Age	Holocene					
Section L-	L17		L1			eco
Species/sample	B20	B21	B23	B24	B25	
Family Hydrophilidae						
Subfamily Helophorinae						
Helophorus splendidus Sahlb.	–	–	–	2	–	**aq**
Subfamily Hydrophilinae						
Hydrobius fuscipes F.	1	–	–	–	–	**aq**
Family Leiodidae						
Subfamily Leiodinae						
Cyrtoplastus irregularis Rtt.?	–	–	–	1	–	**pl**
Leiodes sp.	–	–	–	–	1	**pl**
Family Staphylinidae						
Subfamily Omaliinae						
Eucnecosum tenue LeC.	13	–	1	–	–	**pl**
Olophrum consimile Gyll.	4	–	–	1	–	**mt**
Subfamily Tachyporinae						
Tachinus arcticus Motsch.	28	9	9	60	6	**mt**
T. brevipennis Sahlb.	–	–	–	1	–	**mt**
Subfamily Paederinae						
Lathrobium sp.	1	–	–	–	–	**pl**
Staphylininae gen. indet.	–	–	–	1	–	**pl**
Family Scarabaeidae						
Aphodius sp.	1	–	–	–	–	**xe**
Family Byrrhidae						
Subfamily Byrrhinae						
Morychus viridis Kuzm. et Korot.	53	–	3	12	15	**ss**
Simplocaria arctica Popp.	5	–	–	2	–	**dt**
S. semistriata F.	1	–	–	1	–	**mt**
Subfamily Syncalyptinae						
C*urimopsis cyclolepidia* Muenst.	1	–	–	2	–	**dt**
Family Melyridae						
Troglocollops arcticus L. Medv.	1	–	–	–	–	**ms**
Family Lathridiidae						
Corticaria sp.	5	–	–	–	–	**pl**
Family Chrysomelidae						
Subfamily Chrysomelinae						
Ch. bungei Jac.	–	2	–	–	–	**tt**
Ch. magniceps (Sahlb.)	–	22	3	5	9	**tt**
Ch. septentrionalis Men.	3	–	–	1	1	**mt**
Ch. subsulcata Mnnh.	–	–	–	4	5	**tt**
Chrysolina tolli Jac.	–	2	–	–	4	**tt**
H. hannoverana F.	2	–	–	–	–	**ri**
Phaedon concinnus Steph.	–	–	–	–	1	**me**
Phratora polaris Schn.	1	–	–	–	9	**sh**

Table 28. (Contd.)

Age	Holocene					
Section L-	L17		L1			eco
Species/sample	B20	B21	B23	B24	B25	
Family Brentidae						
Subfamily Apioninae						
Hemitrichapion tschernovi T.-M.	4	–	–	1	–	**dt**
Mesotrichapion wrangelianum Korot.	–	–	–	4	–	**dt**
Apion arcticum Kor.	–	–	–	–	1	**dt**
Apioninae gen. indet.	1	–	–	–	–	**dt?**
Family Brachyceridae						
Subfamily Erirhininae						
Notaris bimaculatus F.	1	–	–	1	1	**ri**
Family Curculionidae						
Subfamily Ceutorhynchinae						
Pelenomus sp.	–	–	–	1	–	**ri**
Tribe Sitonini						
Sitona borealis Kor.	3	–	–	1	1	**dt**
Subfamily Hyperinae						
Hypera diversipunctata Schrank.	1	–	–	–	1	**dt**
H. ornata Cap.	2	–	–	2	1	**dt**
Subfamily Lixinae						
Tribe Cleonini						
Coniocleonus sp.	1	–	–	–	5	**ms**
Stephanocleonus eruditus Faust	1	–	–	–	5	**st**
Stephanocleonus sp.	–	–	–	–	2	**st**
Subfamily Molytinae						
Tribe Lepyrini						
Lepyrus nordenskioeldi Faust	2	–	–	–	13	**sh**
Subfamily Curculioninae						
Tribe Elliscini						
Dorytomus imbecillus Fst.	–	–	–	–	2	**sh**
Dorytomus sp.	1	–	–	–	–	**sh**
Tribe Rhamphini						
Isochnus arcticus Kor.	6	–	–	8	–	**tt**
Order Hymenoptera						
Family Formicidae						
Leptothorax acervorum F.	1	–	–	–	–	**fo**
Hymenoptera gen. indet.	3	2	–	2	–	**oth**
Order Diptera						
Family Chironomidae						
Chironomidae gen. indet. (larvae)	1	–	–	–	–	**aq**
Family Tipulidae						
Tipulidae gen. indet. (larvae)	–	–	–	1	–	**oth**
Sum	322	44	32	209	205	

and could live in this site; however, three species from the assemblage, i.e., *Helophorus splendidus, Hydrothassa hannoverana,* and *Lepyrus nordenskioeldi* are indicative of less severe conditions. In my opinion, the environment in that time was close to the modern state, or slightly warmer.

The next sample (LR-14-R6) comes from elevation of 4.4 m. The sample is poor in insects and close to the previous one, but we have also recorded singular steppe–tundra indicator here, presumably meadow–steppe weevil *Coniocleonus* sp.

Other samples from the Yukagir Formation are also not rich. All of them are dominated by tundra species and include arctic species. In addition, all upper samples (LR-17-R4, B2, R3, R2) contain the group **ss** (*Morychus viridis*). The alteration of "wet" and "dry" conditions shifts towards "more dry" environments (Fig. 26). The upper assemblages belong to the **TU/XE** type, mostly tundra with restricted steppe–tundra elements. Such an entomofauna, with a weak steppe influence and high role of cold resistant species fits well in the paleogeographic position of the site at the margin of unglaciated plain in the north of western Beringia (Tumskoi, 2012). We have not recorded true steppe species or other indicators of high summer temperatures. The environment was more or less close to the modern one, but the climate was probably less affected by open sea moisture. Perhaps, the closest modern analogue of the Middle Pleistocene environment of Bolshoi Lyakhovskii could be the western Chukotka Peninsula, where steppe–tundra relicts, such as *Morychus viridis* and *Poecilus nearcticus* still survive.

The Kuchchugui Formation has been tested in different exposures always with minimum result. A bucket of screened sediment gives half of spoon organic matter, mostly tiny grass roots. Fossil insects were extremely rare in all samples. Most of them belong to flying insects, such as parasitic wasps or flies. We had to combine several Kuchchugui samples to estimate the contribution of particular ecological groups. This combined assemblage includes almost equal amount of tundra groups; **mt** = 36% and **dt** = 39%; the third group is **tt** = 16%; the steppe tundra indicators are represented by individual remains of *Morychus viridis*.

The samples taken from bluish silt under Krest-Yuryakh ice wedge casts are even poorer. The principal ecological composition is close to that of typical Kuchchugui deposits. There is only little difference between insect assemblages from the two Middle Pleistocene units, the Yukagir and Kuchchugui formations in the Lyakhovskii fossil record.

One small sample (LL-17-B22) was taken from the Bychchagy Formation. Fossil insects are not numerous, but diverse. It has yielded tundra and aquatic species: **mt** = 39%, **dt** = 21%, **tt** = 15%, **aq** = 18%; one specimen is the shrub weevil *Lepyrus* sp. The assemblage is indicative of tundra environment, probably corresponding to less severe conditions than at the present time.

The Krest-Yuryakh Formation contrasts dramatically with the older and younger deposits. The sediment is overfull with organic matter. The concentration of fossil insects is rather high, so that fossils are visible without screening. Fallen blocks of the sediment from Krest-Yuryakh cause colorful fossil insect blanket on the sea water. We took half of the usual volume for screening.

A total of four insect samples from two Krest-Yuryakh sections were taken. In section LR-22, we took sample LR-22-B15 from elevation of 2.5 m (first ice wedge cast) and sample LR-22-B16 from elevation of 4 m (second ice wedge cast). Another section (LL-11) was tested similarly, involving a sample from the lower ice wedge cast (LL-11-B17, elevation of 4 m) and sample LL-11-B19 from the second ice wedge cast, elevation 7 m. Despite the elevation difference, these levels are correlated well.

Assemblage LR-22-B15 is equally dominated by tundra species: **mt** = 32% (*Pterostichus* (*Cryobius*) *ventricosus., P.* (*C.*) *pinguedineus, P.* (*C.*) *brevicornis, P. agonus, Diacheila polita, Cholevinus sibiricus*, *Olophrum consimile, Tachinus arcticus, Chrysolina septentrionalis*) and **dt** = 32% (*Curtonotus alpinus, Carabus shilenkovi, Poecilus nearcticus, Pterostichus (Cryobius) nigripalpis, P. (Petrophilus) eximius, Stereocerus haematopus, Amara interstitialis Dicheirotrichus mannerheimi*, *Simplocaria arctica, Curimopsis cyclolepidia*, *Sitona borealis, Hypera ornata, H. diversipunctata*). Arctic species play a minor role, only 3% (*Chrysolina subsulcata, Ch. bungei*). Some insects belong to the plant litter group (*Tachyporus* sp., *Lathrobium* sp., and *Corticaria* sp.) These insects are more typical for the forest zone or shrub tundra. At the same time, the assemblage contains a significant amount of the steppe–tundra indicators, such as *Coniocleonus* sp., (group **ms** = 1%), *Cymindis arctica, Chrysolina brunnicornis bermani, Stephanocleonus eruditus, S. fossulatus* (group **st** = 5%), and *Morychus viridis* (15%). Some species from shrub, riparian, and aquatic groups are relatively thermophilous, including *Dorytomus imbecillus, Colymbetes dolabratus, Aegalia kamtschatica, Agonum impressum, Sericoda quadripunctata, Scymnus* sp., and *Notaris bimaculatus.* This suggests that the fauna was formed under mild climatic conditions. The thermophilous species, plant litter group, and species diversity of tundra species are evidence that the climate was warmer than at present. An increase in the steppe group is an interesting feature. In the Krest-Yuryakh interglacial fauna, warming allowed the establishment of steppe–tundra environment typical for other regions.

Sample LR-22-B16 come from the upper ice wedge cast of the section. The insect assemblage is close to the previous one, but less affected by steppe insects; **ms** = 4%, **ss** = 4%. The main group in the assemblage is **mt** = 37% (*Pterostichus* (*Cryobius*) *ven-*

tricosus, P. (*C.*) *brevicornis, P. costatus, Diacheila polita, Cholevinus sibiricus, Olophrum consimile, Tachinus arcticus*, *Chrysolina septentrionalis*). Dry tundra species (26%) are various, including *Curtonotus alpinus, Carabus shilenkovi, Pterostichus sublaevis, P. (Cryobius) nigripalpis, Dicheirotrichus mannerheimi*, *Hemitrichapion tschernovi, Hypera ornata,* and *H. diversipunctata*. The assemblage includes the **tt** group (5%) (*Chrysolina subsulcata, Ch. bungei, Isochnus arcticus*); **aq** = 9%, **ri** = 5%, **pl** = 3%. This fauna from the upper horizon is indicative of cooling. Species diversity is still high for local faunas, but thermophilous species gradually disappeared from the record.

Another section with Krest-Yuryakh deposits is situated 3.3 km apart from the previous one. The lower sample (LL-11-B17) is correlated with LR-22-B15. The samples are similar in species diversity and ecological structure; **mt** = 40%, **dt** = 24%, **ms** = 2%, **ss** = 6%, **st** = 1%. The assemblage contains a number of thermophilous species, such as *Agabus thomsoni, Colymbetes dolabratus, Gyrinus opacus, Hydrobius fuscipes, Elaphrus riparius, Nebria frigida, Agonum impressum, Cyrtoplastus irregularis, Eucnecosum tenue, Lathrobium* sp., *Philonthus* sp., *Quedius* sp., *Aegalia kamtschatica, Hydrothassa glabra,* and *Notaris bimaculatus*.

The upper sample (LL-11-B19) is correlated with LR-22-B16. We can see a similar trend in faunal changes, i.e., a decrease in species diverse of thermophilous species and the absence of the **st** group. Both samples from the LL-11 site lack arctic species.

The Krest-Yuryakh Formation is evidently an interglacial unit. The combination of increasing steppe–tundra influence with warming is a unique feature which is unusual for other localities. A northern treeless land provides refuges for the steppe–tundra flora and fauna, which required certain summer warm supply and defeated competition with the forest.

The Late Pleistocene Oiagoss Formation was tested by six insect samples. Screening shows little organic content in the sediment, but some samples contain sufficient number of fossil insects.

The first sample (LR-18-B9) was taken from the lower part of the Ice Complex at the elevation of 13.2 m, just above the Kuchchugui unit. It is similar to the samples from Edoma. The ecological structure of the insect assemblage is very simple. Only tundra species are present; the assemblage is dominated by the **dt** group, 58% (*Curtonotus alpinus, Poecilus nearcticus, Pterostichus abnormis, P.* (*Cryobius*) *nigripalpis*); **mt** = 27% (*Pterostichus* (*Cryobius*) sp., *P.* (*C.*) *pinguedineus, Cholevinus sibiricus, Tachinus arcticus, Chrysolina septentrionalis*) and **tt** = 15% (*Chrysolina tolli, Isochnus arcticus*). All species from this short list are cold resistant. The environment was close to the modern one.

The next two samples (LR-5-B6 and LR-5-B7) from elevation of 14.5–17 m are poor, similar in composition. They are also close to the modern environment. Sample LR-18-B10 from elevation of 16.8 m has yielded only three insect specimens, but it is remarkable that one of them is a steppe–tundra indicator, *Morychus viridis*. This means that steppe–tundra species still existed there during the cold stages of the Late Pleistocene.

Sample LR-4-B8 comes from the upper part of the accessible Edoma section, elevation of 21.4 m. The sample is not rich in fossils and the species composition is poor. The ecological structure is close to previous ones. The upper sample (LR-18-B12) from elevation of 22.3 m has yielded only a few specimens of the **mt, dt**, and **tt** groups.

Insect faunas from Lyakhovskii Edoma is usually indicative of conditions close to the modern tundra environment. Only weak traces of steppe–tundra fauna have been observed. The summer temperature was probably around modern one, not lower.

3.3b1. Lyakhovskii Island, Holocene

Holocene insects come from two sites, a low floodplain terrace of the Zimov'e River near its mouth (site LL-1, three samples) and alas deposits (site LL-17, two samples). All samples are rich (Table 28).

Sample LL-17-B20 was taken from the lower horizon of the Holocene alas complex at elevation of 8.5 m (Figs. 26, 28f). The lower sandy bed is full of plant debris and shrub alder remains. Fossil insects are abundant; the sample is the richest one among all insect samples of Lyakhovskii. The assemblage is dominated by the **mt** group (48%) (*Pterostichus* (*Cryobius*) *brevicornis, P.* (*C.*) *ventricosus, P.* (*C.*) *pinguedineus, P.* (*Cryobius*) spp., *P. vermiculosus, P. costatus, Diacheila polita, Cholevinus sibiricus*, *Olophrum consimile, Tachinus arcticus, Chrysolina septentrionalis*). The group is dominated by *Pterostichus* (*Cryobius*) *brevicornis*. Another tundra group **(dt)** plays a less important role (19%), but shows a higher species diversity (*Curtonotus alpinus, Carabus shilenkovi, Bembidion dauricum, Poecilus nearcticus, Pterostichus haematopus, P. sublaevis, Simplocaria arctica, S. semistriata, Curimopsis cyclolepidia, Hemitrichapion tschernovi, Sitona borealis, Hypera ornata, H. diversipunctata*). The third tundra group **tt** is minor (2%); it only includes the weevil *Isochnus arcticus*. The ecological structure of the assemblage is complex (Fig. 26); it includes the **pl, fo, sh, aq**, and **ri** groups; many species of these groups are thermophilous: *Dyschiriodes melancholicus*, *Eucnecosum tenue*, *Lathrobium* sp., *Corticaria* sp., *Hydrobius fuscipes, Hydrothassa hannoverana, Phratora polaris, Dorytomus* sp., and *Notaris bimaculatus*. The ant *Leptothorax acervorum* (**fo** group) is not a direct indicator of forest vegetation; modern distribution of this ant is restricted mostly to the forest zone, but can live also in the forest–tundra or, rarely, in shrub tundra. All of these thermophilous species are indicative of warm climate, possibly sufficiently warm for the forest; however, the absence of tree remains and tree-related insects suggests that forest did not reach this northern area in the early Holocene. The environment was close to the last interglacial one reconstructed based on the Krest-Yuryakh Formation. Insect assemblages are similar in ecological structure. The same strange feature, an increase in steppe component, is observed in the early Holocene entomofauna. The assemblage contains the steppe weevil *Stephanocleonus eruditus*, meadow–steppe *Troglocollops arcticus* and *Coniocleonus* sp., and a high proportion (16%) of *Morychus viridis*. As compared with the previous Late Pleistocene assemblages from the Oiagoss Formation (only rare *Morychus viridis*), the early Holocene fauna shows a considerable increase in the role of steppe taxa. This means that the climate had become sufficiently warm for the existence of steppe–tundra, which could have developed on a treeless land.

This zonal feature provided refuges for steppe–tundra ecosystems during warming. The high Arctic became the last area where large Pleistocene mammals survived until recently (Vartanyan et al., 1993; Boeskorov, 2004).

The upper sample from site LL-17 came from peaty silt at elevation of 13.5 m under a thick solid peat body. This top unit is much younger and its insect assemblage is sharply distinguished by the ecological structure. The assemblage is dominated by arctic species: *Chrysolina tolli, Ch. bungei,* and *Ch. magniceps*. These leaf beetles were recently abundant in Lyakhovskii. The fossils are well preserved, but many elytra are abnormally distorted, probably because of the extreme cold. Other insects belong to the **mt** group (*Pterostichus* (*Cryobius*) *pinguedineus, Pterostichus agonus, Tachinus arcticus)*, singular xerophilous tundra ground beetle *Curtonotus alpinus* and singular aquatic beetle *Hydroporus* sp. The environment was close to the modern one.

Samples from the river terrace are probably stratigraphically intermediate between two alas samples. The first sample from site LL-1 comes from elevation of 1 m. The sample is not abundant, but species diversity is high for the Lyakhovskii sites. It contains some thermophilous species (*Elaphrus riparius, Eucnecosum tenue*) and the steppe–tundra indicator *Morychus viridis*.

The next sample was taken 0.5 m above the first one. The sample is richer, but it is similar in ecological composition to the previous assemblage. The assemblage is dominated by the group **mt** (62%) (*Pterostichus* (*C.*) *brevicornis, P.* (*C.*) *ventricosus, P.* (*Cryobius*) spp.*, P. agonus, Diacheila polita, Cholevinus sibiricus, Olophrum consimile, Tachinus arcticus, Chrysolina septentrionalis*). The second most abundant group is **dt** (20%); the third is **tt** –(8%). We have recorded a number of thermophilous species (*Notaris bimaculatus, Cyrtoplastus irregularis, Helophorus splendidus, Pelenomus* sp.) and the steppe–tundra indicator *Morychus viridis* (5%).

The last sample from the terrace comes from elevation of 2.3 m. The assemblage is rich and species diverse. The ecological structure is very close to the previous ones.

All three insect assemblages are indicative of a warmer climate than at present. The great number of thermophilous species suggests that environments were close to shrub tundra or typical tundra. Even the weevils *Sitona borealis* and *Hypera diversipunctata,* which are common for Beringia, are exotic for the local fauna. These weevils feed on legumes, which are absent in the modern flora of the island.

All insect assemblages studied in Lyakhovskii Island differ from southern faunas. There is no one strong steppe–tundra type of assemblage here. The steppe group plays a minor role or absent; many assemblages are dominated by the mesohygrophilous tundra group; the arctic group is important; and the species diversity is low. Only interglacial faunas show a high species diversity comparable to that of southern faunas. Usual environments of the High Arctic was more tundra-like than steppe–tundra, but the situation changed during interglacials. Thus, a lack of warm supply was a critical factor for the northern part of Beringia.

3.3c. Oiagoss Yar

Fossil insects from Oiagoss Yar (Figs. 1, 6) were studied by Kiselev (Kiselev and Nazarov, 2009). Unfortunately, the samples have no clear age reference (Late Pleistocene). They probably come from the Ice Complex. The fossil insect assemblages studied by Kiselev confirm the Late Pleistocene age of the sediment. The assemblages contain common Late Pleistocene species, including the steppe–tundra indicators (*Morychus viridis, Stephanocleonus eruditus*) and arctic species typical for the north (*Chrysolina tolli, Isochnus arcticus*), while thermophilous species are absent.

The sample studied here (Table 29) were collected by F. Kienast in 2002 during a Russian–German expedition (Kienast et al., 2011). The site is located between the Svyatoi Nos Cape and Merkushina Strelka Peninsula. The sample comes from an ice wedge cast overfull with freshwater mollusks, seeds, and insects at elevation of 3.5 m above sea level. This unit belongs to the Krest-Yuryakh Formation described above (see the Lyakhovskii section). The samples were originally taken for pollen and plant macrofossil analysis; thus, the weight of the sample (0.5 kg) was too small for insect study, but the sediment was extra rich in insect fossils. The fossils are well preserved. The assemblage studied is dominated by insects associated with humid tundra (25%), dry tundra (19%), aquatic (13%), and riparian (13%) habitats. The steppe–tundra indicators are present here, but relatively rare: a few specimens of *Morychus viridis* and meadow–steppe *Troglocollops arcticus,* while true steppe insects are absent. The imaging thing for this northern site is the presence of insects typical for the

Table 29. Insects from the Nagym (Edoma Formation) and Laptev Strait sites (Oiagoss Yar, Svyatoi Nos Cape)

Age	Lower Pleistocene			Last interglacial	Middle Pleistocene			
Section	Nagym			Oiagoss	Svyatoi Nos			
Species/sample N-B	6	5	8	Oya-6	FM-96-1	CH-1	CH-2-4	eco
Sample								
Order Coleoptera								
Family Carabidae								
Subfamily Nebriinae								
Notiophilus aquaticus L.	1	–	1	–	–	–	–	**xe**
Subfamily Carabinae								
Carabus odoratus Motsch.	–	–	–	–	3	–	–	**dt**
Subfamily Elaphrinae								
Blethisa multipunctata (L)	–	–	1	–	–	–	–	**ri**
Diacheila polita Fald.	–	–	3	–	–	1	–	**mt**
Subfamily Trechinae								
Bembidion (*Asioperyphus*) *umiatense* Lth.	–	–	2	–	–	–	–	**ri**
Bembidion (*Notaphus*) *varium* (Ol.)	–	–	–	1	–	–	–	**ri**
B. (*Peryphanes*) *dauricum* Motsch.	–	–	–	–	1	–	–	**dt**
B. (*Peryphanes*) *grapii* Gyll.	1	–	–	–	–	–	–	**dt**
Subfamily Harpalinae								
Tribe Harpalini								
Harpalus amputatus (Say)	–	–	–	1	–	–	–	**ms**
Harpalus sp.	–	–	1	–	–	–	–	**ms?**
Tribe Platynini								
Sericoda quadripunctata (DeG)	–	–	–	–	–	2	–	**ri**
Tribe Pterostichini								
Poecilus (*Derus*) *nearcticus* Lth.	–	–	–	–	3	–	–	**dt**
Pterostichus (*Cryobius*) *brevicornis* (Kby.)	2	–	41	–	–	1	–	**mt**
P. (*Cryobius*) *nigripalpis* Popp.	–	–	2	–	–	–	–	**dt**
P. (*Cryobius*) *pinguedineus* Esch.	1	6	2	–	–	–	7	**mt**
P. (*Cryobius*) *ventricosus* Esch.	–	2	3	4	–	1	6	**mt**
Pterostichus (*Cryobius*) sp.	2	2	1	–	60	4	–	**mt**
P. (*Lenapterus*) *agonus* Horn.	–	1	–	–	1	2	–	**mt**
P. (*Lenapterus*) *costatus* Men.	5	–	1	–	4	–	–	**mt**
P. (*Lenapterus*) *vermiculosus* Men.	–	–	1	–	–	–	2	**mt**
P. (*Tundraphilus*) *sublaevis* Sahlb.	–	1	–	2	7	–	–	**dt**
Pterostichus sp.	–	–	–	–	2	–	–	**dt?**
Stereocerus haematopus (Dej.)	1	–	–	–	4	–	–	**dt**
Tribe Zabrini								
Amara glacialis Mnnh.	3	–	–	–	–	1	–	**dt**
Curtonotus alpinus Payk.	5	15	7	8	50	1	124	**dt**
C. bokori Csiki	–	–	–	1	–	–	–	**dt**
Family Dytiscidae								
Subfamily Agabinae								
Agabus moestus (Curt.)	–	1	–	2	–	–	–	**aq**
Agabus sp.	–	–	–	–	7	3	–	**aq**

Table 29. (Contd.)

Age	Lower Pleistocene			Last interglacial	Middle Pleistocene			
Section	Nagym			Oiagoss	Svyatoi Nos			
Species/sample N-B	6	5	8	Oya-6	FM-96-1	CH-1	CH-2-4	eco
Sample								
Subfamily Colymbetinae								
Colymbetes dolabratus (Payk.)	–	–	–	1	–	–	–	**aq**
Subfamily Hydroporinae								
Hydroporus sp.	1	–	–	–	1	2	–	**aq**
Family Hydrophilidae								
Subfamily Helophorinae								
Helophorus obscurellus Popp.	–	–	–	2	–	–	–	**aq**
H. sibiricus Motsch.	–	–	–	2	–	–	–	**aq**
H. splendidus Sahlb.	–	–	–	2	3	1	1	**aq**
Subfamily Hydrophilinae								
Hydrobius fuscipes F.	–	–	1	–	–	–	–	**aq**
Family Leiodidae								
Subfamily Leiodinae								
Anisotoma sp.	–	–	–	2	–	–	–	**pl**
Cyrtoplastus irregularis Rtt.?	–	–	–	1	–	–	–	**pl**
Subfamily Cholevinae								
Cholevinus sibiricus (Jean.)	–	1	–	5	–	–	–	**mt**
Cholevinus sp.	–	–	–	2	–	–	–	**pl**
Subfamily Coloninae								
Colon sp.	–	–	–	1	–	–	–	**pl**
Family Staphylinidae								
Subfamily Omaliinae								
Olophrum latum Maekl.	–	–	5	–	–	–	–	**pl**
Eucnecosum tenue (LeC.)	–	–	–	2	–	–	–	**pl**
Subfamily Tachyporinae								
Tachinus arcticus Motsch.	33	10	1	1	1	–	10	**mt**
T. brevipennis Sahlb.	–	–	–	6	–	–	–	**mt**
Subfamily Aleocharinae								
Gymnusa sp.?	–	–	–	1	–	–	–	**pl**
Subfamily Paederinae								
Lathrobium longulum Grav.?	–	–	–	1	–	–	–	**pl**
Subfamily Steninae								
Stenus sp.	–	–	–	1	–	–	–	**ri**
Family Scarabaeidae								
Aphodius sp.	–	–	–	1	1	1	–	**xe**
Family Byrrhidae								
Subfamily Byrrhinae								
Morychus viridis Kuzm. et Korot.	3	17	1	3	53	–	–	**ss**
Simplocaria arctica Popp.	–	–	1	–	1	–	–	**dt**
S. elongata J. Sahl	–	–	–	1	–	–	–	**dt**
S. semistriata F.	–	–	2	–	–	–	–	**dt**

Table 29. (Contd.)

Age	Lower Pleistocene			Last interglacial	Middle Pleistocene			
Section	Nagym			Oiagoss	Svyatoi Nos			
Species/sample N-B	6	5	8	Oya-6	FM-96-1	CH-1	CH-2-4	eco
Sample								
Family Bostrichidae								
Stephanopachys substriatus Payk.	1	–	–	–	–	–	–	**fo**
Family Ptinidae								
Subfamily Anobiinae								
Caenocara bovistae Hoffm.	–	–	–	1	–	–	–	**pl**
Family Melyridae								
Troglocollops arcticus L. Medv.	–	–	–	1	–	–	–	**ms**
Family Coccinellidae								
Subfamily Coccinellinae								
Tribe Coccinellini								
Hippodamia arctica Schneid.	–	–	–	1	–	–	–	**ri**
Family Chrysomelidae								
Subfamily Chrysomelinae								
Chrysolina arctica Medv.	–	1	–	–	–	–	1	**ms**
Ch. bungei Jac.	–	–	–	–	–	–	8	**tt**
Ch. magniceps (Sahlb)	–	–	–	–	–	–	1	**tt**
Ch. purpurata Fald.?	–	–	–	–	–	1	–	**st**
Chrysolina septentrionalis Men	3	–	–	–	2	–	4	**mt**
Ch. subsulcata Mnnh.	–	–	–	–	3	–	6	**tt**
Ch. tolli Jac.	–	3	–	–	–	–	4	**tt**
Chrysolina sp.	–	–	–	1	–	–	–	**mt?**
Gonioctena affinis Gyll.	–	–	–	1	–	–	–	**sh**
Hydrothassa hannoverana F.	–	–	–	2	2	–	–	**ri**
Phaedon concinnus Steph.	–	–	–	–	1	–	–	**me**
Family Brachyceridae								
Subfamily Erirhininae								
Notaris bimaculatus F.	–	–	1	–	–	–	–	**ri**
Family Brentidae								
Subfamily Apioninae								
Hemitrichapion tschernovi T.-M.	3	–	1	–	1	1	–	**dt**
Mesotrichapion wrangelianum Kor.	–	–	1	–	–	–	–	**dt**
Family Curculionidae								
Subfamily Ceutorhynchinae								
Ceutorhynchus sp.	–	–	–	–	1	–	–	**dt**
Pelenomus velaris Gyll.?	–	–	–	1	–	–	–	**ri**
Subfamily Entiminae								
Tribe Phyllobini								
Phyllobius virideaeris Laich.	–	–	–	1	–	–	–	**me**
Tribe Sitonini								
Sitona borealis Kor.	1	7	2	–	–	–	–	**dt**

Table 29. (Contd.)

Age	Lower Pleistocene			Last interglacial	Middle Pleistocene			
Section	Nagym			Oiagoss	Svyatoi Nos			
Species/sample N-B	6	5	8	Oya-6	FM-96-1	CH-1	CH-2-4	eco
Sample								
Subfamily Hyperinae								
Hypera diversipunctata Schrank.	1	–	1	–	4	–	–	**dt**
H. ornata Cap.	–	–	–	1	8	–	–	**dt**
Hypera sp.	–	–	–	–	–	1	–	**dt**
Subfamily Lixinae								
Tribe Cleonini								
Stephanocleonus eruditus Faust	–	2	–	–	1	–	–	**st**
S. fossulatus F-W.	–	2	–	–	–	–	–	**st**
Coniocleonus ferrugineus Fahr.	–	–	–	–	1	–	–	**ms**
Coniocleonus sp.	–	–	1	1	2	–	–	**ms**
Subfamily Molytinae								
Tribe Lepyrini								
Lepyrus nordenskioeldi Faust	2	10	1	–	–	–	1	**sh**
Lepyrus sp.	–	–	–	–	15	1	–	**sh**
Subfamily Curculioninae								
Tribe Rhamphini								
Isochnus arcticus Kor.	27	50	–	–	2	–	–	**tt**
I. flagellum Erics.	4	25	–	–	–	–	–	**sh**
Family Saldidae								
Salda littoralis L.?	–	–	–	1	–	–	–	**ri**
Saldula pallipes (F.)	–	–	–	1	–	–	–	**ri**
Family Pentatomidae								
Sciocoris microphthalmus Flor.	–	–	–	1	–	–	–	**fo**
Order Hymenoptera								
Family Formicidae								
Leptothorax acervorum Fabr.	–	–	–	1	–	–	–	**fo**
Hymenoptera gen. indet.	5	2	2	–	–	–	7	**oth**
Order Homoptera								
Cicadellidae gen. Indet	–	–	–	3	–	–	–	**me**
Order Megaloptera								
Family Sialidae								
Sialis sp. (larvae)	4	2	–	2	–	–	–	**aq**
Order Trichoptera								
Thrichoptera gen. indet. (larvae)	–	1	–	5	–	–	1	**aq**
Order Diptera								
Family Tipulidae								
Tipulidae gen. indet. (larvae)	–	–	–	2	–	–	2	**oth**
Diptera gen. indet (pseudopupia)	–	2	2	4	–	–	–	**oth**
Sum	100	156	85	69	245	24	175	

forest zone. We found the ant *Leptothorax acervorum* and the bug *Sciocoris microphthalmus*. Both species presently live in the forest zone, while *Leptothorax acervorum* could have occupied forest–tundra and occasionally shrub tundra. Some other members of the assemblage also correspond to a warmer climate than at the present time. There are riparian species, which live in a less severe climate than that of the arctic coastline (*Bembidion* (*Notaphus*) *varium, Hippodamia arctica, Hydrothassa hannoverana, Pelenomus velaris, Salda littoralis, Saldula pallipes*); aquatic insects (*Colymbetes dolabratus, Helophorus obscurellus, H. sibiricus, H. splendidus*); plant litter beetles (*Anisotoma* sp., *Cyrtoplastus irregularis, Colon* sp., *Eucnecosum tenue, Gymnusa* sp., *Lathrobium longulum*, *Caenocara bovistae,* which lives mostly in the forest zone); shrub beetles *Gonioctena affinis*; and meadow *Phyllobius virideaeris*. Such a high diversity of the secondary groups is typical for the interglacial units. The environment close to forest (forest–tundra or tall shrub tundra) is reconstructed for the last interglacial. The climate was significantly warmer than at present.

Three occasional samples (Table 29) were collected by P. Nikolsky in the vicinity of the Svyatoi Nos section in different years. The samples were taken from the Middle Pleistocene Kuchchugui Formation; they are richer than Kuchchugui insect assemblages taken on the opposite side of the strait (Lyakhovskii Island, see above) and could be useful for reconstruction of the environment of this little known time interval.

Sample FM-96-1 is the richest; the assemblage is rather diverse. It contains a significant proportion of *Morychus viridis* (22%) and individual steppe (*Stephanocleonus eruditus* and very rare *Chrysolina purpurata*) and meadow–steppe species (*Coniocleonus ferrugineus*). The main groups are tundra insects: **dt** = 35% and **mt** = 28%; the arctic group is also present, **tt** = 2%. We can reconstruct a steppe–tundra environment well developed for the region.

Sample CH-1 is poor, but the third sample (CH-2-4) has yielded an assemblage sufficiently abundant for analysis. Despite a great number of specimens (MNI is 175), the diverse is rather low. The assemblage is strongly dominated by the **dt** group (71%), which is mostly represented by the ground beetle *Curtonotus alpinus*. The second most frequent group is **mt** (17%) and the third is **tt** (11%). Only one steppe–tundra indicator, the steppe-meadow leaf beetle *Chrysolina arctica,* has been recorded here. This fauna allows the reconstruction of a severe environment similar to dry grassy tundra.

Unfortunately, stratigraphic correlation between these samples is uncertain, but two Middle Pleistocene insect assemblages were undoubtedly formed in dry environments differing in warm supply; one fauna is indicative of somewhat warmer conditions, but another, cooler climate.

3.3d–3g. Lena Delta Area

The Lena delta area includes numerous islands formed of bedrock, the Pleistocene Ice Complex and the Holocene deposits. Pleistocene deposits were studied in two sections: Buor-Khaya and Nagym.

3.3d. Nagym

The Nagym section is located in the north of the western Lena delta, on the right bank of the Olenek Channel on Ebe-Basyn-Sise Island near a small settlement of Nagym (Figs. 1, 7, 9). The section was repeatedly visited (Lungerstauzen, 1961; Galababa, 1987; Kunitsky, 1989; Grigoriev, 1993), but the most detailed study was performed by the Russian–German Expedition “Lena Delta 2000” in 1998–2000 (Pavlova and Dorozhkina, 2000; Schwamborn et al., 2002; Schirrmeister et al., 2003, 2011). Insect samples were collected by me in 2000.

The composition of the section (Fig. 29) is in general close to that of Buor-Khaya (described below). The section consists of two units: lower sands with grassy beds –(Bulugur Formation) and Ice Complex – (Kobakh Formation). Radiocarbon and thermoluminescence data (Krbetschek et al., 2002, Schirrmeister et al., 2003, 2011) show that both units fit into an early stage of the Late Pleistocene, from 99 to 44 ka.

Nine insect samples (Table 30) were taken from sands of the Bulugur Formation. The number of specimens in particular samples vary; the lower part of the unit (with plant beds) is poorer and the upper, sandy part is richer. Kobakh ice-rich silt is not well represented here; it is only 10 m thick. Three samples come from this unit.

The lower sample (N-B1) is poor; the assemblage contains tundra species, such as *Pterostichus* (*Cryobius*) *brevicornis, P.* (*Cryobius*) *pinguedineus, P.* (*Cryobius*) *ventricosus*, *Tachinus arcticus*, arctic weevil *Isochnus arcticus,* and cold resistant willow weevil *I. flagellum*. The assemblage is apparently indicative of cold and rather wet tundra environment.

The next two samples (N-B2 and N-B3) are similar to each other and, hence, combined. This assemblage contains a number of relatively thermophilous species: *Pelophila borealis, Trechus apicalis, Cymindis vaporariorum*, *Notaris bimaculatus, N. eversmanni*, *Bagous* sp., including members of the forest group: *Badister* sp., *Pissodes* sp., and *Formica gagatoides*. In addition, the assemblage includes individual arctic species and a few specimens of *Morychus viridis*. Despite the small number of specimens, the species diversity is high.

The next sample (N-R2) was screened for rodents, so that some small fossils could have been missed. The assemblage is poor, but its ecological structure is close to the previous one. It contains a number of thermophilous species, such as *Blethisa catenaria, Bembidion (Plataphus) gebleri, Hydrobius fuscipes, Notaris bimac-*

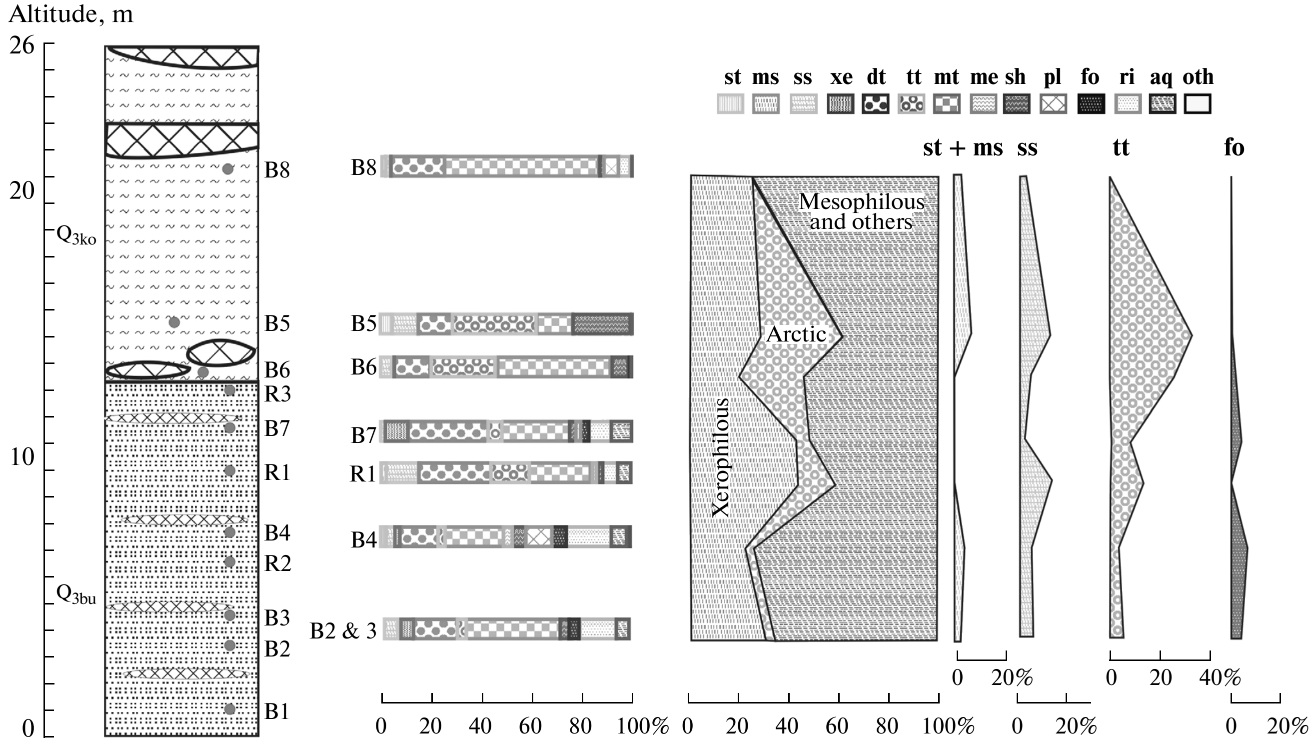


Fig. 29. Stratigraphic scheme and insect assemblages from the Nagym section. For legend, see Figs. 15 and 16. Q_{3bu}) is the Bulugur Formation and Q_{3ko}) is the Kobakh Formation.

ulatus, and the forest weevils *Hylobius piceus* and *Pissodes* sp.

Sample N-B4 comes from the middle part of the sandy unit. It has yielded the largest assemblage in the section (MNI is 275), with a high species diversity, 97 beetle and ant species and many unidentified parasitic wasps, flies, and other insects. Ecological diversity of the assemblage is also high; it includes all ecological groups, from individual steppe insects to forest, meadow, and plant litter taxa. There are many thermophilous species here: *Gyrinus opacus, Notiophilus sylvaticus, Blethisa multipunctata, Diacheila polita, Elaphrus riparius, Dyschiriodes melancholicus, D. politus, Bembidion* (*Bracteon*) *lapponicum, B.* (*Peryphanes*) *grapii, B.* (*Peryphus*) *petrosum*, *B.* (*Plataphus*) *gebleri, Agonum quinquepunctatum, Pterostichus* (*Petrophilus*) *eximius*, *Colymbetes dolabratus, Laccophilus* sp., *Hydrobius fuscipes, Cyrtoplastus irregularis*, *Olophrum consimile, Eucnecosum tenue, Bledius* spp., *Lathrobium* spp., *Philonthus* spp., *Quedius* spp., *Gymnusa* sp., *Aegalia kamtschatica, Heterocerus* sp., *Corticaria* sp., *Stephostethus* sp., *Donacia* sp., *Gonioctena affinis, Phaedon armoraciae*, *Chaetocnema* sp., *Hippuriphila modeeri, Grypus mannerheimi*, *Notaris bimaculatus, N. eversmanni, Bagous limosus, Zacladus radulata, Sitona lineellus, Dorytomus imbecillus,* including forest beetles *Denticollis varians, Luperus* sp., *Magdalis duplicata, Hylobius piceus, Pissodes* sp., *Phloeotribus spinulosus*, *Polygraphus* sp., and ants *Camponotus herculeanus,* and *Leptothorax acervorum*.

All five listed assemblages are indicative of a mild climate, close to that of northern taiga or forest–tundra. Individual steppe species are present; thus, it is possible to propose that there was coexistence of taiga and steppe–tundra communities during this period.

Insect samples from the second part of the Bulugur Formation (N-R1, N-B7, N-R3) have yielded a greater proportion of xerophilous species and fewer forest indicators. Assemblage N-R1 is dominated by the tundra groups: **dt** = 29%, **mt** = 25%, and **tt** = 16%. The proportion of cold resistant species is increased. At the same time, the proportion of the steppe–tundra group **ss** increases to 12%, that is, high for the Nagym record. This cooling interval is considered to be short and individual forest species (*Pissodes* sp.) appeared again in the succeeding assemblage (N-B7).

Significant changes were observed in the upper unit, the Ice Complex. Three samples (Table 29) were taken from the upper silt interbeds. The first two samples (N-B6 and N-B5) come from the unit base. The assemblages include a large proportion of arctic insects, 27 and 34%. The group **tt** includes mostly the weevil *Isochnus arcticus* and a few leaf beetles *Chrysolina tolli*.

The upper sample from unit N-B8 contains only singular specimens of arctic species; it is strongly dom-

Table 30. Insects from the Nagym site, Bulukur Formation

Age	Middle Pleistocene?								
Species/sample N-	B1	B2	B3	R2	B4	R1	B7	R3	eco
Order Coleoptera									
Family Gyrinidae									
Gyrinus opacus Salb.	–	–	–	–	2	2	–	–	**aq**
Family Carabidae									
Subfamily Nebriinae									
Nebria frigida Sahlb.	–	–	–	–	1	–	–	–	**ri**
Notiophilus aquaticus L.	–	1	1	–	3	–	–	–	**xe**
N. sylvaticus Esch.	–	–	–	–	1	–	–	–	**xe**
Pelophila borealis Payk.	–	–	1	–	–	–	–	–	**ri**
Subfamily Carabinae									
Carabus truncaticollis Esch.	–	1	–	–	2	–	–	–	**mt**
Subfamily Elaphrinae									
Blethisa catenaria Brown.	–	–	–	1	–	–	–	–	**mt**
B. multipunctata (L.)	–	–	–	–	1	–	–	–	**ri**
Diacheila polita Fald.	–	–	–	–	8	–	1	–	**mt**
Elaphrus riparius L.	–	–	–	–	1	–	–	–	**ri**
Subfamily Scaritinae									
Dyschiriodes melancholicus Putz.	–	–	–	–	3	–	–	–	**ri**
D. politus (Dej.)	–	–	–	–	1	–	–	–	**ri**
Subfamily Trechinae									
Bembidion (*Asioperyphus*) *umiatense* Lth.	–	1	1	–	7	–	–	–	**ri**
B. (*Bracteon*) *lapponicum* Zeitt.	–	–	–	–	1	1	–	–	**ri**
B. (*Peryphanes*) *dauricum* Motsch.	–	–	–	–	2	–	1	–	**dt**
B. (*Peryphanes*) *grapii* Gyll.	–	–	1	–	12	–	1	–	**dt**
B. (*Peryphus*) *petrosum* Gebl.	–	–	–	–	2	–	–	–	**ri**
B. (*Plataphus*) *gebleri* Gebl.	–	–	–	1	2	1	–	–	**ri**
B. (*Plataphodes*) *arcticum* Lth.	1	–	–		9		1	–	**ri**
Trechus apicalis Motsch.	–	–	1	–	–	–	–	–	**ri**
Subfamily Harpalinae									
Tribe Harpalini									
Badister sp.	–	1	–	–	–	–	–	–	**fo**
Dicheirotrichus mannerheimi Sahlb.	1	–	–	–	2	–	–	–	**dt**
Tribe Lebiini									
Cymindis vaporariorum L.	–	–	1	–	–	–	–	–	**dt**
Tribe Platynini									
Agonum quinquepunctatum Motsch.	–	–	–	–	1	–	–	–	**ri**
Tribe Pterostichini									
Poecilus (*Derus*) *nearcticus* Lth.	–	–	–	–	1	–	1	1	**dt**
Pterostichus (*Cryobius*) *brevicornis* (Kby.)	1	4	2	2	15	2	3	–	**mt**
P. (*Cryobius*) *pinguedineus* Esch.	2	–	1	–	4	3	–	–	**mt**
P. (*Cryobius*) *ventricosus* Esch.	1	1	1	4	4	3	1	1	**mt**
Pterostichus (*Cryobius*) sp.	–	1	1		8	6	2	–	**mt**
P. (*Lenapterus*) *costatus* Men.	–	–	–	–	–	–	1	–	**mt**

Table 30. (Contd.)

Age	Middle Pleistocene?								
Species/sample N-	B1	B2	B3	R2	B4	R1	B7	R3	eco
P. (*Lenapterus*) *vermiculosus* Men.	–	–	1	–	1	–	2	–	**mt**
P. (*Petrophilus*) *abnormis* Sahlb.	–	–	–	–	–	–	1	–	**dt**
P. (*Petrophilus*) *eximius* Mor.	–	–	–	–	1	–	1	–	**dt**
P. (*Petrophilus*) *tundrae* Tschitsch.	–	–	2	–	2	1	–	–	**dt**
P. (*Tundraphilus*) *sublaevis* Sahlb.	–	–	–	1	–	–	–	–	**dt**
Stereocerus haematopus (Dej.)	–	–	–	1	2	2	–	1	**dt**
Tribe Zabrini									
Amara glacialis Mnnh.	–	–	–	–	2	1	2	4	**dt**
A. interstitialis Dej.	–	–	–	–	2	–	–	–	**dt**
Curtonotus alpinus Payk.	–	1	–	1	2	9	2	1	**dt**
C. bokori Csiki	–	–	–	–	–	1	–	–	**dt**
Family Dytiscidae									
Subfamily Agabinae									
Agabus moestus (Curt.)	–	–	–	–	–	–	1	–	**aq**
A. thomsoni (J. Sach.)	–	–	1	–	3	2	1	–	**aq**
Subfamily Colymbetinae									
Colymbetes dolabratus (Payk.)	–	–	–	–	1	–	–	–	**aq**
Subfamily Hydroporinae									
Hydroporus acutangulus Thoms.	–	1	–	–	–	–	–	–	**aq**
Hydroporus sp.	–	–	–	–	3	–	–	–	**aq**
Subfamily Laccophilinae									
Laccophilus sp.	–	–	–	–	1	–	–	–	**aq**
Dytiscidae gen. indet.	–	–	–	–	1	–	–	–	**aq**
Family Hydrophilidae									
Subfamily Helophorinae									
Helophorus splendidus Sahlb.	–	–	–	–	1	–	2	–	**aq**
H. sibiricus Motsch.	–	–	–	–	2	–	–	–	**aq**
Subfamily Hydrophilinae									
Hydrobius fuscipes F.	–	–	–	1	1	–	1	–	**aq**
Subfamily Sphaeridiinae									
Cercyon spp.	–	–	–	–	2	–	–	–	**ri**
Family Leiodidae									
Subfamily Leiodinae									
Cyrtoplastus irregularis Rtt.?	–	–	–	–	4	–	–	–	**pl**
Subfamily Cholevinae									
Cholevinus sibiricus (Jean.)	–	–	–	–	2	–	–	–	**mt**
Colon sp.	–	–	–	–	–	–	1	–	**pl**
Family Staphylinidae									
Subfamily Omaliinae									
Micralymma brevilingue Schiodte	–	–	–	–	1	–	–	–	**mt**
Olophrum consimile Gyll.	–	–	–	–	2	–	1	–	**mt**
Eucnecosum tenue (LeC.)	–	–	–	–	2	–	–	–	**pl**
Subfamily Tachyporinae									
Tachinus arcticus Motsch.	3	3	1	–	11	2	2	–	**mt**

Table 30. (Contd.)

Age	Middle Pleistocene?								
Species/sample N-	B1	B2	B3	R2	B4	R1	B7	R3	eco
Subfamily Oxytelinae									
Bledius spp.	–	–	–	–	2	–	–	–	**ri**
Subfamily Paederinae									
Lathrobium spp.	–	–	–	–	11	–	–	–	**pl**
Subfamily Steninae									
Stenus sp.	–	–	1	–	1	–	–	–	**ri**
Subfamily Staphylininae									
Philonthus spp.	–	–	–	–	2	–	–	–	**pl**
Quedius spp.	–	–	–	–	2	–	–	–	**pl**
Gymnusa sp.	–	–	–	–	7	–	–	–	**pl**
Family Scarabaeidae									
Aegalia kamtschatica Motsch.	–	–	–	–	3	–	–	–	**ri**
Aphodius sp.	–	–	1	–	2	–	4	–	**xe**
Family Byrrhidae									
Subfamily Byrrhinae									
Byrrhus sp.	–	–	–	–	1	–	–	–	**me**
Morychus viridis Kuzm. et Korot.	–	1	2	–	8	8	1	7	**ss**
Simplocaria arctica Popp	–	–	–	–	4	–	–	–	**dt**
S. semistriata F.	–	–	–	–	1	–	–	–	**dt**
Subfamily Syncalyptinae									
Curimopsis cyclolepidia Muenst.	–	–	–	–	1	–	–	–	**dt**
Byrrhidae gen. indet.	–	–	–	–	2	–	–	–	**oth**
Family Heteroceridae									
Heterocerus sp.	–	–	–	–	1	–	–	–	**ri**
Family Elateridae									
Subfamily Dendrometrinae									
Denticollis varians Germ.	–	–	–	–	1	–	–	–	**fo**
Family Lathridiidae									
Subfamily Corticariinae									
Corticaria sp.	–	–	–	–	2	–	–	–	**pl**
Subfamily Lathridiinae									
Stephostethus sp.	–	–	–	–	1	–	–	–	**pl**
Family Chrysomelidae									
Subfamily Donaciinae									
Donacia sp.	–	–	–	–	2	–	–	–	**ri**
Subfamily Chrysomelinae									
Chrysolina septentrionalis Men	–	–	1	–	2	1	–	–	**mt**
Ch. subsulcata Mnnh.	–	–	–	–	–	3	–	–	**tt**
Ch. tolli Jac.	–	–	1	–	1	–	–	–	**tt**
Chrysolina sp.	1	–	–	–	–	–	–	–	**mt?**
Gonioctena affinis Gyll.	–	–	–	–	1	–	–	–	**sh**
Phaedon armoraciae L.	–	–	–	–	1	–	–	–	**me**
Phaedon concinnus Steph.	–	–	–	–	–	1	–	–	**me**

Table 30. (Contd.)

Age	Middle Pleistocene?								
Species/sample N-	B1	B2	B3	R2	B4	R1	B7	R3	eco
Subfamily Galerucinae									
Tribe Alticini									
Chaetocnema sp.	–	–	–	–	9	–	–	–	**me**
Hippuriphila modeeri L.	–	–	–	–	1	–	–	–	**me**
Tribe Luperini									
Luperus sp.	–	–	–	–	1	–	–	–	**fo**
Family Brachyceridae									
Subfamily Erirhininae									
Notaris aethiops (F.)	–	–	–	–	–	–	1	–	**ri**
N. bimaculatus F.	–	–	1	1	2	1	1	–	**ri**
N. eversmanni Faust	–	–	1	–	6	–	–	–	**ri**
Grypus mannerheimi Faust	–	–	–	–	2	–	–	–	**ri**
Family Brentidae									
Subfamily Apioninae									
Hemitrichapion tschernovi T.-M.	–	1	–	–	3	–	–	–	**dt**
Mesotrichapion wrangelianum Kor.	–	–	–	–	–	–	2	–	**dt**
Apioninae gen. indet.	–	–	–	–	2	–	–	–	**dt?**
Family Curculionidae									
Subfamily Bagoinae									
Bagous limosus Gyll.	–	–	–	–	2	–	–	–	**aq**
Bagous sp.	–	–	1	–	–	–	–	–	**aq**
Subfamily Ceutorhynchinae									
Ceutorhynchus sp.	–	–	–	–	–	–	1	–	**dt**
Pelenomus quadrituberculatus F.	–	–	–	–	–	1	–	–	**ri**
Zacladus radulata Hoch.	–	–	–	–	4	–	–	–	**ms**
Subfamily Entiminae									
Tribe Otiorhynchini									
Otiorhynchus cribrosicollis Boh.?	–	–	–	–	1	–	–	–	**ms**
Tribe Sitonini									
Sitona borealis Kor.	1	–	1	–	3	5	3	–	**dt**
S. lineellus Bonsd.	–	–	–	–	1	–	–	–	**me**
Subfamily Hyperinae									
Hypera diversipunctata Schrank.	–	–	–	–	2	–	–	–	**dt**
H. ornata Cap.	–	–	1	–	–	1	–	–	**dt**
Hypera sp.	–	1	–	–	–	–	–	–	**dt**
Subfamily Lixinae									
Tribe Cleonini									
Stephanocleonus eruditus Faust	–	–	–	–	1	–	–	–	**st**
Coniocleonus sp.	–	–	–	–	–	2	–	–	**ms**
Cleonini gen. indet.	–	–	1	–	2	–	–	–	**ms**
Subfamily Mesoptilinae									
Magdalis duplicata Germ.	–	–	–	–	1	–	–	–	**fo**

Table 30. (Contd.)

Age	Middle Pleistocene?								
Species/sample N-	B1	B2	B3	R2	B4	R1	B7	R3	eco
Subfamily Molytinae									
Tribe Hylobiini									
Hylobius piceus DeG.	–	–	–	1	1	–	–	–	**fo**
Tribe Lepyrini									
Lepyrus nordenskioeldi Faust	–	–	1	–	4	2	1	1	**sh**
Tribe Pissodini									
Pissodes sp.	–	–	1	1	1	–	1	–	**fo**
Subfamily Curculioninae									
Tribe Elliscini									
Dorytomus imbecillus Fst.	–	–	–	–	7	–	–	–	**sh**
Tribe Rhamphini									
Isochnus arcticus Kor.	5	–	1	–	7	8	3	–	**tt**
I. flagellum Erics.	4	1	–	–	1	–	–	–	**sh**
Subfamily Scolytinae									
Tribe Ipini									
Ips cembrae Heer	–	–	–	1	–	–	–	–	**fo**
Tribe Phloeotribini									
Phloeotribus spinulosus (Rey.)	–	–	–	–	1	–	–	–	**fo**
Tribe Polygraphini									
Polygraphus sp.	–	–	–	–	3	–	–	–	**fo**
Order Heteroptera									
Family Pentatomidae									
Pentatomidae gen. indet.	–	–	–	–	1	–	–	–	**oth**
Order Hymenoptera									
Family Formicidae									
Camponotus herculeanus L.	–	–	–	–	3	–	–	–	**fo**
Formica gagatoides Ruzs.	–	–	1	–	–	–	–	–	**fo**
Leptothorax acervorum Fabr.	–	–	–	–	2	–	1	–	**fo**
Hymenoptera gen. indet.	4	6	3	–	40	3	2	–	**oth**
Order Megaloptera									
Family Sialidae									
Sialis sp.	3	2	–	–	1	–	3	–	**aq**
Order Trichoptera									
Thrichoptera gen. indet. (larvae)	–	–	–	–	2	–	–	–	**aq**
Order Diptera									
Family Chironomidae									
Chironomidae gen. indet. (larvae)	–	1	–	–	–	–	–	–	**aq**
Diptera fam. indet. (puparia)	2	1	2	1	3	11	3	–	**oth**
Sum	20	19	32	16	275	69	48	16	

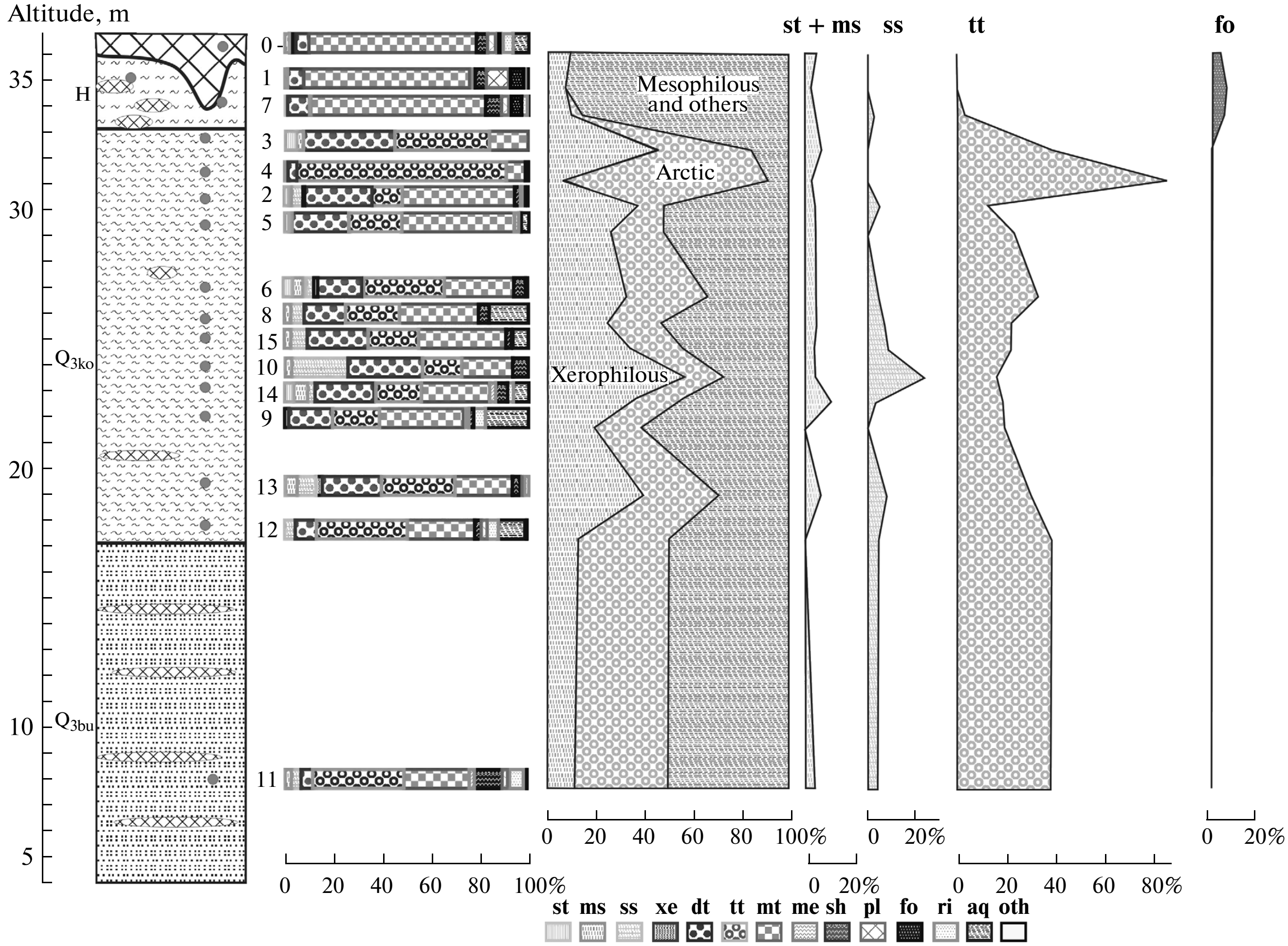


Fig. 30. Stratigraphic scheme and insect assemblages from the Buor-Khaya section.

inated by the **mt** group (62%) (the most popular species is *Pterostichus* (*Cryobius*) *brevicornis*) and includes a number of thermophilous species: *Blethisa multipunctata, Diacheila polita, Hydrobius fuscipes, Olophrum latum,* and *Notaris bimaculatus*.

Judging from radiocarbon data, the cooling interval at the base of the Kobakh Formation is apparently correlated with the MIS4 stage. The second cooling (MIS2) described from the other regional sections of Buor-Khaya and the Bykovsii Peninsula is missed here. An interesting situation is observed in the older Bulugur unit. It is evident that we deal with a warming stage here. Radiocarbon and thermoluminescence data do not provide accurate dating; the oldest date is less than 100 ka. This is probably the terminal stages of the last interglacial, MIS5b or MIS5a.

A feature shared by all Nagym assemblages is the low content of the steppe–tundra indicators and combination of arctic and shrub species. Two close willow weevils *Isochnus arcticus* and *I. flagellum* coexisted throughout the record. They probably fed on the same low willows. A specific climate of a large river valley provided extra warming for this northern area. A similar effect is observed now, rich tundra vegetation with medium-sized shrubs in the protected valley and poor tundra of the arctic type on the plateau.

3.3e. Buor-Khaya

The Buor-Khaya section is located on Kurungnakh Island in the central part of the Lena delta (Figs. 1, 7, 10). There is the third Lena River terrace up to 40 m above the river level (Figs. 30, 31a). The third terrace sequence is rather complicated. Two main units are visible and widely exposed, but the third is seen only locally. The first (lower) unit consists of alluvial–eolian sandy deposits with gravel corresponding to the Bulugur Formation.

This sandy unit is clearly traced throughout the section. The lower part of the unit includes horizontal beds composed of steams and roots of tall grasses. These beds are sometimes resistant and support a subvertical slope. Upward in the section, there are looser sand beds with plant debris.

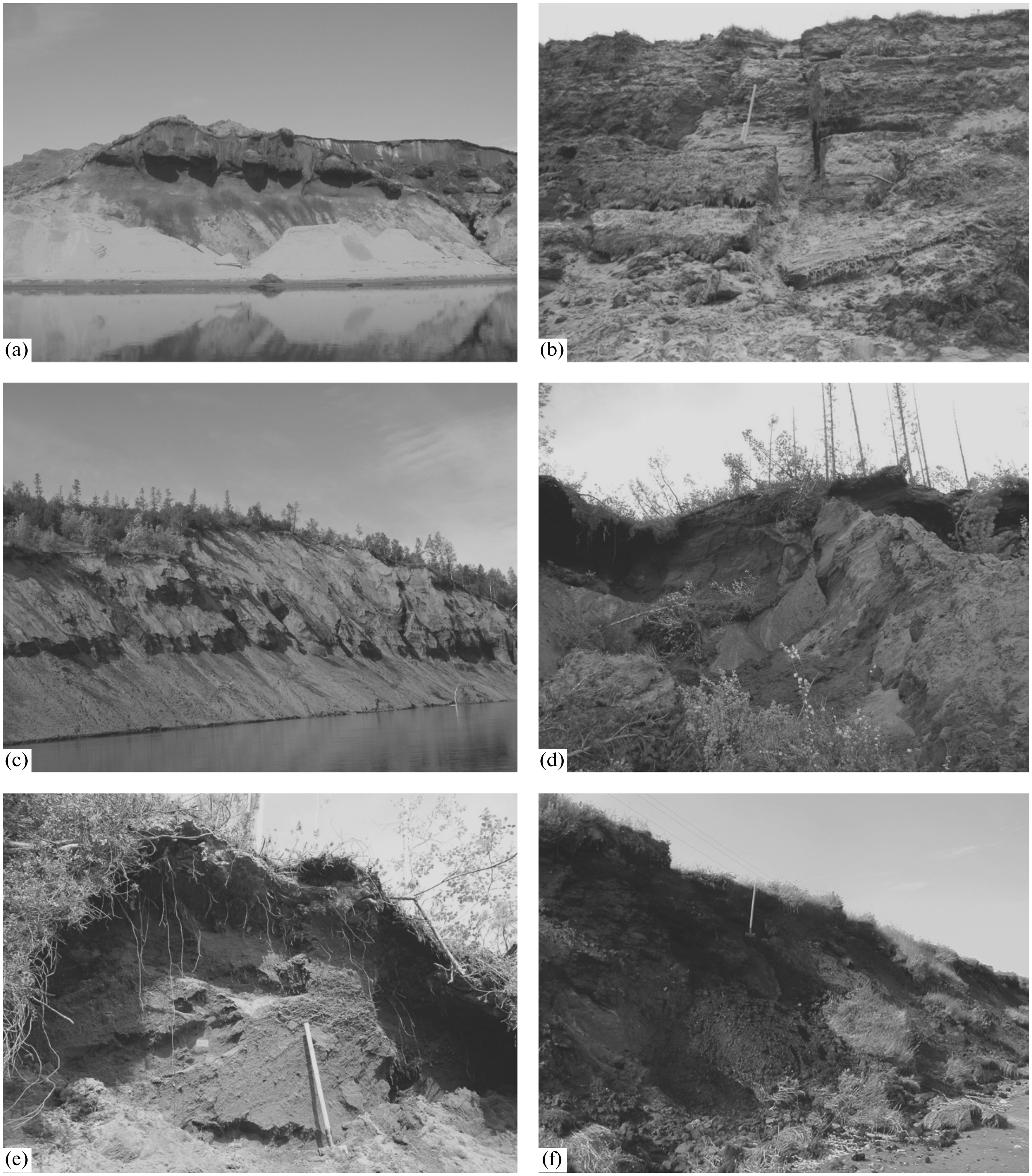


Fig. 31. Photograph of sections from different regions: (a) Buor-Khaya, Lena delta; (b) Samoilov, Lena delta; (c, e) Ice Bluff, Chukotka: (c) general view, (d) upper sandy unit with ice wedge, (e) uppermost sandy unit; (f) Anadyr, Chukotka.

The second unit belongs to the peaty ice-rich Kobakh Formation, which overlies with disconformity the Bulugur Formation (Lungersgauzen, 1961). The border between the formations is clear and sharp. In places, there is gray tiny sand of residual soil. Ice wedges from the upper unit cut sharply into the formation at the border; only narrow tails penetrate into the lower sands.

The Kobakh Formation visually starts from the ice wall. This happens as the ice wedge system is exposed along the strike (similar situation was observed on Lyakhovskii Island). Thick blocks of peat are observed above the ice. This sequence starts from three large interrupted peat beds. Silt deposits with thin peat bed and lenses lie above the lower peats.

The third unit, mostly peaty sediment, follows the Holocene thermokarst depressions (alases) and thermoerosion valleys (logs) are situated on the ice-rich Kobakh Formation, which is partly melted and compressed under it. The Holocene deposits are widespread on the top of the third Lena River terrace and in the first terrace and characterize the relief of the modern landscape.

The chronology is based on the radiocarbon Optical Simulated Luminescence (IR-OSL) methods (Wetterich et al., 2008). The age of the lower sandy unit is uncertain: by IR-OSL, the age interval is from 88 to 65 ka, whereas AMS-dates from the same site fall between 57 and 37 ka. More likely, the Kobakh Formation should be correlated with the Oiagoss Formation or the lower part of the Edoma Formation, although an older age of these sands, at least its lower part, is also possible.

The Ice Complex deposits were dated by AMS from 50 to 33 ka and 17 ka.

The Holocene deposits overlie the Ice Complex unit. This hiatus may be caused by stronger permafrost melting at the beginning of the Holocene, which results in the enforced thermokarst and erosion processes. The Holocene deposits were dated in the uppermost part of the outcrop about 8 ka and 3 ka .

The first insect sample (BKh-B11) (Table 31) was taken from the middle part of the Bulugur Formation at elevation of 8 m. The sediment was not good for screening, because both dense grassy beds and clear sand contain very few fossil insects. We found only one suitable spot with lenses of loose plant debris. Assemblage B-11 is dominated by the tundra groups: **tt** = 38% (*Isochnus arcticus*) and **mt** = 27% (*Pterostichus* (*Cryobius*) *brevicornis, P.* (*Cryobius*) *pinguedineus, P.* (*Cryobius*) *ventricosus, Tachinus arcticus, Chrysolina septentrionalis*). The proportion of xerophilous insects is extremely low, but steppe–tundra indicators are present (*Morychus viridis, Harpalus vittatus vittatus*). Despite the commonly “cold” appearance of the fauna, it includes some thermophilous species, such as *Dyschiriodes melancholicus*, *Quedius* sp., *Bromius obscurus*, *Dorytomus* sp. Surprisingly, shrub insects, primarily *Lepyrus nordenskioeldi,* play a significant role. Such a combination of arctic cold resistant insects with thermophilous species adapted for shrub tundra is quite unusual. This strange combination is probably accounted for by local environment of the river valley, where medium-sized shrubs occupy low wind-protected places near the river, while elevated sites are covered by arctic tundra typical for this area. Environments of this sort are observed in the northern part of the Lena delta near the Nagym section (see above).

Twelve samples come from the ice-rich Kobakh Formation. Despite sharp lithological differences and evident disconformity at the boundary, the lower sample (BKh-B12) from Kobakh silt is very similar to the sample from Bulugur sands. The assemblage is dominated by the arctic group **tt** (37%), the second place belongs to the **mt** group (28%), but the ecological structure of the assemblage is poorer and species diversity is lower. This fauna more closely corresponds to a cold arctic environment.

The next sample from Kobakh Formation (BKh-B13) has yielded more xerophilous species, including individual steppe *Stephanocleonus fossulatus*. The proportion of the **tt** group decreases to 30% and **mt** group, to 24%.

Succeeding eight samples are rather similar. Arctic insects decrease in frequency, but continue to play an important role, 13–20%; the xerophilous part of assemblages is close to its mesophilous part; the steppe–tundra indicators are singular. Only one assemblage (BKh-B10) from the middle part of the unit shows a significant proportion of *Morychus viridis,* 23%. This is the highest frequency of the **ss** group in the sequence.

Sample BKh-B4 from the upper part of the unit (the nearest radiocarbon date is 17 ka) stays out of line. This assemblage includes the highest proportion of the arctic group among Beringian samples, **tt** = 86%. It is correlated with the same horizon in the Bykovsii section (see above) and indicative of extremely cold conditions during the Last Glacial Maximum. Assemblage BKh-B3 returns to the usual structure.

All insect assemblages of the Buor-Khaya section (Tables 31, 32, Fig. 30) are indicative of cold environment, with a high role of low arctic willows (host plant of *Isoshnus arcticus*). Nevertheless, it is evident that the Pleistocene insect fauna from Kurungnakh Island corresponds to steppe–tundra. It includes typical Pleistocene steppe–tundra species, such as the pill beetle *Morychus viridis*; the leaf beetles *Chrysolina brunnicornis* and *Ch. arctica*; the weevils *Coniocleonus cinerascens*, *C. astragali, C. ferrugineus,* and *Stephanocleonus fossulatus* in association with some xerophilous species which were widespread in the Pleistocene steppe–tundra landscape and relatively rare in the modern fauna, such as the weevils *Mesotrichapion wrangelianum, Hemitrichapion tschernovi, Sitona borealis, Hypera ornata,* and others. The assemblage lacks the weevil *Stephanocleonus eruditus,* a typical member of steppe–tundra insect community which is characteristic of Kurungnakh assemblages. This is a significant feature of the section, but not of the local area, while this species is present in most of the samples of neighboring outcrops of the Lena delta (Ebe-Basyn-Sise Island, Nagym section, see below) and Bykovsii Peninsula (Sher et al., 2005).

Table 31. Insects from the Buor-Khaya site (part 1)

Age	Q2?	Late Pleistocene							
Species/sample BKh-B	11	12	13	9	14	10	15	8	eco
Order Coleoptera									
Family Carabidae									
Subfamily Carabinae									
Carabus kolymensis Kryzh. et Bud.	–	–	1	–	–	–	–	–	**ms**
C. truncaticollis Esch.	–	–	–	1	1	–	1	1	**mt**
Carabus sp.	1	1	–	–	–	–	–	–	**oth**
Subfamily Scaritinae									
Dyschiriodes melancholicus Putz.	1	–	–	–	–	–	–	–	**ri**
Subfamily Trechinae									
Bembidion (*Asioperyphus*) *umiatense* Lth.	2	–	–	1	1	–	–	–	**ri**
B. (*Peryphanes*) *dauricum* Motsch.	1	–	–	–	–	–	–	–	**dt**
Subfamily Harpalinae									
Tribe Harpalini									
Harpalus vittatus vittatus Gebl.	1	–	–	–	–	–	–	–	**ms**
Tribe Pterostichini									
Pterostichus (*Cryobius*) *brevicornis* (Kby.)	2	–	–	–	3	–	13	18	**mt**
P. (*Cryobius*) *nigripalpis* Popp.	–	–	7	–	–	–	–	–	**dt**
P. (*Cryobius*) *pinguedineus* Esch.	1	–	2	2	3	3	1	–	**mt**
P. (*Cryobius*) *ventricosus* Esch.	1	–	2	–	1	–	2	–	**mt**
Pterostichus (*Cryobius*) sp.	–	1	10	3	–	–	2	2	**mt**
P. (*Lenapterus*) *costatus* Men.	–	7	1	8	2	–	2	3	**mt**
P. (*Petrophilus*) *abnormis* Sahlb.	–	1	9	1	–	2	6	2	**dt**
P. (*Tundraphilus*) *sublaevis* Sahlb.	1	–	3	–	2	–	4	1	**dt**
Stereocerus haematopus (Dej.)	–	–	1	–	–	–	–	–	**dt**
Tribe Zabrini									
Curtonotus alpinus Payk.	–	2	32	7	3	14	12	12	**dt**
Family Dytiscidae									
Subfamily Agabinae									
Agabus moestus (Curt.)	–	2	–	2	–	–	3	–	**aq**
Agabus sp.	–	–	–	–	2	–	–	1	**aq**
Subfamily Hydroporinae									
Hydroporus acutangulus ? Thoms.	–	4	–	7	2	–	4	–	**aq**
H. lapponum (Gyll.)	–	–	–	–	1	–	–	–	**aq**
Hydroporus sp.	–	–	–	–	–	–	–	1	**aq**
Family Hydrophilidae									
Subfamily Helophorinae									
Helophorus splendidus Sahlb.	–	–	–	1	–	–	3	22	**aq**
Family Leiodidae									
Subfamily Cholevinae									
Cholevinus sibiricus (Jean.)	–	–	27	–	2	2	4	3	**mt**
Family Staphylinidae									
Subfamily Omaliinae									
Eucnecosum tenue LeC.	–	–	1	–	–	–	–	–	**pl**

Table 31. (Contd.)

Age	Q2?	Late Pleistocene							
Species/sample BKh-B	11	12	13	9	14	10	15	8	eco
Subfamily Tachyporinae									
Tachinus arcticus Motsch.	6	6	25	4	6	7	20	21	**mt**
T. brevipennis Sahlb.	–	1	5	1	1	1	3	–	**mt**
Subfamily Steninae									
Stenus sp.	–	2	–	–	–	–	–	–	**ri**
Subfamily Paederinae									
Lathrobium sp.	–	1	–	–	–	–	–	–	**pl**
Subfamily Staphylininae									
Quedius sp.	1	–	–	–	–	–	–	–	**pl**
Family Scarabaeidae									
Aphodius sp.	–	–	7	1	–	–	–	–	**xe**
Family Byrrhidae									
Subfamily Byrrhinae									
Morychus viridis Kuzm. et Korot.	2	2	23	–	2	14	7	7	**ss**
Family Melyridae									
Troglocollops arcticus L. Medv.	–	–	–	–	1	–	–	–	**ms**
Family Chrysomelidae									
Subfamily Chrysomelinae									
Chrysolina arctica Medv.	–	–	1	–	1	–	–	1	**ms**
Ch. brunnicornis wrangeliana Vor.	–	–	–	–	2	–	–	–	**st**
Ch. septentrionalis Men.	2	–	–	–	–	–	1	–	**mt**
Ch. subsulcata Mnnh.	–	–	–	–	1	–	–	–	**tt**
Chrysomela blaisdelli Van Dyke	–	–	1	–	2	–	–	–	**sh**
Hydrothassa hannoverana F.	–	1	–	2	–	–	–	–	**ri**
H. glabra Hbst.	–	–	1	–	–	–	–	–	**ri**
Phaedon concinnus Steph.	–	–	–	1	–	–	–	–	**me**
Subfamily Eumolpinae									
Bromius obscurus L.	1	–	–	–	–	–	–	–	**me**
Family Brentidae									
Subfamily Apioninae									
Hemitrichapion tschernovi T.-M.	–	–	8	1	12	1	8	3	**dt**
Mesotrichapion wrangelianum Kor.	–	1	–	–	–	–	–	1	**dt**
Pseudoprotapion astragali Payk.?	–	–	1	–	–	–	4	1	**ms**
Family Curculionidae									
Subfamily Entiminae									
Tribe Sitonini									
Sitona borealis Kor.	–	–	8	1	–	2	2	3	**dt**
S. lineellus Bonsd.	–	–	–	–	2	–	–	–	**me**
Subfamily Hyperinae									
Hypera diversipunctata Schrank.	–	1	1	–	–	–	2	2	**dt**
H. ornata Cap.	–	–	3	–	–	–	–	1	**dt**
Subfamily Lixinae									
Tribe Cleonini									

Table 31. (Contd.)

Age	Q2?	Late Pleistocene							
Species/sample BKh-B	11	12	13	9	14	10	15	8	eco
Coniocleonus astragali T.-M. et Kor.	–	–	2	–	–	2	–	–	**ms**
C. cinerascens Hochh.	–	–	6	–	–	–	–	–	**ms**
C. ferrugineus Fahr.	–	–	–	–	–	–	–	2	**ms**
Coniocleonus sp.	–	–	3	–	2	–	1	–	**ms**
Stephanocleonus fossulatus F-W.	–	–	1	–	–	–	–	–	**st**
Subfamily Molytinae									
Tribe Lepyrini									
Lepyrus nordenskioeldi Faust	3	1	14	1	1	4	3	6	**sh**
Subfamily Curculioninae									
Tribe Elliscini									
Dorytomus sp.	1	–	–	–	–	–	–	–	**sh**
Tribe Rhamphini									
Isochnus arcticus Kor.	17	20	89	11	12	10	29	32	**tt**
I. flagellum Erics.	1	–	–	–	–	–	–	–	**sh**
Order Heteroptera									
Family Saldidae									
Saldula sp.	–	–	1	–	–	–	–	–	**ri**
Family Corixidae									
Sigara sp.	–	–	1	–	–	–	–	–	**ri**
Order Hymenoptera									
Hymenoptera gen. indet	4	14	25	9	12	1	15	6	**oth**
Order Megaloptera									
Family Sialidae									
Sialis sp.	1	20	8	5	5	4	3	4	**aq**
Order Trichoptera									
Trichoptera gen.indet. (larvae)	2	4	3	–	1	4	–	1	**aq**
Order Diptera									
Family Chironomidae									
Chironomidae gen. indet.	–	–	–	–	–	–	1	–	**aq**
Family Tipulidae									
Tipulidae gen. indet.	–	–	3	–	–	–	–	–	**oth**
Diptera fam. indet. (puparia)	1	1	1	6	7	–	4	1	**oth**
Crustacea, order Cladocera									
Daphnia sp.	–	–	1	–	–	–	2	–	
Sum	45	54	297	56	68	62	137	146	

The Buor-Khaya section has two stratigraphical breaks, so that most of the MIS3 deposits and very important termination of MIS2 (15–12.5 ka) are absent, while the latter essentially differs from the others in the strong domination of steppe insects (Sher et. al., 2005).

The last two samples from the Buor-Khaya section were taken from a Holocene peaty unit (Table 32). An additional sample was taken in 2000 near thermokarst deposits. All Holocene insect assemblages differ significantly from the Pleistocene ones. They are strongly dominated by insects of wet tundra (up to 72%), such as the ground beetles *Diacheila polita, Pterostichus brevicornis*, *P. pinguedineus, P. vermiculosus,* and *P. agonus*, the rove beetles *Olophrum consimile* and *Tachinus brevipennis*. The ground beetles *Pterostichus*

Table 32. Insects from the Buor-Khaya site (part 2)

Age	Late Pleistocene					Holocene			
Species/sample BKh-B	6	5	2	4	3	7	1	00-4	eco
Order Coleoptera									
Family Carabidae									
Subfamily Nebriinae									
Notiophilus aquaticus L.	–	–	1	–	–	–	–	1	**xe**
N. sylvaticus Esch.	–	–	–	–	–	8	9	–	**fo**
Subfamily Carabinae									
Carabus odoratus Motsch.	–	1	–	–	–	–	–	–	**dt**
C. truncaticollis Esch.	–	1	–	–	–	–	–	–	**mt**
Carabus sp.	–	–	1	–	–	–	–	–	**oth**
Subfamily Elaphrinae									
Diacheila polita Fald.	–	–	–	–	–	11	7	5	**mt**
Subfamily Scaritinae									
Dyschiriodes melancholicus Putz.	–	–	–	–	–	1	–	–	**ri**
Dyschiriodes sp.	–	–	1	–	–	–	–	–	**ri**
Subfamily Trechinae									
Bembidion (*Peryphanes*) *dauricum* Motsch.	1	–	–	–	–	1	–	–	**dt**
B. (*Peryphus*) *petrosum* Gebl.?	–	–	–	–	–	–	–	1	**ri**
Subfamily Harpalinae									
Tribe Platynini									
Agonum nitidum Motsh.	–	–	–	–	–	2	–	1	**ri**
Tribe Pterostichini									
Pterostichus (*Cryobius*) *brevicornis* (Kby.)	2	2	1	1	–	55	46	3	**mt**
P. (*Cryobius*) *nigripalpis* Popp.	2	1	–	–	–	–	–	–	**dt**
P. (*Cryobius*) *pinguedineus* Esch.	4	4	3	2	4	7	3	1	**mt**
P. (*Cryobius*) *ventricosus* Esch.	1	2	2	2	–	–	2	4	**mt**
Pterostichus (*Cryobius*) sp.	14	5	–	–	–	–	8	4	**mt**
P. (*Lenapterus*) *agonus* Horn.	–	–	–	–	–	–	–	1	**mt**
P. (*Lenapterus*) *costatus* Men.	1	8	1	–	–	–	–	–	**mt**
P. (*Lenapterus*) *vermiculosus* Men.	–	–	–	–	–	3	3	4	**mt**
P. (*Petrophilus*) *abnormis* Sahlb.	3	–	–	–	–	–	3	–	**dt**
P. (*Petrophilus*) *tundrae* Tschitsch.	–	–	1	–	–	2	–	–	**dt**
P. (*Tundraphilus*) *sublaevis* Sahlb.	4	4	–	2	3	–	1	–	**dt**
Stereocerus haematopus (Dej.)	–	–	–	–	–	–	–	1	**dt**
Tribe Zabrini									
Curtonotus alpinus Payk.	12	11	19	18	25	5	3	2	**dt**
Family Dytiscidae									
Subfamily Agabinae									
Agabus moestus (Curt.)	–	–	–	–	–	–	–	1	**aq**
Agabus sp.	–	1	–	–	–	–	–	–	**aq**
Subfamily Hydroporinae									
Hydroporus acutangulus Thoms.?	2	3	1	–	–	–	1	2	**aq**
Family Hydrophilidae									
Subfamily Helophorinae									
Helophorus splendidus Sahlb.	–	–	–	–	–	–	–	1	**aq**
Helophorus sp.	–	–	–	–	–	1	–	–	**aq**

Table 32. (Contd.)

Age	Late Pleistocene					Holocene			
Species/sample BKh-B	6	5	2	4	3	7	1	00-4	eco
Subfamily Hydrophilinae									
Hydrobius fuscipes F.	–	–	–	–	–	–	–	1	**aq**
Family Leiodidae									
Subfamily Cholevinae									
Cholevinus sibiricus (Jean.)	3	7	21	5	3	–	–	–	**mt**
Family Staphylinidae									
Subfamily Omaliinae									
Holoboreaphilus nordenskioeldi Maekl.	–	–	–	–	–	4	13	2	**pl**
Olophrum consimile Gyll.	–	–	–	–	–	26	13	25	**mt**
Phyllodrepa angustata Maekl.	–	–	–	–	–	1	–	–	**pl**
Subfamily Tachyporinae									
Tachinus arcticus Motsch.	11	22	7	2	1	–	–	–	**mt**
T. brevipennis Sahlb.	5	6	5	24	4	7	15	2	**mt**
Subfamily Steninae									
Stenus sp.	–	–	–	–	–	–	–	1	**ri**
Family Scarabaeidae									
Aphodius sp.	2	–	–	–	–	–	–	–	**xe**
Family Byrrhidae									
Subfamily Byrrhinae									
Byrrhus fasciatus Forst.	–	–	–	–	–	–	1	–	**me**
Morychus viridis Kuzm. et Korot.	6	–	4	–	–	1	–	–	**ss**
Simplocaria arctica Popp.	–	–	–	–	–	–	1	–	**dt**
Family Melyridae									
Troglocollops arcticus L. Medv.	–	–	–	–	–	–	–	1	**ms**
Family Chrysomelidae									
Subfamily Chrysomelinae									
Chrysolina arctica Medv.	1	–	1	2	–	–	–	–	**ms**
Ch. brunnicornis wrangeliana Vor.	–	2	1	–	3	–	–	–	**st**
Ch. bungei Jac.	–	–	–	1	–	–	–	–	**tt**
Ch. septentrionalis Men.	2	2	–	2	–	–	2	–	**mt**
Ch. subsulcata Mnnh.	–	3	–	2	2	–	–	–	**tt**
Ch. tolli Jac.	1	2	2	–	3	–	–	–	**tt**
Chrysomela blaisdelli V. D.	–	–	–	–	–	–	–	1	**sh**
Hydrothassa hannoverana F.	–	–	–	–	–	1	1	1	**ri**
Phaedon concinnus Steph.	–	2	–	–	–	–	–	–	**me**
Phratora vulgatissima L.	–	–	–	–	–	–	–	1	**sh**
Family Brentidae									
Subfamily Apioninae									
Hemitrichapion tschernovi T.-M.	3	5	1	–	–	2	–	–	**dt**
Mesotrichapion wrangelianum Kor.	–	3	2	–	–	–	–	–	**dt**
Pseudoprotapion astragali Payk.?	2	–	–	–	–	–	–	–	**ms**
Apioninae gen. indet.	–	–	–	–	–	2	–	–	**dt?**
Family Brachyceridae									
Subfamily Erirhininae									
Notaris bimaculatus F.	–	–	–	–	–	–	1	–	**ri**

Table 32. (Contd.)

Age	Late Pleistocene					Holocene			
Species/sample BKh-B	6	5	2	4	3	7	1	00-4	eco
Family Curculionidae									
Subfamily Entiminae									
Tribe Sitonini									
Sitona borealis Kor.	3	5	–	–	–	1	–	–	**dt**
Subfamily Hyperinae									
Hypera diversipunctata Schrank.	–	–	–	–	–	–	2	–	**dt**
H. ornata Cap.	–	–	–	–	–	1	–	1	**dt**
Subfamily Lixinae									
Tribe Cleonini									
Coniocleonus sp.	5	1	–	–	2	–	1	–	**ms**
Stephanocleonus fossulatus F-W.	1	–	–	–	–	–	–	–	**st**
Stephanocleonus sp.	2	–	–	–	–	–	–	–	**st**
Subfamily Molytinae									
Tribe Lepyrini									
Lepyrus nordenskioeldi Faust	7	–	2	6	–	1	–	–	**sh**
Subfamily Curculioninae									
Tribe Elliscini									
Dorytomus imbecillus Fst.	–	–	–	–	–	5	–	–	**sh**
D. rufulus amplipennis Tourn.	–	–	–	–	–	3	9	2	**sh**
Tribe Rhamphini									
Isochnus arcticus Kor.	50	23	9	395	24	2	–	–	**tt**
I. flagellum Erics.	–	1	–	–	–	–	–	–	**sh**
Subfamily Scolytinae									
Polygraphus sp.	–	–	–	–	–	–	–	1	**fo**
Order Hymenoptera									
Hymenoptera gen. indet	13	6	12	24	3	11	6	3	**oth**
Order Megaloptera									
Family Sialidae									
Sialis sp.	3	3	–	1	1	–	3	–	**aq**
Order Trichoptera									
Trichoptera gen. indet. (larvae)	–	–	2	3	1	–	–	3	**aq**
Order Diptera									
Family Tipulidae									
Tipulidae gen. indet.	–	–	2	3	–	–	–	–	**oth**
Diptera fam. indet. (puparia)	–	3	1	–	1	4	–	2	**oth**
Crustacea, order Cladocera									
Daphnia sp.	2	–	–	–	–	–	–	–	**aq**
Sum	150	127	86	464	74	153	145	71	

(*Cryobius*) *brevicornis* is most abundant in the samples from the main section; this species is also one of the most common in modern tundra and forest–tundra. The rove beetle *Olophrum consimile* is the dominant in the thermokarst section. This is not surprising, because rove beetles of the genus *Olophrum* prefer boggy habitats, which are typical for the terminal stages of the thermokarst depression succession. There are also a number of other hygrophilous insects in all Holocene assemblages from Kurungnakh: the ground beetles *Dyschiriodes melancholicus, Agonum nitidum,* the rove beetle *Holoboreaphilus nordenskioeldi*, the leaf beetle *Hydrothassa hannoverana*, and the weevil *Notaris bimaculatus*; some forest species have been found: the ground beetle *Notiophilus sylvaticus*, the rove beetle *Phyllodrepa angustata*, and the bark beetle *Polygraphus* sp. The abundance and species diversity of shrub insects is higher than in Pleistocene insect assemblages; they include the leaf beetles *Chrysomela blaisdelli* and *Phratora vulgatissima*, the weevils *Dorytomus imbecillus, D. rufulus amplipennis,* and *Lepyrus nordenskioeldi*.

Based on the insect study, it is possible to recognize three stages of environmental development. The first (>50–32 ka) is the time of existence of a cold variant of steppe–tundra. The second (about 17 ka) is dry and cold tundra. The last, Holocene stage (from 8 ka) is an open tundra-like landscape with undeveloped forest vegetation; the climate was suitable for forest growing, but the time passed after collapse the widespread treeless Pleistocene steppe–tundra community was insufficient.

3.3f, 3g. Lena Delta, Holocene

The Holocene outcrops are numerous; there are relatively low river bluffs (up to 10 m), sometimes almost vertical. A typical bluff consists of regularly bedded sand and peat. The peat beds are usually very compact in contrast to loose sand beds, so that the outcrops are often lamellar in structure. Despite a great number of sites, it was difficult to select those appropriate for insect study. The sandy beds were clear, but the peat beds were too solid and hard for sampling. We found only two more or less suitable Holocene sites, a small island Arga-Bilir-Aryta near large Kurungnakh-Sise Island and two sections on Samoilov Island. Both islands are situated in the northern part of the shrub tundra zone.

3.3f. Arga-Bilir-Aryta Island

The Arga-Bilir-Aryta site (Figs. 7, 10) was tested by the Russian–German expedition in 2000. This is a 7-m-high outcrop; its lower part is mostly sandy, with tiny layers of plant debris. The radiocarbon date of the plant debris from 3.4 m is 3170 ± 50 BP (Kuzmina and Bolshiyanov, 2001).

The middle part of the section is a peat body with tiny sand layers. The peat consists of coarse steams, mostly *Equisetum*, and moss. The upper part is a sandy unit with plant debris, the radiocarbon date from here is 540 ± 60 BP.

Three insect samples were taken from this section (Fig. 32, Table 33). Only the lower sample contains a sufficient number of specimens, while two others are very poor.

Sample A-B2 contains all groups, except **st**. Insects of wet habitats are more important here: **mt** = 29%; **ri** = 20%. Many riparian species from the assemblage, such as *Nebria frigida, Pelophila borealis, Bembidion* (*Notaphus*) *varium, Agonum fuliginosum, Sericoda quadripunctata, Aegalia kamtschatica, Grypus mannerheimi,* and *Lixus paraplecticus* are rare in the Pleistocene. The shrub group is also diverse and includes the leaf beetles *Chrysomela blaisdelli, Gastrolina peltoidea, Gonioctena affinis,* and *Phratora vulgatissima*. The meadow group, which is usually small or absent in the Pleistocene, is represented here by several species: *Berninelsonius hyperboreus, Gastrophysa viridula, Phaedon armoraciae,* and *Phyllobius virideaeris*. The plant litter group includes quite common *Corticaria* sp. and very rare for western Beringia *Leiodes* sp. The assemblage contains some forest indicators, such as the beetles *Dromius quadraticollis, Phosphuga atrata,* and the ant *Camponotus herculeanus*. This assemblage is clearly indicative of forest–tundra environment. At the same time, individual steppe–tundra beetles remain in the sample: *Morychus viridis* and *Troglocollops arcticus*.

The deposits were formed in a large river valley. In such a dynamic environment, the possibility of reworking of older material is high, but on the other hand, some steppe–tundra relicts still live in this area. The pill beetle *Morychus viridis* is recorded from the lower Lena River, Bulun (Kuzmina and Korotyaev, 1987). Modern beetles were also collected in the Lena delta in Belaya Skala site close to Tit-Ary Island (collected by A.I. Tsybulsky in the Ust'-Lena Nature Reserve). Belaya Skala is the northernmost point of forest vegetation with steppe-like patches in the Lena River valley, so that Arga-Bilir-Aryta Island, which was forested in the mid-Holocene, could provide suitable environment for Pleistocene relicts.

Other two samples from Arga-Bilir-Aryta Island include only a few beetle specimens mostly from wet habitats. These samples are more modern-like; they include mostly tundra and riparian species without steppe–tundra relicts. Sample Ar-1 includes one forest species, the ant *Camponotus herculeanus*. This species is recorded in modern tundra environment of the Lena delta area, because ants are transported with drifting woods from the river upstream. Numerous flying female *Camponotus herculeanus* were observed in the town of Tiksi by me each field season, but they never produce successful nests.

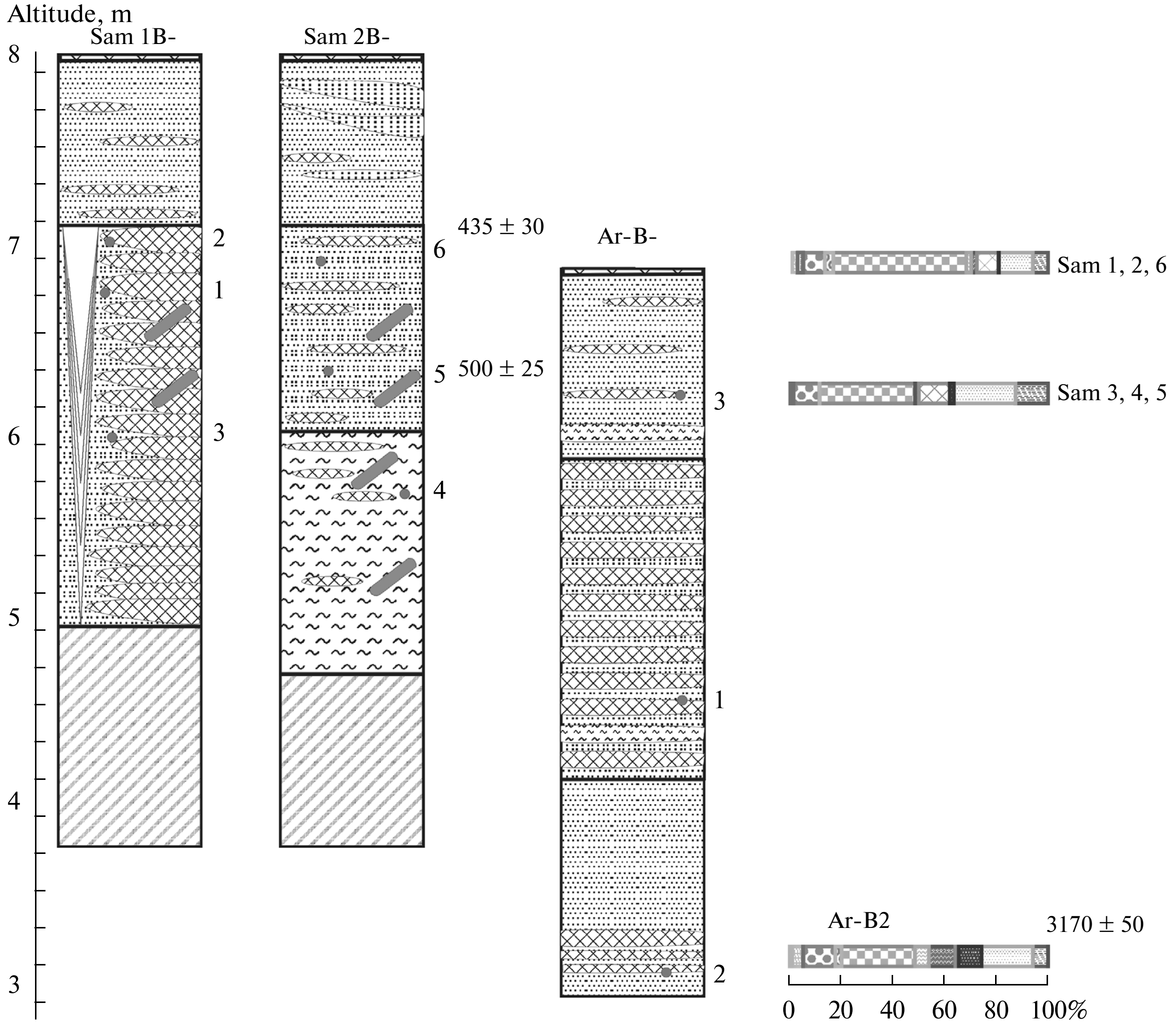


Fig. 32. Stratigraphic scheme and insect assemblages from the Holocene sections of the Lena delta. For legend, see Fig. 16.

3.3g. Samoilov Island

Typical Holocene river terrace were studied on Samoilov Island. This small island in the middle of the Lena delta (Figs. 7, 10) is well studied, because it is easily accessible and has a research station. For our research, a good point is a low possibility of reworking. The closest Pleistocene outcrop is located downstream from the island. The age and general composition of the section (Fig. 32) is close to that of the terrace of Arga-Bilir-Aryta Island. We sampled the middle-upper part of the section, which is relatively young. The radiocarbon age of the sample from elevation of 6.6 m is 230 ± 25 BP and that of 6.2 m is 500 ± 25 BP (Schwamborn et al., 2002).

We took six samples (Fig. 32, Table 33) from two sections. All samples are very poor in beetles, but rich in other insect remains, such as cases of caddis flies. Insect assemblages closely correspond to modern environment of a large river delta. The section contains abundant buried woods (as well as the modern surface of the island). The wood pieces were transported from the upstream forest. One specimen found in young insect assemblages from Samoilov Island is the forest ground beetle *Dromius quadraticollis*. This beetle lives under bark and could have been transported with drifting wood. Such a tundra–riparian assemblage, with a single forest species distinctly differs from a true forest fauna with diverse forest, meadow, shrub, and plant litter insects.

3.4. Chukotka Peninsula

The Chukotka Peninsula (Figs. 1, 12) is a key area for Quaternary Beringian studies, but it remains an under-studied part of Siberia. Only the western areas, such as the Chaun Lowland and Aion Island and the Main River Ice Bluff in south-central Chukotka have extensive and significant Quaternary outcrops of loess-like deposits that provide the opportunity of multi-proxy environmental reconstructions of the past. Fossil insects from all of these sections were stud-

Table 33. Insects from the Arga-Bilir-Aryta and Samoilov sites, Lena delta

Age	Holocene									
Section	Arga—Bilar—Aryta			Samoilov						
Species/sample BKh-02-B	2	1	3	Samoilov 1			Samoilov 2			eco
Sample Sam-B				1	2	3	4	5	6	
Order Coleoptera										
Family Carabidae										
Subfamily Nebriinae										
Nebria frigida Sahlb.	1	–	–	–	–	–	–	–	–	**ri**
Notiophilus aquaticus L.	–	–	–	2	–	–	1	–	–	**xe**
Pelophila borealis Payk.	1	–	–	–	–	–	–	–	–	**ri**
Subfamily Carabinae										
Carabus truncaticollis Esch.	1	–	–	–	–	–	–	–	–	**mt**
Subfamily Elaphrinae										
Blethisa catenaria Brown.	1	–	–	–	–	–	–	–	–	**mt**
Diacheila polita Fald.	2	2	–	1	–	–	–	–	–	**mt**
Subfamily Scaritinae										
Dyschiriodes melancholicus Putz.	–	–	–	1	–	1	–	–	–	**ri**
Subfamily Trechinae										
Bembidion (*Asioperyphus*) *umiatense* Lth.	–	1	–	–	–	–	–	1	1	**ri**
B. (*Peryphus*) *petrosum* Gebl.?	–	1	–	–	–	–	–	–	–	**dt**
B. (*Notaphus*) *varium* (Oliver)	1	–	1	–	–	–	–	–	–	**ri**
B. (*Peryphanes*) *grapii* Gyllenhal	–	–	1	–	–	–	–	–	–	**dt**
B. (*Plataphodes*) *arcticum* Lindroth	1	–	–	–	1	–	–	2	–	**ri**
Subfamily Harpalinae										
Tribe Harpalini										
Dicheirotrichus mannerheimi Sahlb.	–	–	1	–	–	–	–	–	–	**dt**
Tribe Lebiini										
Dromius quadraticollis Mor.?	1	–	–	–	–	–	–	–	1	**fo**
Tribe Platynini										
Agonum fuliginosum Panz.	1	–	–	1	–	2	–	–	–	**ri**
A. quinquepunctatum Motsch.	–	–	1	–	–	–	–	–	–	**ri**
Sericoda quadripunctata (DeG)	1	–	–	–	–	–	1	–	–	**ri**
Tribe Pterostichini										
Pterostichus (*Cryobius*) *brevicornis* (Kby.)	3	2	5	6	1	–	–	–	2	**mt**
P. (*Cryobius*) *pinguedineus* Esch.	–	–	–	–	2	–	–	–	–	**mt**
P. (*Cryobius*) *ventricosus* Esch.	3	–	–	–	–	–	2	1	2	**mt**
Pterostichus (*Cryobius*) sp.	2	–	–	1	–	–	–	–	–	**mt**
P. (*Lenapterus*) *agonus* Horn.	–	–	–	2	–	–	–	–	–	**mt**
P. (*Petrophilus*) *magus* Mnnh.		2								
P. (*Tundraphilus*) *sublaevis* Sahlb.	2	–	1	–	–	–	–	–	–	**dt**
Stereocerus haematopus (Dej.)	1	–	–	–	–	–	–	–	–	**dt**
Tribe Zabrini										
Amara glacialis Mnnh.	1	–	–	–	–	–	–	–	–	**dt**
Curtonotus alpinus Payk.	2	–	–	2	1	–	–	–	–	**dt**

Table 33. (Contd.)

Age	Holocene									
Section	Arga–Bilar–Aryta			Samoilov						
Species/sample BKh-02-B	2	1	3	Samoilov 1			Samoilov 2			eco
Sample Sam-B				1	2	3	4	5	6	
Family Dytiscidae										
Subfamily Agabinae										
Agabus moestus (Curt.)	–	1	–	–	–	–	–	–	–	**aq**
A. lapponicus (Thoms.)?	–	1	–	–	–	–	–	–	–	**aq**
A. thomsoni (J.Sach.)	–	–	–	–	–	4	–	–	–	**aq**
Agabus sp.	2	–	–	1	–	–	–	–	–	**aq**
Subfamily Hydroporinae										
Hydroporus acutangulus Thoms.	1	1	–	–	–	–	–	–	–	**aq**
H. tuberculatus Gyll.	–	–	–	–	–	–	1	–	–	**aq**
Hydroporus sp.	–	–	–	1	–	–	1	–	1	**aq**
Family Hydrophilidae										
Subfamily Sphaeridiinae										
Cercyon spp.	–	–	–	1	–	–	–	1	–	**ri**
Family Leiodidae										
Subfamily Leiodinae										
Leiodes sp.	–	–	–	–	–	–	–	–	1	**pl**
Subfamily Cholevinae										
Cholevinus sibiricus (Jean.)	–	–	–	–	–	–	1	–	–	**mt**
Family Silphidae										
Subfamily Silphinae										
Phosphuga atrata L.	1	–	–	–	–	–	–	–	–	**fo**
Family Staphylinidae										
Subfamily Omaliinae										
Eucnecosum tenue (LeC.)	1	–	–	–	–	–	1	1	–	**pl**
Holoboreaphilus nordenskioeldi Maekl.	–	–	–	–	–	1	–	–	–	**pl**
Olophrum consimile Gyll.	5	1	1	2	–	–	1	–	–	**mt**
Olophrum latum Maekl.	–	–	–	–	–	1	–	–	–	**pl**
Subfamily Tachyporinae										
Tachinus arcticus Motsch.	3	–	–	1	2	–	–	2	–	**mt**
T. brevipennis Sahlb.	–	–	–	6	2	–	7	2	–	**mt**
Subfamily Staphylininae										
Quedius sp.	–	–	–	1	1	1	–	–	–	**pl**
Staphylinidae gen. indet.	–	1	–	–	–	–	–	–	–	**pl**
Family Scarabaeidae										
Aegalia kamtschatica Motsch.	2	–	–	–	–	–	–	–	–	**ri**
Aphodius sp.	1	–	–	–	–	–	–	–	–	**xe**
Family Byrrhidae										
Subfamily Byrrhinae										
Morychus viridis Kuzm.et Korot.	2	–	–	–	1	–	–	–	–	**ss**
Symplocaria semistriata F	–	–	–	–	–	–	–	–	1	**dt**
Subfamily Syncalyptinae										
Curimopsis cyclolepidia Muenst.	–	–	–	1	–	–	1	1	–	**dt**

Table 33. (Contd.)

Age	Holocene									
Section	Arga–Bilar–Aryta			Samoilov						
Species/sample BKh-02-B	2	1	3	Samoilov 1			Samoilov 2			eco
Sample Sam-B				1	2	3	4	5	6	
Family Elateridae										
Subfamily Dendrometrinae										
Berninelsonius hyperboreus (Gyll.)	1	1	–	–	–	–	–	–	–	**me**
Family Melyridae										
Troglocollops arcticus L. Medv.	1	–	–	–	–	–	–	–	–	**ms**
Family Coccinellidae										
Subfamily Coccinellinae										
Tribe Scymnini										
Scymnus sp.	–	1	–	–	–	–	–	–	–	**ri**
Tribe Coccinellini										
Coccinellini gen. indet.	1	–	–	–	–	–	–	–	–	**oth**
Family Lathridiidae										
Subfamily Corticariinae										
Corticaria sp.	–	–	–	–	1	–	–	–	–	**pl**
Family Chrysomelidae										
Subfamily Donaciinae										
Donacia sp.	–	–	–	–	–	–	–	1	–	**ri**
Chrysolina septentrionalis Men	–	–	–	1	–	–	–	–	–	**mt**
Chrysomela blaisdelli Van Dyke	1	–	–	–	–	–	–	–	–	**sh**
Gastrolina peltoidea Gebl.	2	–	–	–	–	–	–	–	–	**sh**
Gastrophysa viridula Deg.	1	–	–	–	–	–	–	–	–	**me**
Gonioctena affinis Gyll.	1	–	–	–	–	–	1	–	–	**sh**
Phaedon armoraciae L.	–	–	–	1	–	–	–	–	–	**me**
Phratora vulgatissima L.	2	–	–	–	–	–	–	–	–	**sh**
Family Brachyceridae										
Subfamily Erirhininae										
Notaris bimaculatus F.	3	1	1	–	–	–	–	–	–	**ri**
Grypus mannerheimi Faust	2	–	–	–	–	–	–	–	–	**ri**
Family Curculionidae										
Subfamily Ceutorhynchinae										
Pelenomus quadrituberculatus F.	–	–	–	1	–	–	–	–	–	**ri**
Subfamily Entiminae										
Tribe Phyllobini										
Phyllobius virideaeris Laich.	1	–	–	–	–	–	–	–	–	**me**
Tribe Sitonini										
Sitona borealis Kor.	1	–	–	–	–	–	–	–	–	**dt**
S. lineellus Bonsd.	1	–	–	–	–	–	–	–	–	**me**
Subfamily Hyperinae										
Hypera diversipunctata Schrank.	–	–	–	–	–	–	1	–	–	**dt**
H. ornata Cap.	1	–	–	–	–	–	–	–	–	**dt**
Hypera sp.	–	–	–	–	–	–	–	1	–	**dt**

Table 33. (Contd.)

Age	Holocene									
Section	Arga–Bilar–Aryta			Samoilov						
Species/sample BKh-02-B	2	1	3	Samoilov 1			Samoilov 2			eco
Sample Sam-B				1	2	3	4	5	6	
Subfamily Lixinae										
Tribe Lixini										
Lixus paraplecticus L.	1	–	–	–	–	–	–	–	–	**ri**
Subfamily Molytinae										
Tribe Lepyrini										
Lepyrus nordenskioeldi Faust	–	1	–	–	1	–	–	–	–	**sh**
Lepyrus sp.	1	–	–	–	–	–	–	–	–	**sh**
Subfamily Curculioninae										
Tribe Elliscini										
Dorytomus rufulus amplipennis Tourn.	–	1	–	–	–	–	–	–	–	**sh**
Dorytomus sp.	–	–	–	–	1	–	–	–	–	**sh**
Tribe Rhamphini										
Isochnus arcticus Kor.	2	–	–	1	1	1	–	–	–	**tt**
Order Heteroptera										
Family Corixidae										
Sigara sp.	–	–	–	–	1	–	–	–	–	**aq**
Family Saldidae										
Salda littoralis L	–	–	–	1	1	1	–	–	–	**ri**
Order Hymenoptera										
Family Formicidae										
Camponotus herculeanus L.	4	1	–	–	–	–	1	–	–	**fo**
Hymenoptera gen. indet.	3	–	1	7	–	–	2	–	–	**oth**
Order Megaloptera										
Family Sialidae										
Sialis sp.	1	–	–	4	–	–	3	2	–	**aq**
Order Trichoptera										
Thrichoptera gen. indet., larvae	–	–	–	58	32	112	–	–	–	**aq**
Order Diptera										
Family Chironomidae										
Chironomidae gen. indet. (larvae)	1	–	–	1	–	–	–	–	–	**aq**
Family Tipulidae										
Tipulidae gen. indet. (larvae)	1	–	–	1	–	–	–	1	–	**aq**
Diptera fam. indet. (puparia)	10	3	1	2	–	–	–	–	–	**oth**
Crustacea, order Cladocera										
Daphnia sp.	3	–	–	6	–	1	–	–	–	**aq**
Sum	70	19	12	35	17	12	20	13	9	

ied by Kiselev (Kiselev, 1980a, 1980b, 1981; Kiselev and Nazarov, 2009). The study is unequal; Kiselev visited only western sites and collected detailed sample sequences there. The Main River was visited by his colleagues, so that insect sampling was the secondary task of field work and we had only preliminary results. In 2004, I had an opportunity to continue this work.

3.4a. Main River

The Main River area (Figs. 12, 13) contains the best exposed and continuous Quaternary section among all Chukotka sites. The modern vegetation is larch forest; stone pine, birch, and aspen also occur. This area is sufficiently warm to provide restricted agriculture; local people from the closest villages plant vegetables in open ground, which is unusual for Chukotka.

The first mentioning of alluvial Quaternary deposits and the first geological map of the Main River valley was produced at the beginning of the 20th century (Polevoi, 1915). The age and formation of these deposits is widely debatable. Vtyurin (1964) and Tomirdiaro (1972) focused on the lithology and permafrost features of the exposure. Tomirdiaro's interpretation of mid- and late-Pleistocene ice-rich sediments of aeolian origin was doubted by Svitoch (1980), who found resemblance with the Middle Pleistocene Turkutsky Formation (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 most of the deposits in three key exposures on the Main River (Ust'-Aldan (Aldan Mouth), Mamontovyi Obryv (Mammoth Bluff), and Ledovyi Obryv (Ice Bluff)) is now secure (Dort-Golts, 1982; Kotov and Ryabchun, 1986; Kotov, 1988, 2002; Kotov et al., 1989; Lozhkin et al., 2000; Anderson and Lozhkin, 2002). In the Ice Bluff exposure, a series of radiocarbon dates (conventional ages) range from 42.0 ± 1.3 ka near the section base to 19.5 ± 0.5 near the top; the uppermost material was dated late-Holocene (Anderson and Lozhkin 2002).

The Main River Ice Bluff exposure (Figs. 31c, 33) extends for about 1 km at an elevation of 30 m on the left bank of the Main River. In the 1970s and 1980s, the section was better exposed, particularly its 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 floodplain; thermokarst lake deposits; and peat that developed after lake drainage and dated 42 ka) are presently covered. The northern exposure is dominated upward by ice-rich deposits that are similar to widespread Edoma sediments on the coastal Yakutian lowlands. The southern portion of the exposure is dominated upward by a further sequence of superimposed thermokarst lake deposits. 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. 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. During the summer of 2004 insect sampling, (Tables 34–38) was one of the main tasks of fieldwork. The lowest sample (B9) comes from a sandy unit with small ice-wedge casts positioned 3 m above river level. Based on its position above river level, this bed is tentatively assigned to the first, alluvial–floodplain unit (Kotov and Ryabuchun 1986), but fossil insects from here are not in concordance with an aquatic environment and, furthermore, an overlying peat layer was not observed; the stratigraphic relation of this unit to other units described is thus uncertain. All other insect samples collected in the 2004 field season were taken from the ice-rich upper part of the section. A total of 48 samples were taken and screened for insect remains.

Radiocarbon data show that the deposits in question were formed approximately between 33 and 16 ka (Kuzmina et al., 2011). 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 (ca. 1 m per 800), are also applied to the side trenches near the top of the section, the sediment of the left trench (IB-3a) would be older, but the sediment of the right trench (IB-6) is younger than sediments in IB-2 at the same level. The bedding in the upper part of the section looks oblique (Figs. 31d, 31e).

The first fossil insects from this locality were sampled by a Svitoch expedition in 1975. Using the description of the sequence by Kiselev (1980b), our new samples are correlated with those taken previously. The richest previously collected insect samples (Kiselev's LO.2 and 3) come from the lower, presently inaccessible part of the exposure represented by shallow-water lake sediment and these contained a great 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 deposits or Edoma). Sample LO.5 comes from the southern part of the exposure and again contains a significant number 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 Edoma in the upper part of the exposure and correlated with samples taken in 2004 from an elevation of 24–26 m above river level.

Insect faunas recovered from old (Kiselev, 1981) and our new samples are similar, with the exception of

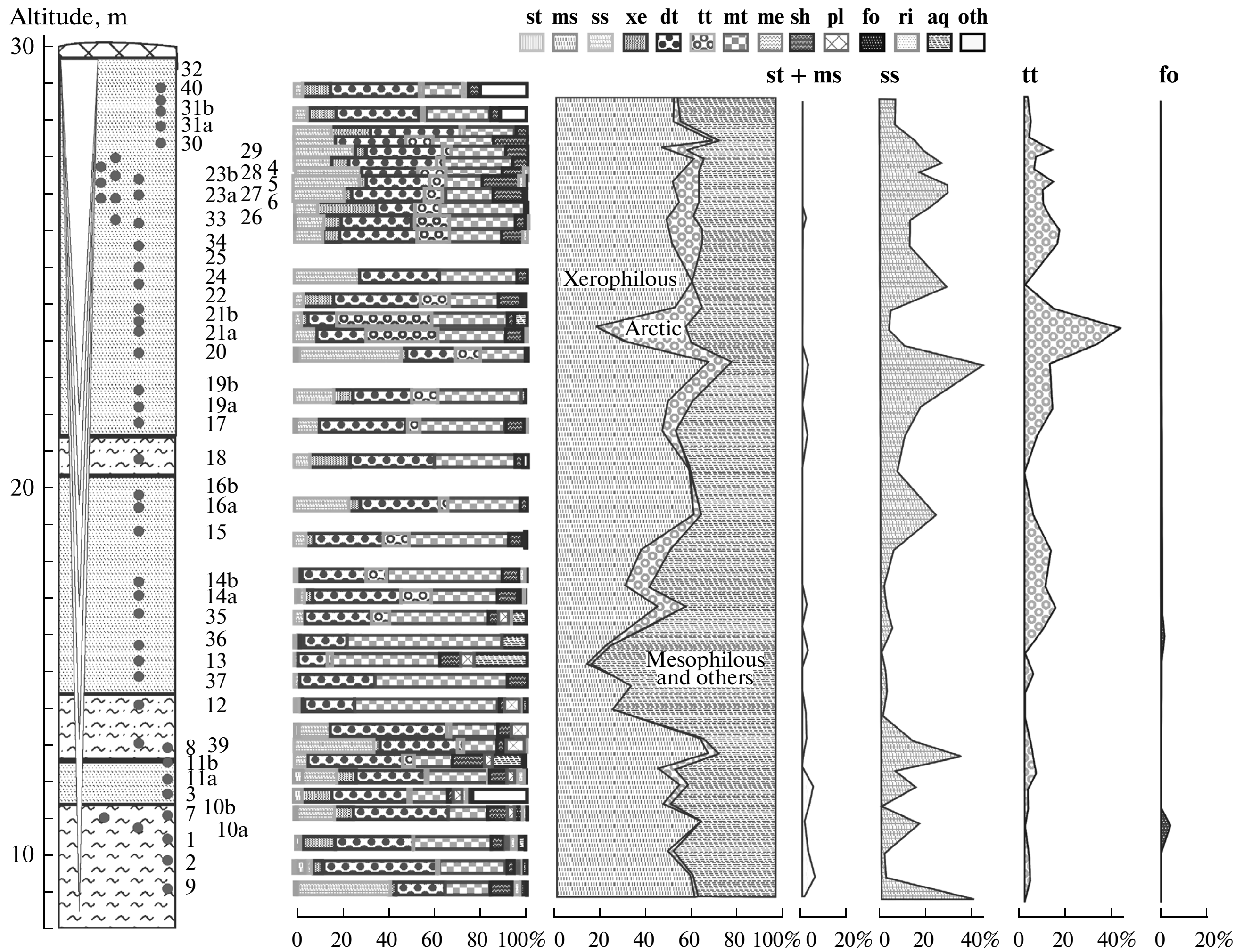


Fig. 33. Stratigraphic scheme of the Late Pleistocene deposits and insect assemblages from the Ice Bluff, Main River, Chukotka. For legend, see Figs. 15 and 16.

aquatic species, which are known only from previous studies. Other observations, such as an almost complete absence of thermophilous steppe insects and abundance of the dung beetle *Aphodius* sp., were noted in both the previously collected and new samples and illustrate the peculiarity of the local entomofauna.

The oldest and lowest sample from 2004 was taken in trench IB-4b. The insect samples were taken from gray sand; there was no visual organic matter, but plant and insect remains were recovered after screening.

Sample ChM-B9 (Table 34) is dominated by *Morychus viridis* (40%). The next three most frequent groups are **dt** (22%), **mt** (19%), and **sh** (11%); other groups are minor (**ms, xe, ri, aq, oth**) or absent (**st, tt, me, pl, fo**). One interesting specimen is the leaf beetle *Chrysomela blaisdelli*, which feeds on willow and is rarely found to the 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 two lowermost samples, while containing a relatively low percentage of steppe–tundra indicators, contain a single individual of the true steppe ground beetle *Cymindis arctica* and a few remains of the meadow–steppe weevil *Coniocleonus* sp. The relative proportions of the pill beetle *Morychus viridis* increases from 1–2% in the lower samples to 33% in the upper sample of sequence B-8. There are also single occurrences of the arctic weevil *Isochnus arcticus* and the arctic leaf beetle *Chrysolina tolli*.

The majority of samples (29 in all) were taken in the main cut, IB-2b, between ca. 11 and 26 m above the river (see Table 2 and Fig. 4). It should be noted that the lower samples (B-11a, B-11b, and B-39) overlap the upper samples of cut IB-1 in elevation, but they are represented by different fossil insect assemblages; assemblages B-11a, B-11b, and B-39 have a less pro-

Table 34. Insects from the Main site, Late Pleistocene (part 1)

Section	4b	1					5	2			
Species/sample ChM-B	9	2	1	7	3	8	38	10	11a	11b	eco
Order Coleoptera											
Family Carabidae											
Subfamily Nebriinae											
Notiophilus aquaticus L.	2	4	25	4	11	1	–	–	3	–	**xe**
Subfamily Carabinae											
Carabus odoratus Motsch.	–	–	1	–	–	–	–	–	–	–	**dt**
Carabus sp.	1	–	–	–	–	–	–	–	–	–	**mt?**
Subfamily Elaphrinae											
Elaphrus riparius L.	1	–	–	–	–	–	–	–	–	–	**ri**
Elaphrus splendidus F.-W.	–	1	2	–	–	–	–	–	–	–	**ri**
Subfamily Trechinae											
Bembidion (*Peryphanes*) *dauricum* Motsch.	–	–	–	–	–	1	–	–	–	–	**dt**
Bembidion (*Plataphodes*) sp.	–	–	2	–	–	–	–	–	–	–	**ri**
Subfamily Harpalinae											
Tribe Harpalini											
Dicheirotrichus mannerheimi Sahlb.	–	–	–	1	2	9	–	1	1	–	**dt**
Harpalus vittatus alaskensis Lth.	1	1	–	–	–	–	–	1	–	–	**ms**
Tribe Lebiini											
Cymindis arctica Kryzh. et Em.	–	1	1	–	–	–	–	–	–	–	**st**
Tribe Pterostichini											
Pterostichus (*Cryobius*) *brevicornis* (Kby.)	2	2	3	1	2	3	–	–	2	–	**mt**
P. (*Cryobius*) *nigripalpis* Popp.	–	–	–	–	–	2	–	–	–	–	**dt**
P. (*Cryobius*) *pinguedineus* Esch.	–	–	9	1	1	1	–	–	–	–	**mt**
P. (*Cryobius*) *ventricosus* Esch.	1	–	5	–	–	1	–	–	2	–	**mt**
Pterostichus (*Cryobius*) sp.	12	4	22	6	6	2	2	3	8	4	**mt**
P. (*Lenapterus*) *agonus* Horn.	–	–	2	–	1	–	–	–	–	1	**mt**
P. (*Lenapterus*) *vermiculosus* Men.	–	–	–	1	–	1	–	–	–	–	**mt**
P. (*Petrophilus*) *abnormis* Sahlb.	–	–	1	–	–	–	–	–	–	1	**dt**
P. (*P.*) *montanus* (Motsch.)	–	–	1	–	–	–	–	–	–	2	**dt**
P. (*Tundraphilus*) *sublaevis* Sahlb.	–	1	1	1	1	–	–	–	1	–	**dt**
Stereocerus haematopus (Dej.)	2	4	12	4	1	7	–	2	2	–	**dt**
Tribe Zabrini											
Amara glacialis Mnnh.	2	–	–	–	–	–	–	–	–	–	**dt**
Curtonotus alpinus Payk.	19	18	20	10	9	10	3	1	11	10	**dt**
C. bokori Csiki	–	–	1	–	–	–	–	–	–	–	**dt**
Family Dytiscidae											
Subfamily Agabinae											
Agabus moestus (Curt.)	–	–	2	–	1	–	–	–	2	4	**aq**
A. thomsoni (J. Sach.)	–	2	3	–	–	–	–	–	–	–	**aq**
Agabus sp.	1	–	–	–	–	–	–	–	–	–	**aq**
Subfamily Hydroporinae											
Hydroporus acutangulus Thoms.?	–	–	2	–	–	–	–	–	–	4	**aq**
Family Hydrophilidae											
Subfamily Helophorinae											
Helophorus splendidus Sahlb.	1	–	–	–	–	–	–	–	–	–	**aq**

Table 34. (Contd.)

Section	4b	1				5	2			
Species/sample ChM-B	9	2	1	7	3	8	38	10	11a	11b	eco
Subfamily Sphaeridiinae											
Cercyon sp.	–	–	–	–	–	1	–	–	–	–	**ri**
Family Leiodidae											
Subfamily Leiodinae											
Cyrtoplastus irregularis Rtt.	–	–	1	–	1	7	–	2	1	–	**pl**
Family Staphylinidae											
Subfamily Omaliinae											
Micralymma brevilingue Schiodte	–	–	2	–	–	–	–	–	1	–	**mt**
Olophrum latum Maekl.	–	2	2	2	2	2	2	2	2	2	**pl**
Subfamily Tachyporinae											
Tachinus arcticus Motsch.	–	2	–	–	–	–	–	–	–	4	**mt**
T. brevipennis Sahlb.	10	19	13	1	3	6	2	–	9	–	**mt**
Tachyporus sp.	–	–	–	1	–	–	–	–	–	–	**pl**
Family Scarabaeidae											
Aphodius sp.	–	1	2	2	–	2	1	–	4	–	**xe**
Family Byrrhidae											
Subfamily Byrrhinae											
Morychus viridis Kuzm. et Korot.	55	2	1	11	–	34	6	8	13	3	**ss**
Simplocaria sp.	–	–	–	–	–	1	–	–	–	–	**dt**
Subfamily Syncalyptinae											
C*urimopsis cyclolepidia* Muenst.	–	–	–	2	–	–	–	–	1	2	**dt**
Family Ptinidae											
Subfamily Anobiinae											
Caenocara bovistae Hoffm.	–	–	–	1	–	–	–	–	–	–	**fo**
Family Coccinellidae											
Subfamily Coccinellinae											
Coccinella fulgida Wat. ?	–	–	1	–	22	–	–	–	–	–	**oth**
Coccinella sp.	–	–	–	–	–	–	–	–	–	1	**oth**
Hippodamia arctica Schneid.	–	–	1	1	2	–	–	–	–	–	**ri**
Family Chrysomelidae											
Subfamily Chrysomelinae											
Chrysolina septentrionalis Men.	1	–	3	2	1	1	–	–	1	1	**mt**
Ch. tolli Jac.	–	–	1	–	–	–	–	–	–	1	**tt**
Chrysomela blaisdelli V. D.	6	–	–	–	–	–	–	–	–	–	**sh**
Hydrothassa hannoverana F.	1	–	–	–	–	–	–	–	–	–	**ri**
Phaedon armoraciae L.	–	–	–	–	–	–	–	–	1	–	**me**
Plagiodera versicolora Laich.	1	–	–	–	–	–	–	–	–	–	**sh**
Family Brentidae											
Subfamily Apioninae											
Hemitrichapion tschernovi T.-M.	–	1	1	–	–	–	–	–	–	1	**dt**
Mesotrichapion wrangelianum Kor.	4	3	4	–	4	4	–	–	5	2	**dt**
Pseudoprotapion astragali Payk.	–	–	1	–	–	–	–	–	–	–	**ms**
Family Brachyceridae											
Subfamily Erirhininae											
Notaris aethiops F.	–	–	1	–	–	–	–	–	–	–	**ri**

Table 34. (Contd.)

Section	4b	1					5	2			
Species/sample ChM-B	9	2	1	7	3	8	38	10	11a	11b	eco
Family Curculionidae											
Subfamily Ceutorhynchinae											
Pelenomus velaris Gyll.	–	–	–	–	–	–	–	–	3	–	**ri**
Subfamily Entiminae											
Tribe Sitonini											
Sitona borealis Kor.	3	1	3	–	1	–	–	–	2	1	**dt**
Subfamily Hyperinae											
Hypera diversipunctata Schrank.	–	–	8	3	7	–	1	1	3	4	**dt**
H. ornata Cap.	–	19	6	7	4	–	–	–	–	1	**dt**
Subfamily Lixinae											
Tribe Cleonini											
Coniocleonus ferrugineus Fahr.	–	3	–	–	2	–	–	1	–	–	**ms**
C. vinocurovi T.-M. et Kor.	–	–	–	–	–	–	–	–	3	–	**ms**
Coniocleonus sp.	–	–	2	1	–	–	–	–	–	–	**ms**
Subfamily Molytinae											
Tribe Lepyrini											
Lepyrus gemellus Kby.	–	–	4	4	–	–	–	–	–	–	**sh**
L. nordenskioeldi Faust	4	–	4	1	1	2	–	–	5	5	**sh**
L. volgensis Fst.	–	4	3	–	1	–	–	–	–	3	**sh**
Subfamily Curculioninae											
Tribe Elliscini											
Dorytomus rufulus amplipennis Tourn.	–	–	–	1	–	–	–	–	–	–	**sh**
Tribe Rhamphini											
Isochnus arcticus Kor.	–	1	–	–	1	3	–	–	1	2	**tt**
I. flagellum Erics.	4	1	–	–	–	1	–	–	1	–	**sh**
Order Heteroptera											
Family Saldidae											
Salda sp.	2	–	–	–	–	–	–	–	–	–	**ri**
Saldula sp.	–	–	1	–	–	–	–	–	–	–	**ri**
Family Pentatomidae											
Aelia sp.	–	1	–	–	1	–	–	–	–	–	**ms**
Pentatomidae gen. indet	–	–	–	1	–	–	–	–	–	–	**oth**
Order Megaloptera											
Family Sialidae											
Sialis sp.	–	–	–	–	–	1	–	–	–	–	**aq**
Order Diptera											
Diptera gen. indet (pseudopupia)	–	–	–	–	–	–	–	–	1	–	**oth**
Sum	136	98	180	70	88	102	17	22	88	59	

Table 35. Insects from the Main site, Late Pleistocene (part 2)

Section	3										
Species/sample ChM-B	39	12	37	13	36	35	14a	14b	15	16a	eco
Order Coleoptera											
Family Carabidae											
Subfamily Carabinae											
Carabus arvensis Hbst.	–	–	–	–	–	–	1	–	–	–	**fo**
C. shilenkovi O. Berl.	–	–	–	–	–	–	1	–	–	–	**dt**
C. truncaticollis Esch.	–	1	–	–	–	1	–	1	–	–	**mt**
Carabus sp.	–	–	–	–	–	–	–	–	1	–	**oth**
Subfamily Trechinae											
Bembidion (*Peryphanes*) *dauricum* Motsch.	1	–	–	–	–	–	–	–	–	–	**dt**
Subfamily Harpalinae											
Tribe Harpalini											
Dicheirotrichus mannerheimi Sahlb.	–	–	1	–	–	1	–	1	–	–	**dt**
Tribe Lebiini											
Cymindis arctica Kryzh. et Em.	1	1	–	–	1	–	1	–	–	–	**st**
Tribe Pterostichini											
Pterostichus (*Cryobius*) *brevicornis* (Kby.)	–	26	8	–	7	–	–	5	1	–	**mt**
P. (*Cryobius*) *pinguedineus* Esch.	–	–	1	–	3	2	–	–	3	–	**mt**
P. (*Cryobius*) *ventricosus* Esch.	1	3	1	2	3	2	1	–	–	2	**mt**
Pterostichus (*Cryobius*) sp.	6	19	12	14	18	15	13	32	8	3	**mt**
P. (*Lenapterus*) *agonus* Horn.	–	–	–	–	2	1	–	1	–	–	**mt**
P. (*Lenapterus*) *costatus* Men.	–	1	–	3	2	–	–	–	–	–	**mt**
P. (*Lenapterus*) *vermiculosus* Men.	–	–	–	1	1	–	1	5	–	–	**mt**
P. (*Petrophilus*) *abnormis* Sahlb.	–	–	–	–	–	–	1	1	–	–	**dt**
P. (*P.*) *montanus* (Motsch.)	–	–	–	–	1	–	1	–	–	–	**dt**
P. (*Tundraphilus*) *sublaevis* Sahlb.	1	2	–	–	–	1	–	–	–	–	**dt**
Stereocerus haematopus (Dej.)	2	5	6	2	3	2	6	9	3	4	**dt**
Tribe Zabrini											
Amara glacialis Mnnh.	–	–	–	–	–	1	–	–	1	1	**dt**
A. interstitialis Dej.	–	–	–	–	–	–	–	–	–	–	**dt**
Curtonotus alpinus Payk.	14	9	5	3	4	8	13	8	7	3	**dt**
C. bokori Csiki	–	–	–	–	–	–	–	–	–	1	**dt**
Family Dytiscidae											
Subfamily Agabinae											
Agabus moestus (Curt.)	–	1	–	6	2	1	–	2	–	–	**aq**
Agabus sp.	–	–	–	–	–	–	1	–	1	–	**aq**
Subfamily Hydroporinae											
Hydroporus acutangulus Thoms.?	–	–	–	4	2	5	–	–	–	–	**aq**
H. lapponum (Gyll.)	–	–	–	1	–	–	–	–	–	–	**aq**
Hydroporus sp.	–	1	–	–	1	–	–	–	–	–	**aq**
Family Hydrophilidae											
Subfamily Helophorinae											
Helophorus splendidus Sahlb.	–	–	–	2	2	–	–	–	–	–	**aq**
Subfamily Sphaeridiinae											
Cercyon sp.	–	–	–	–	–	–	1	–	–	–	**ri**
Family Leiodidae											
Subfamily Leiodinae											
Cyrtoplastus irregularis Rtt.	2	4	–	–	–	2	–	–	–	–	**pl**
Family Staphylinidae											
Subfamily Omaliinae											
Olophrum latum Maekl.	2	2	–	–	–	–	–	–	–	–	**pl**
Subfamily Tachyporinae											
Tachinus brevipennis Sahlb.	2	7	1	6	5	16	19	12	20	6	**mt**

Table 35. (Contd.)

Section	3										
Species/sample ChM-B	39	12	37	13	36	35	14a	14b	15	16a	eco
Subfamily Steninae											
Stenus sp.	–	–	–	–	–	–	–	1	–	–	**ri**
Subfamily Paederinae											
Lathrobium sp.	–	–	–	3	–	2	–	–	–	–	**pl**
Family Scarabaeidae											
Aphodius sp.	–	1	–	–	1	–	5	1	3	2	**xe**
Family Scirtidae											
Cyphon sp.	–	–	–	–	–	–	–	1	–	–	**ri**
Family Byrrhidae											
Subfamily Byrrhinae											
Morychus viridis Kuzm. et Korot.	6	1	1	1	–	4	3	2	4	7	**ss**
Subfamily Syncalyptinae											
Curimopsis cyclolepidia Muenst.	2	–	–	1	–	2	2	4	1	–	**dt**
Family Coccinellidae											
Subfamily Coccinellinae											
Hippodamia arctica Schneid.	–	1	–	–	–	–	–	–	–	–	**ri**
Family Chrysomelidae											
Subfamily Chrysomelinae											
Chrysolina septentrionalis Men.	–	–	–	–	–	–	2	1	1	–	**mt**
Ch. subsulcata Mnnh.	–	–	–	–	–	–	1	–	–	–	**tt**
Ch. tolli Jac.	–	–	–	1	–	3	1	–	–	–	**tt**
Family Brentidae											
Subfamily Apioninae											
Hemitrichapion tschernovi T.-M.	1	–	1	–	–	–	3	2	2	–	**dt**
Mesotrichapion wrangelianum Kor.	1	–	–	1	1	2	–	2	1	–	**dt**
Family Curculionidae											
Subfamily Ceutorhynchinae											
Ceutorhynchus sp.	–	–	–	–	–	–	1	–	–	–	**dt**
Subfamily Entiminae											
Tribe Sitonini											
Sitona borealis Kor.	–	–	–	–	1	1	4	2	1	1	**dt**
Subfamily Hyperinae											
Hypera diversipunctata Schrank.	–	2	–	–	–	6	13	3	3	2	**dt**
H. ornata Cap.	–	3	–	–	2	–	2	–	4	–	**dt**
Subfamily Lixinae											
Tribe Cleonini											
Coniocleonus sp.	–	–	–	–	–	–	1	–	–	–	**ms**
Subfamily Molytinae											
Tribe Lepyrini											
Lepyrus gemellus Kby.	–	1	–	2	–	1	2	1	–	–	**sh**
L. nordenskioeldi Faust	2	1	4	1	–	2	5	2	2	1	**sh**
L. volgensis Fst.	–	–	–	–	–	–	–	2	–	–	**sh**
Subfamily Curculioninae											
Tribe Elliscini											
Dorytomus sp.	–	1	–	1	–	–	–	–	–	–	**sh**
Tribe Rhamphini											
Isochnus arcticus Kor.	1	–	–	–	–	4	14	10	9	2	**tt**
I. flagellum Erics.	–	–	–	1	–	–	5	3	3	–	**sh**
Order Heteroptera											
Family Saldidae											
Salda sp.	–	–	–	–	–	1	–	–	–	–	**ri**
Order Diptera											
Diptera gen. indet (pseudopupia)	–	–	1	–	–	–	–	–	–	–	**oth**
Sum	45	93	41	56	62	86	124	114	79	35	

Table 36. Insects from the Main site, Late Pleistocene (part 3)

Section	2										
Species/sample ChM-B	16b	18	17	19a	19b	20	21a	21b	22	24	eco
Order Coleoptera											
Family Carabidae											
Subfamily Nebriinae											
Notiophilus aquaticus L.	–	4	–	–	1	1	–	1	–	–	**xe**
Subfamily Carabinae											
Carabus odoratus Motsch.?	–	–	–	–	–	–	–	–	1	–	**dt**
C. truncaticollis Esch.	–	–	2	–	–	–	–	–	–	–	**mt**
Carabus sp.	–	1	–	–	–	–	–	–	–	–	**oth**
Subfamily Elaphrinae											
Elaphrus riparius L.	–	–	–	–	–	–	1	–	–	–	**ri**
Subfamily Harpalinae											
Tribe Pterostichini											
Pterostichus (*Cryobius*) *brevicornis* (Kby.)	–	–	–	–	–	1	–	–	–	–	**mt**
P. (*Cryobius*) *pinguedineus* Esch.	–	–	–	–	2	2	–	–	–	1	**mt**
P. (*Cryobius*) *ventricosus* Esch.	1	–	–	1	2	–	–	–	–	–	**mt**
Pterostichus (*Cryobius*) sp.	2	2	7	3	2	5	2	2	2	7	**mt**
P. (*Lenapterus*) *agonus* Horn.	–	–	–	–	–	–	1	–	–	–	**mt**
P. (*L.*) *costatus* Men.	–	–	–	1	–	–	–	–	–	–	**mt**
P. (*Lenapterus*) *vermiculosus* Men.	–	–	–	–	–	–	–	–	–	1	**mt**
P. (*Tundraphilus*) *sublaevis* Sahlb.	–	–	1	1	–	–	–	1	–	–	**dt**
Stereocerus haematopus (Dej.)	1	–	6	–	1	3	–	–	2	1	**dt**
Tribe Zabrini											
Amara glacialis Mnnh.	1	1	–	1	–	1	1	–	1	1	**dt**
Curtonotus alpinus Payk.	4	3	7	4	2	9	6	5	4	5	**dt**
Family Dytiscidae											
Subfamily Agabinae											
Agabus sp.	–	–	–	–	–	–	–	2	1	–	**aq**
Subfamily Hydroporinae											
Hydroporus sp.	–	–	–	–	–	–	–	1	–	–	**aq**
Family Hydrophilidae											
Subfamily Helophorinae											
Helophorus splendidus Sahlb.	–	–	–	1	–	–	–	1	–	–	**aq**
Family Staphylinidae											
Subfamily Omaliinae											
Micralymma brevilingue Schiodte	–	–	–	–	–	–	–	–	1	–	**mt**
Subfamily Tachyporinae											
Tachinus arcticus Motsch.	–	3	6	2	4	–	3	9	1	–	**mt**
T. brevipennis Sahlb.	4	7	2	4	–	5	7	9	4	–	**mt**
Family Scarabaeidae											
Aphodius sp.	1	3	–	4	–	1	–	1	6	–	**xe**
Family Byrrhidae											
Subfamily Byrrhinae											
Morychus viridis Kuzm. et Korot.	7	3	5	4	6	29	5	2	2	9	**ss**
Subfamily Syncalyptinae											
Curimopsis cyclolepidia Muenst.	–	–	1	–	–	1	2	–	3	–	**dt**

Table 36. (Contd.)

Section	2										
Species/sample ChM-B	16b	18	17	19a	19b	20	21a	21b	22	24	eco
Family Chrysomelidae											
Subfamily Chrysomelinae											
Chrysolina septentrionalis Men.	–	2	4	–	1	–	2	1	2	2	**mt**
Ch. subsulcata Mnnh.	–	–	–	–	–	2	–	–	–	–	**tt**
Chrysomela blaisdelli V. D.	–	–	1	–	–	–	–	–	–	–	**sh**
Family Brentidae											
Subfamily Apioninae											
Hemitrichapion tschernovi T.-M.	–	–	1	–	–	–	–	–	–	1	**dt**
Mesotrichapion wrangelianum Kor.	1	4	2	2	1	–	1	–	1	1	**dt**
Family Curculionidae											
Subfamily Entiminae											
Tribe Sitonini											
Sitona borealis Kor.	–	2	2	1	–	–	1	2	4	2	**dt**
Subfamily Hyperinae											
Hypera diversipunctata Schrank.	1	3	2	–	2	–	–	–	1	–	**dt**
H. ornata Cap.	–	1	–	–	–	–	–	–	1	–	**dt**
Subfamily Lixinae											
Tribe Cleonini											
Coniocleonus sp.	–	–	1	–	–	1	–	–	–	–	**ms**
Subfamily Molytinae											
Tribe Lepyrini											
Lepyrus gemellus Kby.	–	–	–	–	–	–	1	–	–	–	**sh**
L. nordenskioeldi Faust	–	1	4	–	–	1	3	2	4	1	**sh**
Subfamily Curculioninae											
Tribe Rhamphini											
Isochnus arcticus Kor.	–	–	3	4	3	5	16	27	6	–	**tt**
I. flagellum Erics.	1	–	–	–	–	–	–	–	1	–	**sh**
Order Heteroptera											
Family Corixidae											
Sigara sp.	–	–	1	–	–	–	–	–	–	–	**ri**
Order Trichoptera											
Thrichoptera gen. indet. (larvae)	–	–	–	–	–	–	–	1	–	–	**aq**
Sum	24	40	58	33	27	67	52	66	48	32	

nounced steppe component. The sediments also differ, suggesting that one or another section contains displaced material or that the sections are not coeval. In trench IB-2b, we focus on samples above the radiocarbon date of 29.78 ±0.21 ka.

The assemblages from samples B-12–B-15, from ca. 12 m to ca. 18 m above datum and, according to the radiocarbon dates, representing a period from ca. 30 to ca. 25 ka ^{14}C , show a gradual decrease in the proportions of steppe–tundra indicators and all xerophilous groups, while the proportion of mesophilous tundra insects increases (up to 61%, sample B-12); the shrub group is significant (7–9%). One of the assemblages (B-13, 14.8m) contains abundant remains of aquatic insects (the aquatic scavenger beetles *Hydroporus acutangulus, H. lapponum*, and *Agabus moestus*). These features, along with the high frequency of mesophilous tundra and shrub groups, the lesser role of xerophilous species, unstable presence of steppe insects, which are poor in species diversity, and permanent presence of

Table 37. Insects from the Main site, Late Pleistocene (part 4)

Section	2						3			3a	
Species/sample ChM-B	25	34	33	23a	23b	23c	6	5	4	26	eco
Order Coleoptera											
Family Carabidae											
Subfamily Nebriinae											
Notiophilus aquaticus L.	–	–	–	12	2	1	–	–	1	14	**xe**
Subfamily Carabinae											
Carabus truncaticollis Esch.	–	–	–	–	–	–	–	–	–	1	**mt**
Subfamily Trechinae											
Bembidion (*Peryphanes*) sp.	–	–	–	–	–	–	–	–	–	1	**ri**
Subfamily Harpalinae											
Tribe Harpalini											
Harpalus vittatus alaskensis Lth.	–	2	–	–	–	–	–	–	–	1	**ms**
Tribe Pterostichini											
Pterostichus (*Cryobius*) *brevicornis* (Kby.)	–	–	–	–	–	–	2	1	–	1	**mt**
P. (*Cryobius*) *pinguedineus* Esch.	–	–	–	2	–	–	–	–	–	2	**mt**
P. (*Cryobius*) *ventricosus* Esch.	–	–	–	–	–	–	–	–	1	1	**mt**
Pterostichus (*Cryobius*) sp.	1	1	1	4	4	2	2	2	6	20	**mt**
P. (*Lenapterus*) *costatus* Men.	–	–	–	–	–	–	–	1	–	1	**mt**
P. (*Lenapterus*) *vermiculosus* Men.	–	–	–	–	–	–	–	–	–	1	**mt**
P. (*Petrophilus*) *abnormis* Sahlb.	–	–	–	–	–	–	–	–	–	4	**dt**
P. (*Tundraphilus*) *sublaevis* Sahlb.	–	–	–	–	–	–	–	–	1	1	**dt**
Stereocerus haematopus (Dej.)	1	–	1	3	2	2	1	1	2	5	**dt**
Tribe Zabrini											
Amara glacialis Mnnh.	–	1	1	–	–	–	1	1	1	6	**dt**
A. interstitialis Dej.	–	1	–	–	–	–	–	–	–	–	**dt**
Curtonotus alpinus Payk.	1	1	6	4	5	6	8	10	11	51	**dt**
C. bokori Csiki	–	–	–	–	1	–	1	–	–	–	**dt**
Family Dytiscidae											
Subfamily Agabinae											
Agabus sp.	–	–	–	–	–	–	–	1	–	–	**aq**
Subfamily Hydroporinae											
Hydroporus acutangulus Thoms.?	–	–	–	–	–	–	1	–	–	–	**aq**
Family Hydrophilidae											
Subfamily Helophorinae											
Helophorus splendidus Sahlb.	–	–	–	–	–	–	–	–	–	1	**aq**
Family Staphylinidae											
Subfamily Omaliinae											
Micralymma brevilingue Schiodte	–	–	1	–	–	–	–	–	–	–	**mt**
Subfamily Tachyporinae											
Tachinus arcticus Motsch.	–	–	1	15	6	2	–	–	1	46	**mt**
T. brevipennis Sahlb.	–	–	6	–	5	–	9	5	6	20	**mt**
Family Scarabaeidae											
Aphodius sp.	1	5	3	3	1	1	2	2	1	9	**xe**
Family Byrrhidae											
Subfamily Byrrhinae											
Morychus viridis Kuzm. et Korot.	2	7	5	6	6	4	13	19	14	44	**ss**
Subfamily Syncalyptinae											
Curimopsis cyclolepidia Muenst.	–	–	1	–	–	–	2	–	1	7	**dt**

Table 37. (Contd.)

Section	2						3			3a	
Species/sample ChM-B	25	34	33	23a	23b	23c	6	5	4	26	eco
Family Chrysomelidae											
Subfamily Chrysomelinae											
Chrysolina arctica Medv.	–	–	–	–	–	–	–	–	–	1	**ms**
Ch. septentrionalis Men.	–	–	–	–	–	–	–	1	–	6	**mt**
Hydrothassa hannoverana F.	–	–	–	–	–	–	–	1	–	–	**ri**
Family Brentidae											
Subfamily Apioninae											
Hemitrichapion tschernovi T.-M.	–	–	1	–	–	–	2	1	–	5	**dt**
Mesotrichapion wrangelianum Kor.	–	–	3	1	5	2	2	1	1	11	**dt**
Family Curculionidae											
Subfamily Ceutorhynchinae											
Ceutorhynchus sp.	–	–	–	–	–	–	–	–	1	2	**dt**
Subfamily Entiminae											
Tribe Sitonini											
Sitona borealis Kor.	–	–	1	1	–	–	–	2	–	4	**dt**
Subfamily Hyperinae											
Hypera diversipunctata Schrank.	–	–	–	–	–	1	–	3	2	5	**dt**
H. ornata Cap.	–	–	–	1	–	–	2	–	–	9	**dt**
Subfamily Lixinae											
Tribe Cleonini											
Coniocleonus cinerascens Hochh.	–	–	–	–	–	–	–	–	–	1	**ms**
C. zherichini T.-M. et Kor.	–	–	–	–	–	–	–	–	–	1	**dt**
Subfamily Molytinae											
Tribe Lepyrini											
Lepyrus gemellus Kirby	–	–	–	–	–	–	–	–	–	1	**sh**
Lepyrus nordenskioeldi Faust	–	–	3	–	1	2	4	8	3	15	**sh**
L. volgensis F.	–	–	–	–	–	–	2	2	1	–	**sh**
Lepyrus sp.	–	1	–	1	–	–	–	–	–	–	**sh**
Subfamily Curculioninae											
Tribe Rhamphini											
Isochnus arcticus Kor.	–	–	6	6	–	2	5	6	2	54	**tt**
I. flagellum Erics.	–	–	1	–	–	–	2	2	1	–	**sh**
Order Heteroptera											
Family Saldidae											
Salda sp.	–	–	1	–	–	–	–	–	–	–	**ri**
Order Hymenoptera											
Family Formicidae											
Hymenoptera gen. indet.	–	–	–	–	–	–	–	1	–	–	**oth**
Order Megaloptera											
Family Sialidae											
Sialis sp.	–	–	–	–	–	–	–	1	–	11	**aq**
Order Trichoptera											
Thrichoptera gen. indet. (larvae)	–	–	–	–	–	–	–	1	–	2	**aq**
Order Diptera											
Diptera gen. indet (pseudopupia)	–	–	–	–	–	–	–	–	–	3	**oth**
Sum	6	19	42	59	38	25	61	70	57	352	

Table 38. Insects from the Main site (part 5) and Anadyr site

Site	Main								Anadyr				
Age	Late Pleistocene									Holocene			
Section	3a			6									
Species/sample ChM-B	27	28	29	30	31a	31b	40	32					eco
Sample A–B									4	1	3	2	
Order Coleoptera													
Family Gyrinidae													
Gyrinus sp.	–	–	–	–	–	–	–	–	–	2	1	1	**aq**
Family Carabidae													
Subfamily Nebriinae													
Nebria frigida Sahlb.	–	–	–	–	–	–	–	–	–	–	1	1	**ri**
Notiophilus aquaticus L.	–	–	–	8	2	1	–	4	2	–	–	–	**xe**
Pelophila borealis Payk.	–	–	–	–	–	–	–	–	–	2	–	–	**ri**
Subfamily Carabinae													
Carabus truncaticollis Esch.	–	–	–	–	–	–	1	–	–	3	–	–	**mt**
C. vietinghoffi Adams	–	–	–	–	–	–	–	–	–	–	1	–	**fo**
Subfamily Elaphrinae													
Blethisa multipunctata (L.)	–	–	–	–	–	–	–	–	–	–	1	–	**ri**
Diacheila polita Fald.	–	1	–	–	–	–	–	–		1	3	2	**mt**
Elaphrus riparius L.	–	1	–	–	–	–	–	–	–	–	–	–	**ri**
Subfamily Trechinae													
Bembidion (*Peryphanes*) sp.	–	–	–	–	–	–	–	–	–	–	–	–	**dt**
Subfamily Patrobinae													
Patrobus septentrionis Dej.	–	–	–	–	–	–	–	–	–	–	1	–	**ri**
Subfamily Harpalinae													
Tribe Platynini													
Agonum sp.	–	–	–	–	–	–	–	–	–	–	1	–	**ri**
Tribe Pterostichini													
Pterostichus (*Cryobius*) *brevicornis* (Kby.)	–	1	–	–	4	–	–	–	–	6	3	1	**mt**
P. (*Cryobius*) *pinguedineus* Esch.	–	–	1	1	–	–	–	–	–	–	–	–	**mt**
P. (*Cryobius*) *ventricosus* Esch.	–	–	–	–	–	–	1	–	–	–	–	1	**mt**
Pterostichus (*Cryobius*) sp.	–	3	3	6	–	2	–	2	14	1	–	–	**mt**
P. (*Lenapterus*) *agonus* Horn.	–	–	–	–	–	–	–	–	–	4	1	2	**mt**
P. (*Lenapterus*) *costatus* Men.	–	–	–	–	–	–	–	–	–	–	1	–	**mt**
P. (*Lenapterus*) *vermiculosus* Men.	1	–	–	–	–	–	–	–	–	–	–	–	**mt**
P. (*Petrophilus*) *magus* Man.	–	–	–	–	–	–	–	–	–	–	2	–	**fo**
P. (*Petrophilus*) *tundrae* Tschitsch	–	–	1	–	–	–	–	–	–	–	–	–	**dt**
P. (*Tundraphilus*) *sublaevis* Sahlb.	–	1	–	–	–	1	–	–	2	–	–	–	**dt**
Stereocerus haematopus (Dej.)	1	1	1	3	1	4	1	2	4	–	1	–	**dt**
Tribe Zabrini													
Amara glacialis Mnnh.	1	–	1	1	2	–	–	1	–	–	–	–	**dt**
Curtonotus alpinus Payk.	–	6	8	4	4	3	1	5	10	2	1	–	**dt**
Family Dytiscidae													
Subfamily Agabinae													
Agabus moestus (Curt.)	–	–	–	–	–	–	–	–	1	–	–	2	**aq**
A. thomsoni (J. Sach.)	–	–	–	–	–	–	–	–	–	–	–	1	**aq**
Agabus spp.	–	–	–	–	–	–	–	–	–	7	8	2	**aq**

Table 38. (Contd.)

Site	Main									Anadyr			
Age	Late Pleistocene									Holocene			
Section	3a			6									
Species/sample ChM-B	27	28	29	30	31a	31b	40	32					eco
Sample A–B									4	1	3	2	
Subfamily Colymbetinae													
Colymbetes dolabratus (Payk.)	–	–	–	–	–	–	–	–	–	–	1	1	**aq**
Rhantus notatus Fabr.	–	–	–	–	–	–	–	–	–	2	–	–	**aq**
Subfamily Hydroporinae													
Hydroporus sp.	–	–	–	–	–	–	–	–	–	1	2	2	**aq**
Family Hydrophilidae													
Subfamily Helophorinae													
Helophorus splendidus Sahlb.	–	–	–	–	–	–	–	–	–	–	1	–	**aq**
Subfamily Hydrophilinae													
Hydrobius fuscipes F.	–	–	–	–	–	–	–	–	–	2	2	–	**aq**
Family Leiodidae													
Subfamily Cholevinae													
Cholevinus sibiricus (Jean.)	–	–	–	–	–	–	–	–	–	1	–	–	**mt**
Family Staphylinidae													
Subfamily Omaliinae													
Olophrum latum Maekl.	–	–	–	–	–	–	–	–	–	1	–	–	**pl**
O. rotundicolle Sahlb.	–	–	–	–	–	–	–	–	–	3	–	–	**pl**
Olophrum sp.	–	–	–	–	–	–	–	–	–	–	–	1	**pl**
Subfamily Tachyporinae													
Tachinus arcticus Motsch.	–	–	9	3	4	–	–	1	–	–	–	–	**mt**
T. brevipennis Sahlb.	–	7	2	2	2	1	2	4	1	–	–	–	**mt**
Family Scarabaeidae													
Aphodius sp.	3	–	–	2	3	–	–	2	1	–	–	–	**xe**
Family Scirtidae													
Cyphon variabilis (Thun.)	–	–	–	–	–	–	–	–	–	–	–	1	**ri**
Family Byrrhidae													
Subfamily Byrrhinae													
Byrrhus sp.	–	–	–	–	–	–	–	–	–	–	1	–	**me**
Morychus viridis Kuzm. et Korot.	3	14	11	9	2	1	1	2	1	–	–	–	**ss**
Simplocaria arctica Popp	–	–	–	–	–	–	–	–	1	–	–	–	**dt**
Subfamily Syncalyptinae													
Curimopsis cyclolepidia Muenst.	–	1	1	–	–	1	–	1	1	–	–	–	**dt**
Family Elateridae													
Subfamily Dendrometrinae													
Limonius sp.	–	–	–	–	–	–	–	–	–	1	–	–	**ri**
Family Coccinellidae													
Subfamily Coccinellinae													
Coccinella transversoguttata Fald.?	–	–	–	–	2	4	8	10	–	–	–	–	**oth**
Family Chrysomelidae													
Subfamily Chrysomelinae													
Chrysolina septentrionalis Men.	–	1	1	1	1	–	–	1	1	–	–	–	**mt**

Table 38. (Contd.)

Site	Main									Anadyr			
Age	Late Pleistocene									Holocene			
Section	3a			6									
Species/sample ChM-B	27	28	29	30	31a	31b	40	32					eco
Sample A–B									4	1	3	2	
Ch. subsulcata Mnnh.	–	–	–	–	–	–	–	–	3	–	–	–	**tt**
Ch. tolli Jac.	–	–	–	–	–	–	–	–	3	–	–	–	**tt**
Phaedon concinnus Steph.	–	–	–	–	–	–	–	–	1	–	–	–	**me**
Phratora polaris Schn.	–	–	–	–	–	–	–	1	–	–	–	–	**sh**
Ph. vulgatissima L.	–	–	–	–	–	–	–	–	–		–	1	**sh**
Plagiodera versicolora Laich.	–	–	–	–	–	–	–	–	–	1	–	–	**sh**
Family Brentidae													
Subfamily Apioninae													
Hemitrichapion tschernovi T.-M.	–	–	–	2	–	–	–	–	–	–	–	–	**dt**
Mesotrichapion wrangelianum Kor.	–	1	3	3	–	–	2	4	–	–	–	–	**dt**
Family Brachyceridae													
Subfamily Erirhininae													
Notaris bimaculatus F.	–	–	–	–	–	–	–	–	–	1	1	–	**ri**
N. eversmanni Faust	–	–	–	–	–	–	–	–	–	17	1	4	**ri**
Family Curculionidae													
Subfamily Entiminae													
Tribe Phyllobini													
Phyllobius virideaeris Laich.	–	–	–	–	–	–	–	1	–	–	–	–	**me**
Tribe Sitonini													
Sitona borealis Kor.	–	–	–	3	1	–	–	2	–	–	–	–	**dt**
Subfamily Hyperinae													
Hypera diversipunctata Schrank.	–	1	4	6	–	–	2	4	–	–	–	–	**dt**
H. ornata Cap.	–	–	–	–	1	–	–	–	–	–	–	–	**dt**
Subfamily Lixinae													
Subfamily Molytinae													
Tribe Lepyrini													
Lepyrus nordenskioeldi Faust	–	2	9	3	–	–	1	2	2	1	–	1	**sh**
Lepyrus sp.	1	–	–	–	2	–	–	–	–	–	–	–	**sh**
Subfamily Curculioninae													
Tribe Elliscini													
Dorytomus imbecillus Fst.	–	–	–	–	–	–	–	–	1	–	–	–	**sh**
Tribe Rhamphini													
Isochnus arcticus Kor.	–	7	7	1	1	–	1	1	11	–	–	–	**tt**
I. flagellum Erics.	–	–	–	–	–	–	–	–	1	–	–	–	**sh**
Order Megaloptera													
Family Sialidae													
Sialis sp.	–	–	–	7	–	–	–	–	–	–	–	–	**aq**
Order Trichoptera													
Thrichoptera gen. indet. (larvae)	–	–	–	–	–	–	–	–	–	23	–	–	**aq**
Order Diptera													
Diptera gen. indet (pseudopupia)	–	–	–	1	–	–	–	–	–	12	2	–	**oth**
Sum	10	48	62	58	32	18	21	50	61	59	35	24	

the arctic group are typical for the MIS3 interval and this faunal sequence is in agreement with the features of in the Bykovsii fossil insect fauna (Sher et al., 2005).

Upward in the section (samples B-16–B-20, ca. 18–22 m), radiocarbon dating shows 25.44 ± 0.13 (ca. 18 m) and 21.05 ± 0.10 ka (ca. 23 m). Xerophilous taxa again dominate: **dt** is up to 37% and **ss** is up to 43% (sample B-20). All samples contain the arctic weevil *Isochnus arcticus*.

Three succeeding samples, B-21a, B-21b, and B-22, are close to each other and characterized by an increase in the frequency of arctic species up to 41% in assemblage B-21b. This set of samples, which are closely spaced, are dated ca. 21 ka. 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 the left of the main trench, and trench IB-6, which lies to the right. Samples B-30, B-31, and B-32 (from the right trench, IB-6) are similar; they contain a small proportion of steppe–tundra indicators, although most of the insects are xerophilous. The three samples contain abundant ladybird beetles of the genus *Coccinella*, apparently *C. transversoguttata*. The fossil ladybird is not perfectly preserved because of the minimal chitin and rounded shape; we extracted many isolated pieces and calculated the Minimum Numbers of Individuals (see Elias, 1994) using the best preserved parts. The radiocarbon date of this unit is 15.81 ± 0.075 ka; this is the youngest date obtained. The lower sample (B-30) from trench IB-6 overlaps in height the upper sample (B-23b) of trench IB-2, but we suspect that the age of insect assemblage B-30 is younger than B-23b; as mentioned above, the levels dated 19.85 ± 0.08 ka (^{14}C) in IB-2 and 15.81 ± 0.075 (^{14}C) in IB-6 are separated by less than 1 m; this means either a sudden decrease in sedimentation rate or displacement of material between the two trenches. The second possibility seems more probable for this section (see above).

Samples from trenches IB-3 and IB-3a can be combined, because the trenches belong to the same section; IB-3 was made early in the field season and IB-3a is a renovation of an old trench. The radiocarbon date 20.90 ± 0.11 ka ^{14}C lies ca. 1 m above the date of 20.83 ± 0.09 ka of IB-2 trench, probably reflecting a local tectonic disruption of deposits (see above). Fossil insect assemblages from IB-3 and IB-3a are well correlated with sequence IB-2. The arctic weevil *Isochnus arcticus* is present (11–15%), but less significant than it was before; and the indicator of cold steppe *Morychus viridis* is abundant (14–29%). In addition, the most abundant assemblage (B-26, dated 20.90 ± 0.11 ka) contains single remains of two meadow–steppe species, the weevil *Coniocleonus cinerascens* and the leaf beetle *Chrysolina arctica*.

The most important insect groups in the Main River Ice Bluff assemblages are the mesic and hygrophilous tundra groups and dry tundra group. Taiga insects are virtually absent in the assemblage; one generalist tree species whose habitat is restricted to the forest zone, *Caenocara bovistaeis*, is present in one sample. The steppe elements are present, but the faunas diverge taxonomically from those of other western Beringian areas. They are similar to other faunas in the fact that the cryophyte–steppe pill beetle *Morychus viridis* plays an important role; however, thermophilous steppe insects are almost completely absent. For example, the weevil *Stephanocleonus eruditus* is one of the most tolerant and common thermophilous steppe insects across sites in western Beringia, except for the Ice Bluff, where it is not recorded. In contrast, the thermophilous steppe ground beetle *Cymindis 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, in the Ice Bluff site, *Cymindis arctica* is recorded in six samples from the lower part of the exposure. Furthermore, the great abundance of dung beetles (*Aphodius*) unusual for northeastern Asia further underlines the unusual nature of the steppe–tundra faunal group in this locality.

3.4b. Anadyr

In addition to the main geological works on the Main River in summer 2004, our research group visited a low terrace near Anadyr (Figs. 12, 31e), where Holocene peat is present. The section is situated on the right bank of the Anadyr Bay not far from the town of Anadyr. The age of the peat beds is around 6 ka (A. Kotov, personal communication).

The Anadyr section consists of two units: the lower unit is composed of gray silt with a small ice wedge cast at the top (Figs. 31e, 34). The second unit is a thick peat body, with an uneven base and lenses of silty sediment.

The composition of the two units became clear only after careful cleaning of the section. At first sight, the whole terrace is peaty, because the lower silt deposits are eroded more rapidly and the upper peat beds overhangs the section. Fossil insect assemblages proof our guess that the units differ in age (similar to the case of Mamontovyi Bysagasa, see above).

The lower sample (A-B4) was taken from silt (Fig. 34, Table 38). The assemblage is dominated by three tundra groups in almost equal proportions: **dt** = 30%, **tt** = 28%, and **mt** = 26%. The high frequency of arctic species, such as *Isochnus arcticus*, *Chrysolina tolli,* and *Ch. subsulcata* is indicative of a severe environment comparable to that of the last glacial maximum (LGM) recorded in the Ice Bluff section. The assemblage also contains individual specimens of

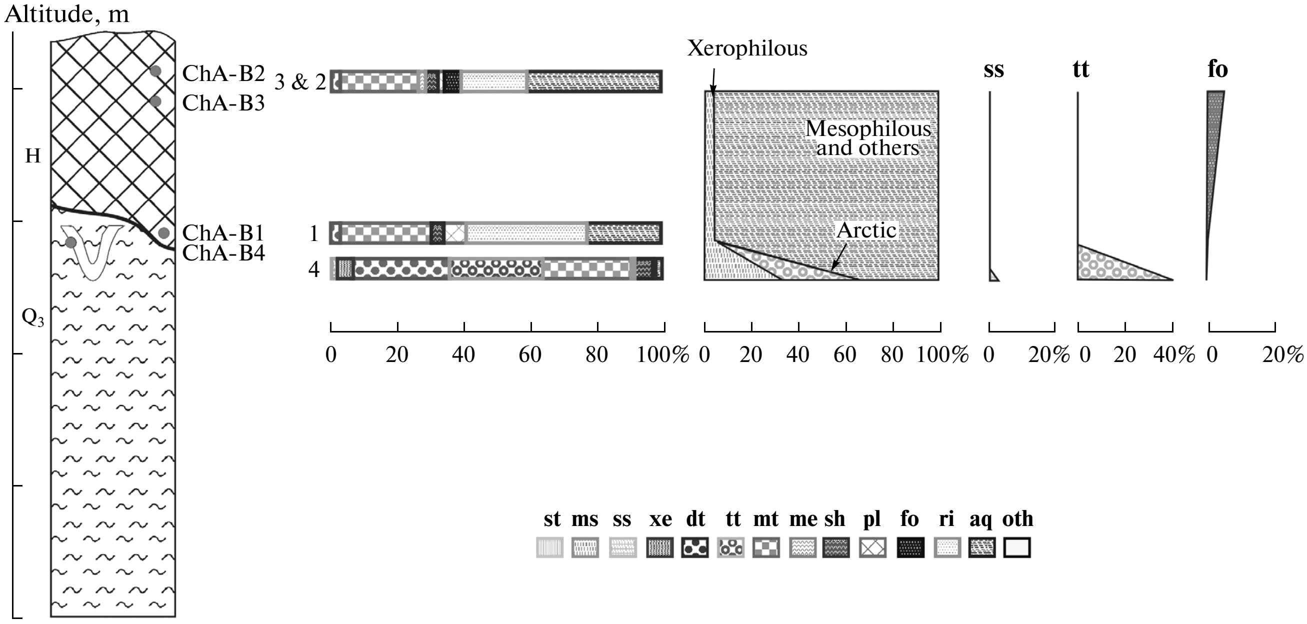


Fig. 34. Stratigraphic scheme and insect assemblages from the Anadyr site, Chukotka. For legend, see Figs. 15 and 16.

Morchus viridis, the easternmost record in western Beringia.

Three samples from the peat unit have yielded a sharply different insect fauna. Each of three assemblages is dominated by aquatic and riparian species. The lower peat sample (A-B1) includes mostly riparian species, such as *Pelophila borealis, Limonius* sp., *Notaris bimaculatus,* and abundant *N. eversmanni* (species rarely occurring in fossil assemblages). Aquatic insects are also diverse, including *Gyrinus* sp., *Agabus* spp., *Rhantus notatus, Hydroporus* sp., and *Hydrobius fuscipes*. In addition to beetles, the assemblage contains many caddis fly and fly remains. We have recorded some indicators of relatively warm environments probably close to the modern shrub tundra; there are shrub species *Plagiodera versicolora* and plant litter inhabitants *Olophrum latum* and *O. rotundicolle*.

Two upper samples from the peat beds are small, but diverse in species, we have combined them. Assemblage A-B2,3 is dominated by aquatic taxa: *Gyrinus* sp., *Agabus moestus, A. thomsoni*, *Colymbetes dolabratus, Hydroporus* sp., *Helophorus splendidus*, and *Hydrobius fuscipes.*

The riparian group is also important here: *Nebria frigida, Patrobus septentrionis, Agonum* sp., *Cyphon variabilis, Notaris bimaculatus*, and *N. eversmanni*. Two species found in the assemblage, which live in the forest zone (*Carabus vietinghoffi, Pterostichus magus*), are indicative of warmer conditions than in the modern environments.

The mesophilous tundra group is well represented in the peat samples, but the species compositions of the typical Pleistocene species and Holocene associations significantly differ. The **mt** group of samples A-B1, 2, 3 includes *Carabus truncaticollis* and *Diacheila polita*, which are rare in the Pleistocene. *Pterostichus* (*Cryobius*) *brevicornis* became the most abundant species among *Cryobius* (in the Pleistocene, this beetle is present, but other species of the subgenus are more abundant). These features are observed in other Holocene sites across western Beringia.

3.4c. Amguema River

Several small sites have been studied at the Amguema River (Fig. 12) in 1989. The expedition was focused on modern insects of relict steppe areas, so geological works played a secondary role and fossil insects were collected to reconstruct the past environment of the relict steppe; whether the Amguema steppe is a long-lived local environment or recent recolonization.

We sampled all available sections (Fig. 35, Table 39), i.e., three river floodplain terraces, a peat bed near the top of a 60-m-high river bluff, and Pleistocene ice-rich section (one sample) similar to the Late Pleistocene Ice Complex. The age of the sediment is uncertain. Pleistocene deposits in the Amguema River valley were previously studied by Kotov (2002). He worked in the same area of the Amguema Power Station (as our team did). Kotov's team did not find a proper exposure, but excavated a slope test pit and discovered sandy–silty ice-rich deposits with ice wedges. The radiocarbon age from the sample taken in plant remains from 11–12 m of depth is 20.60 ± 0.60 ka (Kotov, 2002).

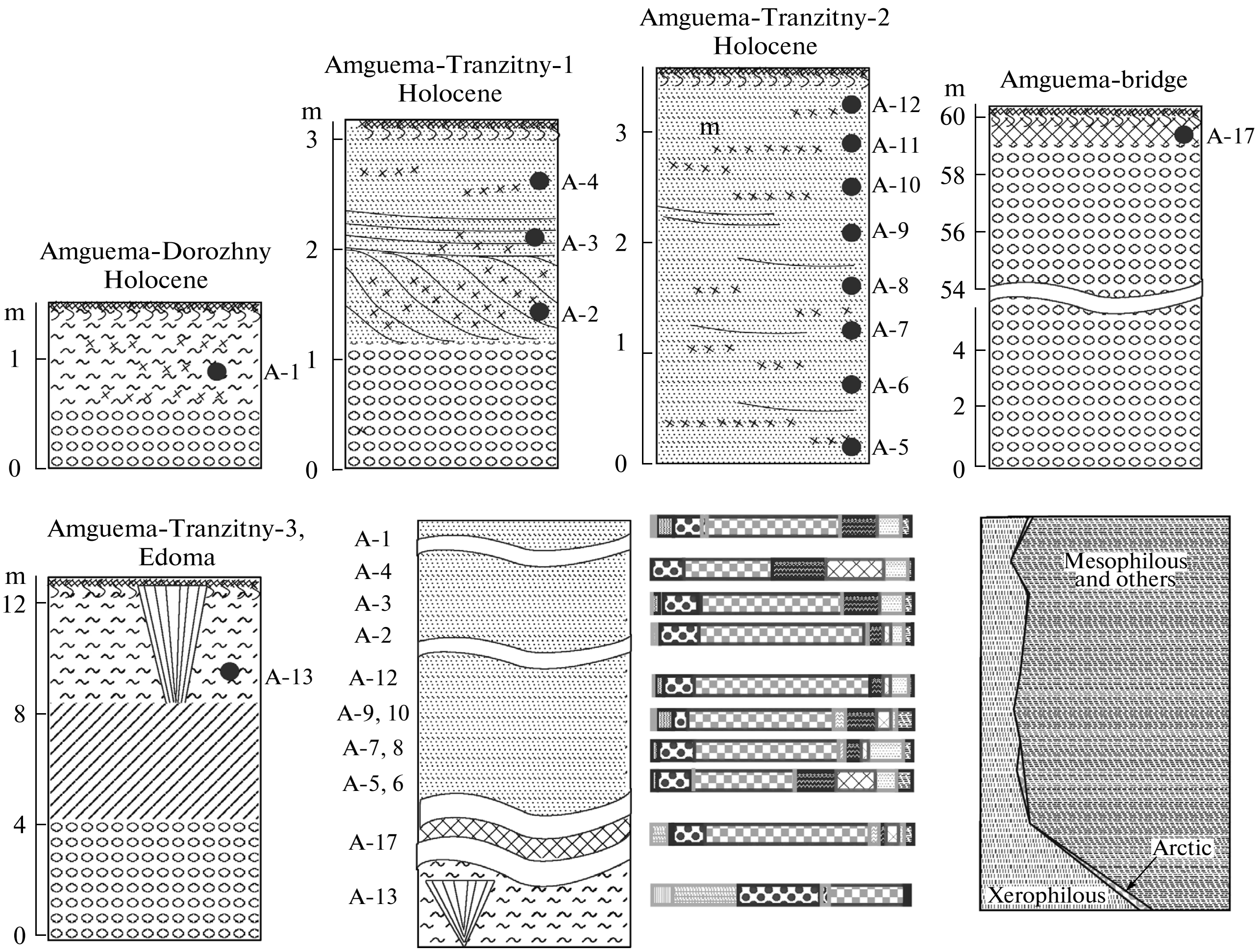


Fig. 35. Stratigraphic scheme and insect assemblages from the Amguema River, Chukotka. For legend, see Fig. 16.

The first river floodplain terrace of the Amguema River was formed in the middle Holocene. Radiocarbon date from a depth of 3 m of a 11-m-high terrace is 3.63±0.03 ka (Anderson and Lozhkin, 2002). The lower terraces are apparently younger.

Sample A-13 comes from Late Pleistocene Edoma-like deposits near an ice wedge at elevation of 9 m, section Tranzitnyi-3. (Fig. 35). The assemblage is dominated by xerophilous species: **dt** = 33%, **ss** = 26%, and **st** = 7%. Thus, the structure is typical for the Pleistocene steppe–tundra communities. Steppe insects are represented by only one species, the leaf beetle *Chrysolina brunnicornis*. Anyway, the existence of the steppe group is an important feature of the fauna. Steppe insects are well represented in Late Pleistocene assemblages of the western Chukotka Peninsula (Kiselev, 1981; Kiselev and Nazarov, 2009), but almost absent in the southeastern part of the region (Kiselev, 1981; Kuzmina et al., 2011). The Amguema area is geographically close to the western Chukotka and the fauna follows this regional setting. We can guess that these deposits are older or younger than the date 20 ka, which comes from similar deposits of the nearby section, because the insect fauna is clearly indicative of steppe–tundra environment, distinguished from the cold tundra reconstructed for the last glacial maximum in the Ice Bluff section (see above).

Sample A-17 was taken from a peat bed near the top of the modern ground surface. The assemblage is strongly dominated by mesophilous tundra species (69%). Aquatic and riparian beetle species are not well represented, but we have found abundant head remains of larval Tipulidae, which require wet environments. The most interesting feature of the fauna is the presence of a significant amount of *Morychus viridis* (8%) in such a modern looking "wet" assemblage. This confirms the theory of long existing steppe-like patches in this area. The section "near bridge" is located directly in the modern steppe, where living *M. viridis* were collected; thus, we can propose that this steppe has existed for at least several hundred years.

Single *Morychus viridis* remains were also found in the river terraces sections covered by ordinary tundra

Table 39. Insects from the Amguema sites

Age	Q_3	Holocene													
Section	Trans3	Dor.	Trans1			Trans2								Bridge	eco
Species/sample Am-B	13	1	2	3	4	5	6	7	8	9	10	11	12	17	
Order Coleoptera															
Family Carabidae															
Subfamily Nebriinae															
Nebria frigida Sahlb.	–	–	–	–	–	–	–	–	–	–	–	–	1	–	**ri**
Notiophilus aquaticus L.	–	4	1	3	–	3	1	1	2	2	2	1	3	1	**xe**
Subfamily Carabinae															
Carabus truncaticollis Esch.	–	–	–	–	–	–	–	–	–	1	–	–	–	1	**mt**
Subfamily Elaphrinae															
Blethisa multipunctata (L)	–	–	–	–	1	–	–	–	–	–	–	–	–	–	**ri**
Diacheila polita Fald.	–	3	3	4	2	2	1	1	3	3	1	2	6	2	**mt**
Elaphrus lapponicus Gyll.	–	–	–	–	1	–	1	–	–	–	–	–	–	–	**ri**
Elaphrus sp.	–	–	–	–	–	–	–	–	–	–	–	–	1	–	**ri**
Subfamily Trechinae															
Bembidion (*Asioperyphus*) *umiatense* Lth.	–	–	–	5	–	–	–	–	3	–	–	–	–	–	**ri**
B. (*Peryphus*) *petrosum* Gebl.?	–	1	–	–	–	–	–	–	–	–	–	–	–	–	**ri**
B. (*Plataphodes*) *arcticum* Lth.	–	4	–	2	–	–	–	2	2	–	–	–	2	–	**ri**
B. (*Plataphus*) *geblery* Gebl.	–	–	–	–	–	–	1	–	1	–	–	–	–	–	**ri**
B. (*Plataphus*) *hyperboraeorum* Munst	–	–	–	3	1	3	–	–	4	2	–	2	1	–	**ri**
Bembidion sp.	–	–	–	1	–	–	–	–	–	–	–	–	–	1	**ri**
Subfamily Harpalinae															
Tribe Harpalini															
Dicheirotrichus mannerheimi Sahlb.	–	–	–	1	–	–	–	–	–	–	–	–	–	–	**dt**
Harpalus sp.	–	–	–	–	–	–	–	–	–	1	–	–	1	–	**ms?**
Tribe Platynini															
Agonum exaratum (Mannh.)	–	–	1	1	–	–	–	–	1	–	–	–	1	–	**ri**
Tribe Pterostichini															
Pterostichus (*Cryobius*) *brevicornis* (Kby.)	–	12	2	9	1	–	–	6	1	2	–	2	1	2	**mt**
P. (*Cryobius*) *pinguedineus* Esch.	2	6	8	30	7	4	2	3	10	3	3	4	9	14	**mt**
P. (*Cryobius*) *ventricosus* Esch.	4	1	20	15	3	5	3	1	9	9	2	8	32	22	**mt**
Pterostichus (*Cryobius*) sp.	–	1	–	5	–	–	–	1	2	–	–	–	–	–	**mt**
P. (*Lenapterus*) *agonus* Horn.	–	1	1	–	–	–	–	–	–	1	–	–	–	3	**mt**
P. (*Petrophilus*) *tundrae* Tschitsch.	–	–	2	1	–	1	–	–	1	–	–	–	–	–	**dt**
P. (*Petrophilus*) *abnormis* Sahlb.	–	–	–	–	–	–	–	–		–	–	–	1	–	**dt**
P. (*Tundraphilus*) *sublaevis* Sahlb.	–	1		3	–	–	–	–	1		1	2	2	–	**dt**
Stereocerus haematopus (Dej.)	1	2	1	6	3	1	–	–	–	–	–	–	2	3	**dt**
Tribe Zabrini															
Amara interstitialis Dej.	–	–	–	2	–	–	–	1	–	–	–	–	–	–	**dt**
A. glacialis Mnnh.	2	–	–	1	1	1	–	–	–	–	–	–	–	2	**dt**
Curtonotus alpinus Payk.	13	1	–	2	1	1	–	–	4	–	1	–	1	1	**dt**
Curtonotus bokori Csiki	1	–	–	–	–	–	–	–	–	–	–	–	–	–	**dt**
Family Dytiscidae															
Subfamily Agabinae															
Agabus moestus (Curt.)	–	–	2	2	1	3	–	1	–	–	–	1	2	1	**aq**

Table 39. (Contd.)

Age	Q_3	Holocene													
Section	Trans3	Dor.	Trans1			Trans2								Bridge	eco
Species/sample Am-B	13	1	2	3	4	5	6	7	8	9	10	11	12	17	
A. thomsoni (J.Sach.)	–	–	–	–	–	–	–	–	1	–	–	–	–	–	**aq**
Subfamily Hydroporinae															
Hydroporus acutangulus Thoms.?	–	–	–	–	–	–	–	–	–	1	–	–	–	–	**aq**
Hydroporus morio Aubé	–	3	–	–	–	–	–	1	–	–	–	–	–	–	**aq**
Hydroporus sp.	–	–	1	2	1	2	–	–	1	–	1	–	1	2	**aq**
Subfamily Colymbetinae	–	–	–	–	–	–	–	–	–	–	–	–	–	–	
Colymbetes sp.	–	–	–	–	–	–	1	–	–	–	–	–	–	–	**aq**
Dytiscidae gen. indet.	–	–	–	1	–	–	–	–	–	–	1	–	–	–	**aq**
Family Hydrophilidae															
Subfamily Helophorinae															
Helophorus oblongus LeC	–	–	–	–	–	–	–	–	–	1	–	–	–	1	**aq**
H. splendidus Sahlb.	–	1	–	–	–	–	–	–	–	–	–	–	–	1	**aq**
Subfamily Sphaeridiinae															
Cercyon sp.	–	–	1	–	–	–	–	–	–	–	–	–	–	–	**pl**
Family Staphylinidae															
Subfamily Omaliinae															
Eucnecosum tenue LeC.	–	1	1	–	11	3	–	–	1	1	–	1	2	1	**pl**
Olophrum consimile Gyll.	–	5	6	5	4	3	3	2	5	3	1	3	3	1	**mt**
Subfamily Tachyporinae															
Tachinus arcticus Motsch.	17	3	6	8	3	7	–	3	6	3	8	2	6	22	**mt**
Subfamily Steninae															
Stenus sp.	–	–	–	–	–	–	–	–	–	–	–	–	1	–	**ri**
Subfamily Paederinae															
Lathrobium sp.	–	–	1	1	1	–	–	1	–	–	1	–	1	–	**pl**
Staphylinidae gen. indet.	–	–	–	–	–	–	–	–	1	2	–	–	–	5	**pl**
Family Byrrhidae															
Subfamily Byrrhinae															
Byrrhus fasciatus Forst.	–	1	–	–	–	1	–	–	1	1	–	–	–	4	**me**
Morychus viridis Kuzm. et Korot.	20	–	2	2	–	–	–	–	–	–	–	–	–	7	**ss**
Simplocaria arctica Popp.	–	–	–	2	–	–	–	–	–	–	–	–	–	1	**dt**
Subfamily Syncalyptinae															
Curimopsis cyclolepidia Muenst.	–	–	1	–	–	–	–	–	–	–	–	–	1	–	**dt**
Family Melyridae															
Troglocollops arcticus L. Medv.	–	1	–	–	–	–	–	–	–	–	–	–	–	–	**ms**
Family Elateridae															
Berninelsonius hyperboreus (Gyll.)	–	–	1	1	–	–	–	1	–	1	–	–	–	–	**me**
Family Chrysomelidae															
Subfamily Chrysomelinae															
Chrysolina brunnicornis Weise	6	–	–	–	–	–	–	–	–	–	–	–	–	–	**st**
Ch. instabilis Maekl.	–	–	1	–	–	–	–	–	–	–	–	–	–	–	**dt**
Ch. septentrionalis Men	–	1	1	3	–	–	–	–	–	–	–	–	3	–	**mt**
Ch. tolli Jac.	–	1	–	–	–	1	–	–	–	–	–	–	–	–	**tt**
Chrysolina sp.	–	–	–	–	–	–	–	–	1	–	–	–	–	–	**mt?**

Table 39. (Contd.)

Age	Q_3	Holocene													
Section	Trans3	Dor.	Trans1			Trans2								Bridge	eco
Species/sample Am-B	13	1	2	3	4	5	6	7	8	9	10	11	12	17	
Family Brentidae															
Subfamily Erirhininae															
Notaris acridulus L.	–	–	–	–	1	–	–	–	–	–	–	–	–	–	**ri**
N. aethiops F.	–	–	1	1	–	1	1	–	–	–	–	–	–	–	**ri**
N. bimaculatus F.	–	–	1	1	–	–	–	–	–	–	–	–	–	–	**ri**
Grypus mannerheimi Faust	–	–	–	–	1	–	–	–	–	–	–	–	–	–	**ri**
Subfamily Apioninae															
Mesotrichapion wrangelianum Kor.	–	1	2	–	–	–	–	2	1	1	–	1	3	3	**dt**
Hemitrichapion tschernovi T.-M.	–	–	–	1	–	–	–	–	–	–	–	–	–	–	**dt**
Family Curculionidae															
Subfamily Bagoinae															
Bagous sp.?	–	–	–	–	–	–	–	–	–	–	1	–	–	–	**aq**
Subfamily Ceutorhynchinae															
Pelenomus sp.	–	1	–	–	–	–	–	–	–	–	–	–	–	1	**ri**
Subfamily Entiminae															
Sitona borealis Kor.	8	–	1	1	1	–	–	–	–	1	–	–	–	3	**dt**
S. lineellus Bonsd.	–	–	–	–	–	–	–	–	–	–	1	–	–	–	**me**
Subfamily Hyperinae															
Hypera diversipunctata Schrank.	–	1	2	–	1	2	–	–	2	1	–	–	–	1	**dt**
H. ornata Cap.	–	–	–	1	–	–	–	–	1	–	–	–	3	–	**dt**
Subfamily Molytinae															
Tribe Lepyrini															
Lepyrus canadensis Csy.	–	1	4	–	1	–	–	1	2	–	1	1	2	–	**sh**
L. nordenskioeldi Fst	1	2	–	4	–	1	1	–	–	1	–	1	–	1	**sh**
Subfamily Curculioninae															
Tribe Elliscini															
Dorytomus imbecillus Fst.	–	–	–	3	7	2	3	1	–	–	–	–	–	–	**sh**
D. rufulus amplipennis Tourn.	–	3	4	10	4	1	–	–	2	2	4	1	2	1	**sh**
Tribe Rhamphini															
Isochnus arcticus Kor.	3	–	–	–	–	–	–	–	–	–	–	–	–	–	**tt**
I. flagellum Erics.	1	–	1	–	–	–	–	–	–	–	–	–	–	–	**oth**
Order Hymenoptera															
Hymenoptera gen. indet.	–	2	–	–	1	–	–	1	–	–	1	2	1	–	**oth**
Order Megaloptera															
Family Sialidae															
Sialis sp.	–	1	–	–	–	–	–	–	–	–	–	–	–	–	**aq**
Order Trichoptera															
Trichoptera gen. indet. (larvae)	–	1	–	1	–	–	–	1	–	–	1	–	–	1	**aq**
Order Diptera															
Family Chironomidae															
Chironomidae gen. indet.	–	1	–	–	–	–	1	–	–	–	–	–	–	1	**aq**
Family Tipulidae															
Tipulidae gen. indet. (larvae)	–	1	–	–	–	–	1	1	2	1	–	1	–	18	**aq**
Diptera fam. indet. (puparia)	30	2	1	7	4	–	1	–	5	–	3	–	10	91	**oth**
Sum	79	69	79	143	58	48	18	29	69	43	29	32	94	108	

vegetation (samples A-2, A-3), but most of the samples from these three sections does not provide evidence of old steppes. The species composition of insects from 12 alluvial samples is close to the modern state and corresponds to shrub–grassy tundra. Despite a high possibility of transportation in alluvial deposits, insect remains in the river valley localities mostly agree with local environments.

CHAPTER 4. INSECT FAUNAS FROM THE PLIOCENE TO HOLOCENE AND ENVIRONMENT RECONSTRUCTION

Neogene insect assemblages of western Beringia are rather rare and available insects are too few to provide a detailed reconstruction (Elias et al., 2006). We know that the Miocene assemblage from Ary-Mas has yielded mostly aquatic and riparian insects and probably includes some extinct species. The steppe–tundra indicators are absent here, although the scarcity of insects prevents reliable conclusions.

The Pliocene Begunov Formation from the Krestovka River, Kolyma Lowland, has mostly yielded tundra species and only one specimen belongs to the weevil tribe Cleonini. This identification means that we deal with the genus *Coniocleonus* (most of species belong to the **ms** group and one species, *C. zherichini,* to the **dt** group) or *Stephanocleonus* (**st** group). Thus, this fossil is probably the first sign of steppe–tundra community.

The early stage of the Early Pleistocene (in the recent stratigraphic scheme) is represented by the Kutuyakh Beds from the Krestovka River. Fossil insects are not numerous here, insect assemblages include tundra and forest species. At the top of the unit, the number of forest insect decreases and some xerophilous steppe–tundra indicators appear. There are the pill beetle *Morychus viridis*, weevils of the tribe Cleonini and a problematic fossil described by Kiselev (1981) as *Crosita* sp. The first reliable evidence of a steppe–tundra environment was found in the Kutuyakh Beds; thus, a steppe–tundra community was established in the Early Pleistocene.

The Early Pleistocene Chukochinsky Horizon of the Oler Formation is more widespread. Fossil insects from the stratotype on the Chukochya River and from the Krestovka River have been studied by Kiselev (1981). All samples contain steppe–tundra indicators, but their proportions vary through the section. The highest frequency of *Morychus viridis* and other steppe species is recorded in the upper part of the unit: subhorizon 1e in the Chukochya section and horizon IVa in the Krestovka section.

The Oler Formation is well recognizable in the field, but the boundary between the Early Pleistocene Chukochinsky Horizon and Middle Pleistocene Akansky Horizon is not very clear and only a paleomagnetic study can provide accurate division. Some samples come from supposedly, but not doubtless Chukochinsky Horizon. Based on the Chukochya and Krestovka sections, it is shown that steppe–tundra insect communities, including the **S-T/SS** type, have been existing since Early Pleistocene. Many other samples come from the "Oler Formation" and we have to operate with a wider age interval, Early–Middle Pleistocene.

Using the database QINSIB (Kuzmina, 2013), the types of insect communities are compared through the time and regions. The time intervals were chosen by importance: Late Neogene, Early–Middle Pleistocene, last interglacial (Late Pleistocene, MIS5), Early Pleistocene–middle Late Pleistocene (MIS4–3), latest Late Pleistocene (last glacial maximum, MIS2), and early Holocene. The table includes only large assemblages (where MNI is greater than 50).

Table 40 shows that, in Early–Middle Pleistocene insect faunas, steppe species play a secondary role. The western regions (Lena delta and Laptev Strait) were mostly occupied by tundra (**TU/TU**) or, to some extent, by steppe–tundra (**TU-XE**) types. Steppe species were more frequent in the Middle Kolyma region (Sededema section), but a lack of data could have caused misrepresentation.

Insect assemblages from the Yana–Indigirka Lowland are dominated by the moderate steppe–tundra **S-T/S-T** type. The best studied Early–Middle Pleistocene insect assemblages come from the Kolyma Lowland. This area is also dominated by the moderate steppe–tundra type **S-T/S-T**, but some steppe ecotypes, such as **S-T/SS** and **S-T/ST,** are also present. In other regions (Chukotka, Middle Indigirka, and Upper Kolyma), old insect assemblages have not been studied. Thus, it is possible to conclude that the Kolyma Lowland fits to the steppe–tundra environment better than other regions in question.

In a search for general patterns through the time, we cannot propose reliable conclusions. In some section, such as Alazeya in the Kolyma Lowland (Kuzmina, 1989), the **S-T/SS** and **S-T/ST** types appear in the terminal Early Pleistocene and terminal Middle Pleistocene, but this pattern has not been observed in other sections.

The last interglacial units are not well studied in western Beringia due to a lack of proper sections. Only a few sections reliably dated MIS5 are known: Alazeya, Bolshoi Lyakhovskii Island, and Oiagoss Yar. Insect assemblages from the Kuobakh Beds of the Alazeya section (Kuzmina, 1989) contain a significant number of forest species (Table 5, Fig. 15), along with aquatic, riparian, meadow, and plant litter groups, which are rare in typical steppe–tundra faunas. Single steppe–tundra indicators are also present here. The high proportion of forest insects are indicative of interglacial environments and the climate close to the modern one or even warmer.

The next example is assemblages studied from the Krest-Yuryakh Formation of Lyakhovskii Island

Table 40. Geographical distribution of the faunal types in western Beringia

Age/Region type	Kolyma Lowland	Middle Kolyma	Upper Kolyma	Yana–Indigirka Lowland	Middle Indigirka	Lena delta	Laptev Strait	Western Chukotka	Southeastern Chukotka
Neogene	Number of assemblages								
TU/TU	1								
TU/XE	2								
Early–Middle Pleistocene									
TU/TU	2			1			1		
TU/XE	7	2		7		5	3		
TU/S-T	21	2		9		1			
S-T/S-T	47	1		27					
S-T/SS	9								
S-T/ST	4								
Interglacial MIS5									
TU/XE	2						4		
TU/S-T							1		
Late Pleistocene (*MIS4–MIS3*)									
TU/TU				1		1	4		1
TU/XE				1	3	4	1	5	31
TU/S-T	2	3		10	1	21	3	14	8
S-T/S-T	18	1		16		6	1	10	
S-T/SS	9			14			2	7	
S-T/MS	1								
S-T/ST	1			1				2	
Late Pleistocene (*MIS2*)									
TU/TU						4			
TU/XE						12			7
TU/S-T						11			
S-T/S-T	3					3		3	2
S-T/SS	5					4			
S-T/MS	7							3	
S-T/ST	1							2	
Early Holocene									
TU/TU			3			1	1	2	
TU/XE	1		2			11	2	14	
TU/S-T	3					5	2	8	
S-T/S-T	2							4	

(Andreev et al., 2004) and Oiagoss Yar (Kienast et al., 2011). These northern faunas almost lack forest species, but an increase in the plant litter, meadow, shrub, aquatic, and riparian groups is indicative of significant warming. In addition, interglacial faunas from the northern sites are characterized by an increase in the frequency of steppe insects. They include thermophilous steppe weevils *Stephanocleonus eruditus* and *S. fossulatus,* which are extremely rare for the northern areas. Interglacial warming was favorable not only for shrub tundra, but also for steppe–tundra. The northern regions remained treeless during the interglacial and provided a refuge for steppe–tundra communities.

Late Pleistocene insects are known throughout western Beringia. Northwestern faunas include fewer steppe species. Lena delta assemblages are dominated by the moderate steppe–tundra type **TU/S-T**; the **TU/XE** and **S-T/S-T** types are less abundant and the **TU/TU** type is rare. Northern faunas (Laptev Strait) include more steppe-free assemblages (type **TU/TU**) and a smaller proportion of **TU/XE, TU/S-T, S-T/S-T,** and **S-T/SS**.

The Yana–Indigirka Lowland provides more favorable conditions for steppe–tundra faunas. The dominant type here is **S-T/S-T**, the second most common group is **S-T/SS** and the third is **TU/S-T**. Other types (**TU/TU, TU/XE,** and **S-T/ST**) are infrequent. Anyway, we can see the strong steppe–tundra type **S-T/ST**, which has not been recorded in the northwestern areas.

In the Kolyma Lowland, the steppe component played a greater role. The dominant type is **S-T/ST**, the second most important is **S-T/SS,** and **S-T/ST** and **S-T/MS** are infrequent. Even weak tundra-like types have not been recorded here.

Late Pleistocene assemblages from the Middle Kolyma belong to the **S-T/S-T** and **TU/S-T** types.

The most interesting situation is observed in the Middle Indigirka area. Only a few Late Pleistocene samples have been examined (Kiselev and Nazarov, 2009), but this region is very important due to modern relict steppes (Berman et al., 2001a, 2011). The question is how long these steppes existed in this area. If the fossil record shows the existence of steppe–tundra communities in the past, these steppes should be regarded as relict. Unfortunately, only three fossil insect assemblages are available. Two of them belong to the **TU/XE** type and one, to the **TU/S-T** type. Fossil assemblages from the Middle Indigirka contain individual *Stephanocleonus* sp.*, Chrysolina perforata, Otiorrhynchus cribrosicollis*, and *Morychus viridis*, but most of insects belong to aquatic, riparian, and tundra species. Thus, the steppe–tundra component was weak in this area compared with the Kolyma or Yana–Indigirka lowlands. This problem needs further study. In any event, we know that some steppe–tundra species were present here since the Late Pleistocene.

Insect faunas from the western Chukotka Peninsula slightly differ from that of the neighboring Kolyma Lowland. They are dominated by the moderate steppe–tundra type **TU/S-T**; the second most frequent is **S-T/S-T**; other faunas belong to the **S-T/SS, TU/XE,** and **S-T/ST** types. Steppe–tundra environment was less developed here, but it certainly existed.

A different situation is observed in the southeastern Chukotka Peninsula. Most of the assemblages belong to the **TU/XE** type, that is, they contain only single steppe–tundra indicators and lack true steppe species. Considerably fewer assemblages contain individual steppe species and belong to the **TU/S-T** type. Only two assemblages from the lower unit of the Ice Bluff section belong to the **S-T/S-T** type. The steppe group is restricted to only one species, the ground beetle *Cymindis arctica*. Thus, the local environment was more tundra-like rather than steppe–tundra.

The last glacial maximum is a distinctive time, which shows significant zoogeographical differences in the steppe–tundra environment. The best studied area is the Lena delta. We have two detailed records of this time: Bykovsii (Sher et al., 2005) and Buor-Khaya (Wetterich et al., 2008). According to the presently accepted classification, most of the assemblages in this area belong to slightly steppe–tundra type **TU/XE** and **TU/S-T**; some faunas are steppe-free (**TU/TU**) and some belong to the **S-T/S-T** type. In addition, we recorded assemblages of the **S-T/SS** type at the top of the section, which reflect post-last glacial maximum time. In the majority of samples, the steppe group is represented by individual *Stephanocleonus eruditus*. The last glacial maximum is characterized by faunas with a high proportion of cold resistant weevil *Isochnus arcticus*. A number of assemblages in both sections are dominated by this species. Such feature indicates severe climate during last glacial maximum. Similar faunas with a high proportion of *Isochnus arcticus* were also recorded in the southeastern Chukotka Peninsula (Kuzmina et al., 2011).

Insect assemblages probably of the last glacial maximum of the western Chukotka Peninsula (Kiselev and Nazarov, 2009) are different. They belong to strong steppe–tundra **S-T/MS, S-T/ST,** and **S-T/S-T** types; cold resistant species are not numerous. During this cold time, steppe–tundra was established here with certainty. Similarly, even more pro-steppe regularity was in the Kolyma Lowland. The most popular type here is **S-T/MS**, the second most frequent is **S-T/SS**; the types **S-T/ST** and **S-T/S-T** are also present. In other regions, insect assemblages corresponding to the last glacial maximum have not been studied.

We can see a great difference between the Kolyma and nearby West Chukotka areas, on the one hand, and the northwestern part of western Beringia, on the other hand. Certainly, the Kolyma+West Chukotka was the area of the best developed steppe–tundra environment during the whole of the Late Pleistocene, including the last glacial maximum.

The collapse of the steppe–tundra environment is considered to be at the Pleistocene–Holocene boundary (Sher, 1997a, 1997b). A great extinction of large Pleistocene mammals (mammoth) or local extinction (horse, bison, saiga) in western Beringia were correlated with environmental changes near 10 ka. We know that some large mammal species survived the transition (Boeskorov, 2004) in the refuges on Wrangel Island, the Taimyr Peninsula, Lena delta, and Lyakhovskii Island. Insects have more chances to survive in microhabitats due to their small size.

Most of the studied Early Holocene insect assemblages contain steppe–tundra indicators. In the Lena delta, the majority of assemblages belong to the weak steppe–tundra type **TU/XE**, some belong to the type **TU/S-T**, and only one assemblage is steppe-free (type **TU/TU**). Early Holocene faunas from Bolshoi Lyakhovskii Island also include the **TU/XE, TU/S-T**, and **TU/TU** types. The proportion of steppe insects even increased here, as compared with poor Pleistocene communities of this northern site.

Early Holocene faunas of the Kolyma Lowland contain **TU/XE, TU/S-T**, and **S-T/S-T** types. Early Holocene insects of the western Chukotka are most thoroughly studied. The dominant type here is **TU/XE**, other faunas belong to the **TU/S-T, S-T/S-T**, and **TU/TU** types. A dramatic decrease in the steppe influence in this most prominent steppe–tundra zone is evident, but it is obvious that the steppe–tundra environment survived the boundary here.

A number of Early Holocene insect faunas are recorded in the Upper Kolyma region. The assemblages belong to the **TU/TU** and **TU/XE** types, with relatively high proportions of forest, plant litter, and riparian species.

At least restricted areas of the steppe–tundra environment survived the great Pleistocene extinction. The northern part of Beringia was more favorable for such environments than the southern part. The key point was probably competition of the treeless landscape and forest invasion. Sea transition from the north and forest expansion from the south narrowed the steppe–tundra zone to a critical size in the Early Holocene, until it was closed completely in the recent time (Kuzmina and Sher, 2006).

Distribution of steppe–tundra variations in time and space shows that the most prominent time for this environment was the Late Pleistocene and the most prominent area was the Kolyma Lowland. The biogeographical zones became more distinct during the "warming" periods in the last interglacial and in the Early Holocene. Warming provided favorable conditions for steppe insects in the northern region and steppe–tundra community was shifted to the north and occupied treeless landscape.

CHAPTER 5. STEPPE–TUNDRA AS A UNIQUE PLEISTOCENE ENVIRONMENT OF BERINGIA

5.1. Term Steppe–Tundra

The first mentioning of mixed faunas goes back to Nehring (1880), who studied mammals from the Thiede and Westeregeln sites in Germany. He explained the mixed species composition by the low temperature and overlap of the natural zones. Later, Tugarinov (1929) suggested the idea of the unique tundra–steppe environment, which provids habitats for animals with different ecological requirements.

The term tundra–steppe in the recent references has been used since the publication of Grichuk and Grichuk (1960). Russian scientists traditionally use the term "tundra–steppe" (Sher, 1976, 1990).

American authors prefer the term steppe–tundra (Guthrie, 1968; Hibbert, 1982), which has the same meaning and is sometimes translated as 'tundra–steppe" (Guthrie, 1976), or 'mammoth steppe" (Guthrie, 1986, 2001).

5.2. Arguments for and against the Steppe–Tundra Theory

The problem of mixed faunas was discussed by Brauner (1934) and Kuznetsov-Ugamsky (1934). They suggested many alternative reasons for this phenomenon, such as taphonomy (mechanical mixture of fossils from different beds), an increase in the species ranges further to the north or further to the south, changes in species ecology, seasonal migrations, etc. These main alternative explanations stated almost a century ago are still discussed.

Insects from northeastern Asia (Kiselev, 1981; Kuzmina, 1989; Kiselev and Nazarov, 2009) support the steppe–tundra theory, taking this landscape for a special unique environment which existed during the Pleistocene in the northern ice-free regions, such as western Beringia. Many experts in mammal and plant paleontology, geologists, modern botanists, entomologists, and climatologists made their contribution to this theory (Grichuk and Grichuk, 1960; Giterman, 1963; Sher, 1967, 1976, 1982, 1988, 1990, 1997c, 1997d; Yurtsev, 1976, 1981; Vangengeim, 1977; Kaplina, 1981; Grichuk, 1984; Velichko et al., 2002; Alfimov and Berman, 2004; and others).

At the same time, many researchers disagree with the steppe–tundra theory (Arkhangelov et al., 1983; Popov, 1983; Solov'ev and Stanisheva, 1983; and others). The major disagreement is whether the humidity was high or low. Actually, the ice-rich sediment may suggest a high humidity during the coldest period of the Pleistocene. "It is hard to imagine such a dry environment during the deposition process that corresponds to a wet polygonal landscape. The Edoma sections support this statement; the cryolithological appearance of this deposits (large ice wedges and segregation ice in the sediment) suggest a high humidity of the active layer" (Arkhangelov et al., 1983, p. 96). Popov (1983) adheres to a similar point of view. He believes that Edoma deposits were formed in a floodplain water-rich environment with boggy vegetation. The region with Edoma deposits was described as the "Great Alluvial Plain." This region escaped an increase in continental climate (which should theoretically follow an intense land growth in Beringia during glaciations) because of the great influence of water streams in the alluvial plain. Xerophilous vegetation reconstructed on the basis of palynology could have occupied small dry islands and slope edges. Popov suggests that steppe mammals adapted to the wet tundra-like environment and migrated in the winter to the forest–tundra or steppe areas of central Yakutia. The supporters of the "wet" Pleistocene hypothesis consider insect data as secondary and rarely mention them.

Some damage was made by dry climate enthusiastic followers. One of the most discussed problems in the 1970s–1980s was the eolian origin of the Edoma Formation. The research team of Tomirdiaro (1975, 1980, 1984; Tomirdiaro et al., 1984; Tomirdiaro and Chernen'ky, 1987) accepted the theory of extremely dry, cold, and windy steppe–tundra environment. Dust carried by wind deposited loess sediment, which was the only source of the Edoma Formation. This statement was criticized by adepts of multisource origin of the ice-rich Edoma Formation (Arkhangelov, et al., 1983), but together with doubtful loess theory, the authors also refused the dry climate and steppe–tundra vegetation.

Tomirdiaro works provoked criticism because of the categorical style of his articles and a lack of factual material, but the eolian theory has recently become more popular in western Beringia (Morozova and Velichko, 1996; Gubin, 1997, 1999). The eolian origin of similar ice-rich silty deposits in eastern Beringia is better substantiated (McDowell and Edwards, 2001; Muhs et al., 2003; Sanborn et al., 2006; Roberts et al., 2007) and supported by modern observations (Laxton et al., 1996). The richness of the loess soil helps to explain the high productivity of the steppe–tundra environment (Laxton et al., 1996).

5.3. Insects in the Steppe–Tundra Environment

Fossil insects provide strong support to the steppe–tundra theory (Kiselev, 1981; Kuzmina and Ponomarenko, 2001). For the diversity of fossil Quaternary insects, see Figs. 36–41. Almost all West Beringian Pleistocene insect faunas contain steppe–tundra indicators, species that are rare or absent in the modern tundra or forest–tundra. Insect combinations follow a certain pattern. This pattern allows us to make generalizations and even use the types of steppe–tundra faunas in our discussions. The fossil fauna type reflects (with taphonomic distortion) a past biocenose. The fact that we can recognize certain types and use them as indicators (see above) suggests that insect assemblages under study are not a mechanical mixture. The regularity suggests that steppe and tundra species actually lived together within the same landscape and were members of an integrated system.

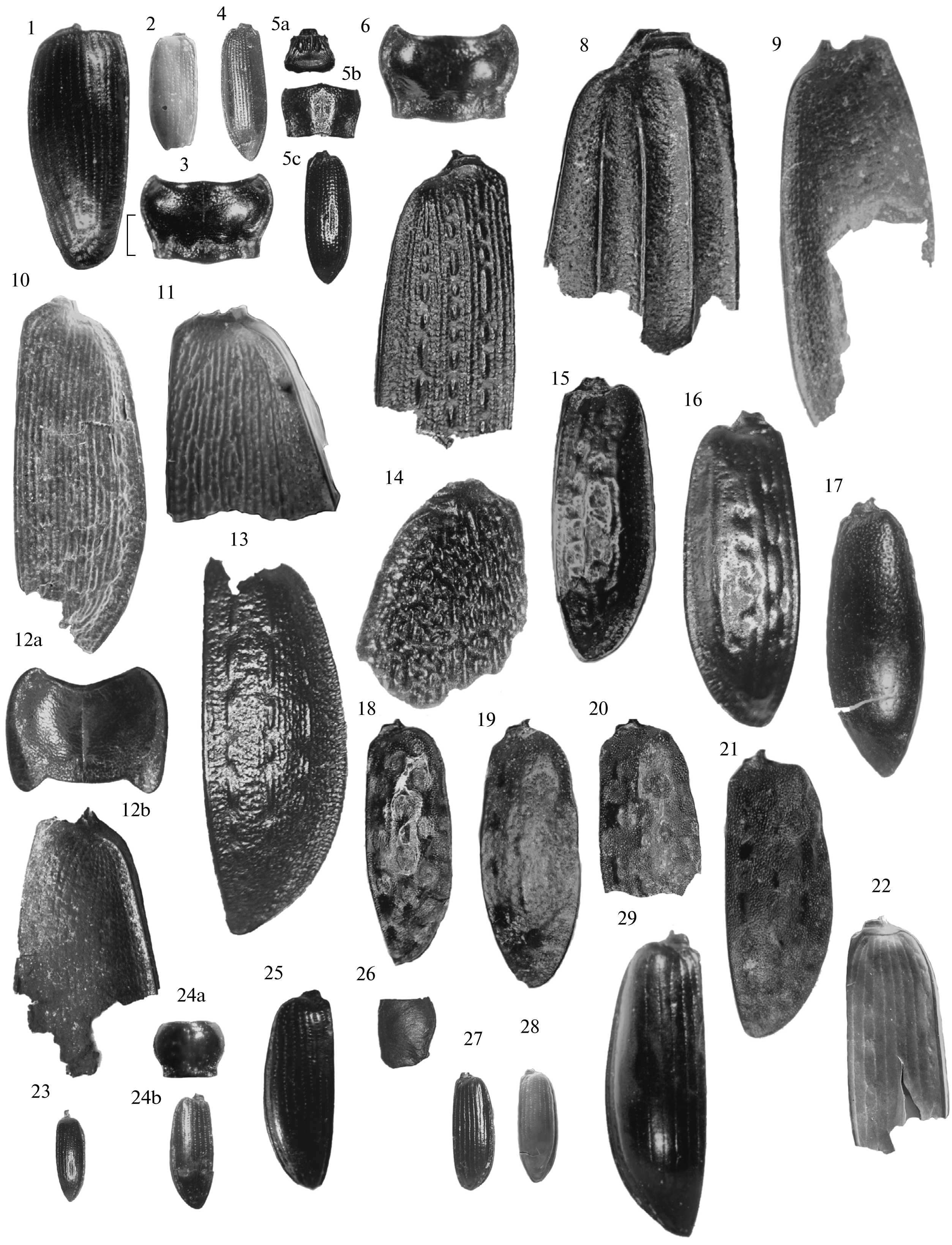
The first attempts at the typification were made by the author for the Alazeya fossil insect assemblages (Kuzmina, 1989). At present, with addition of new data from the northern and western sites, the system has become more general, but the main features remain the same. Here we use seven types of commonly nonforest insect faunas (see Chapter 1). One type (**TU/TU**) is indicative of strictly tundra environments, but other six are more or less affected by steppe species. It is possible to recognize weak (**TU/XE, TU/S-T**), moderate (**S-T/S-T**), and strong (**S-T/MS, S-T/SS, S-T/ST**) steppe–tundra types.

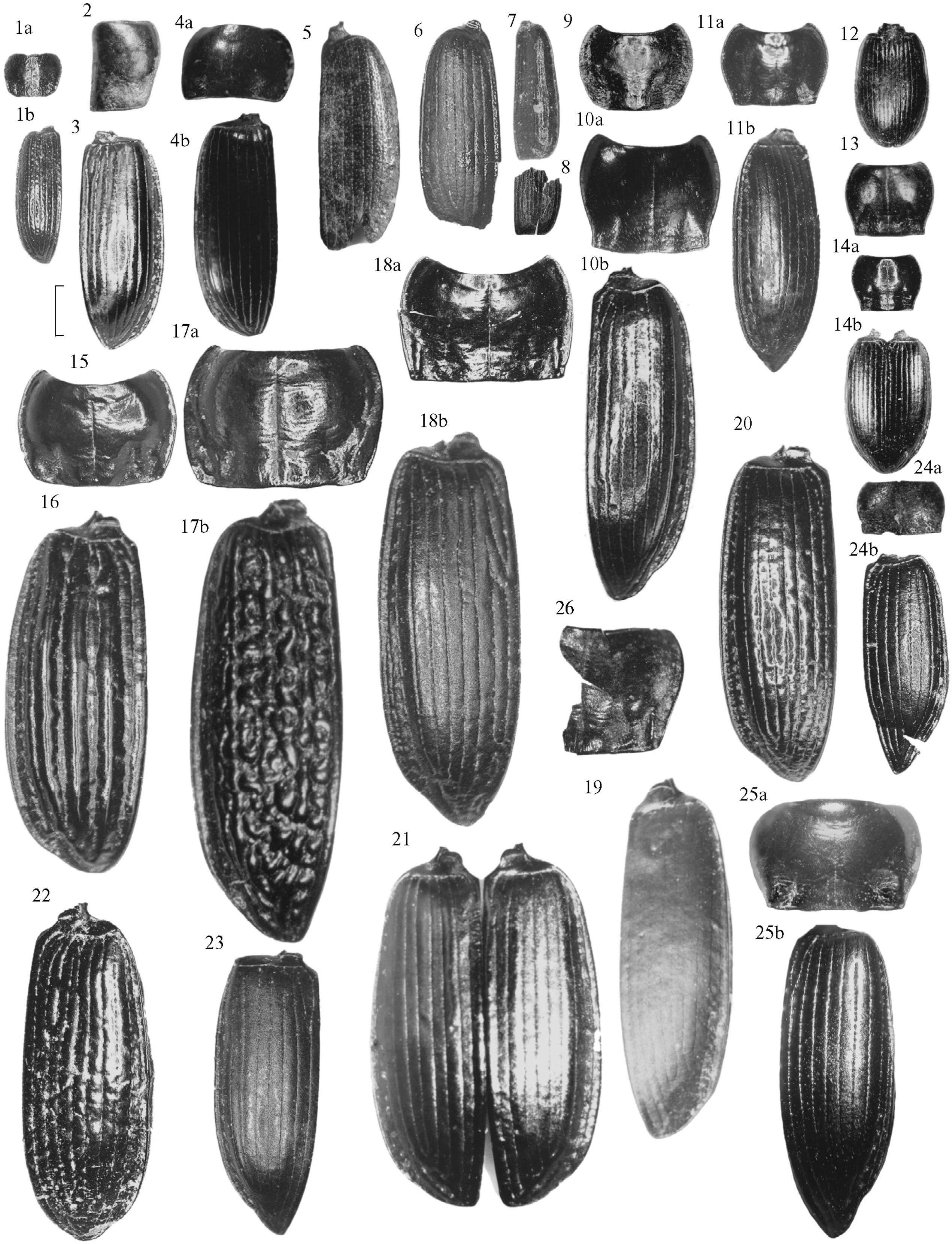
Most of the Pleistocene steppe–tundra insect faunas are very close to each other in species composition. It is interesting that Pleistocene samples are characterized by a short species list and large number of specimens, while Holocene faunas are richer in species and less abundant. The steppe–tundra insect natural association seems very simple and uniform. We have a core of the most popular species (Kuzmina, 2014) or group of species (Table 41).

Fossil beetles identified to genus, such as *Bembidion* sp., *Agabus* sp., and *Hydroporus* sp. are also abundant. Other species are less frequent. A large part of the insect list (185 specimens of 683) are rare species, which were found only in 1 or 2 samples.

Some of the most widespresd species are better presented in fossil insect assemblages. The average proportion of MNI is 2–3% (Table 41), although the following species are more frequent: *Morychus viridis*, *Curtonotus alpinus*, *Tachinus arcticus*, *Isochnus arcticus,* and *Phyllobius kolymensis*. The highest value is shown by the pill beetle *Morychus viridis*. It is the most remarkable member of the Pleistocene community, even according to its frequency in the fauna, it occupies the third place after the ground beetles *Pterostichus* (*Cryobius*) spp. and *Curtonotus alpinus*. The share of *Morychus viridis* sometimes reaches 80% of the sample volume; this species is most abundant in the Pleistocene of western Beringia. Unexpectedly, *Morychus viridis* is a strictly stenotopic species. Its modern habitat is limited to the so-called "hemicryophytous steppe," poorly vegetated spots with xerophilous sedges and tiny moss (Berman et al., 2001a). The incredibly high role of *Morychus viridis* is indicative of such environments which were very common in the Pleistocene, in contrast to the modern state.

We can see a high role of phytophagous insects in the core of steppe–tundra community. Using phytophages and their host plants, we can reconstruct certain aspects of plant community better than using direct methods, palynological and plant macrofossil study (Table 42).


1
2
3
4
5a
5b
5c
6
7
8
9
10
11
12a
12b
13
14
15
16
17
18
19
20
21
22
23
24a
24b
25
26
27
28
29


1a
2
4a
5
6
7
9
11a
12
1b
3
4b
8
10a
11b
13
14a
18a
10b
17a
15
14b
18b
20
24a
16
17b
24b
26
19
25a
21
22
23
25b

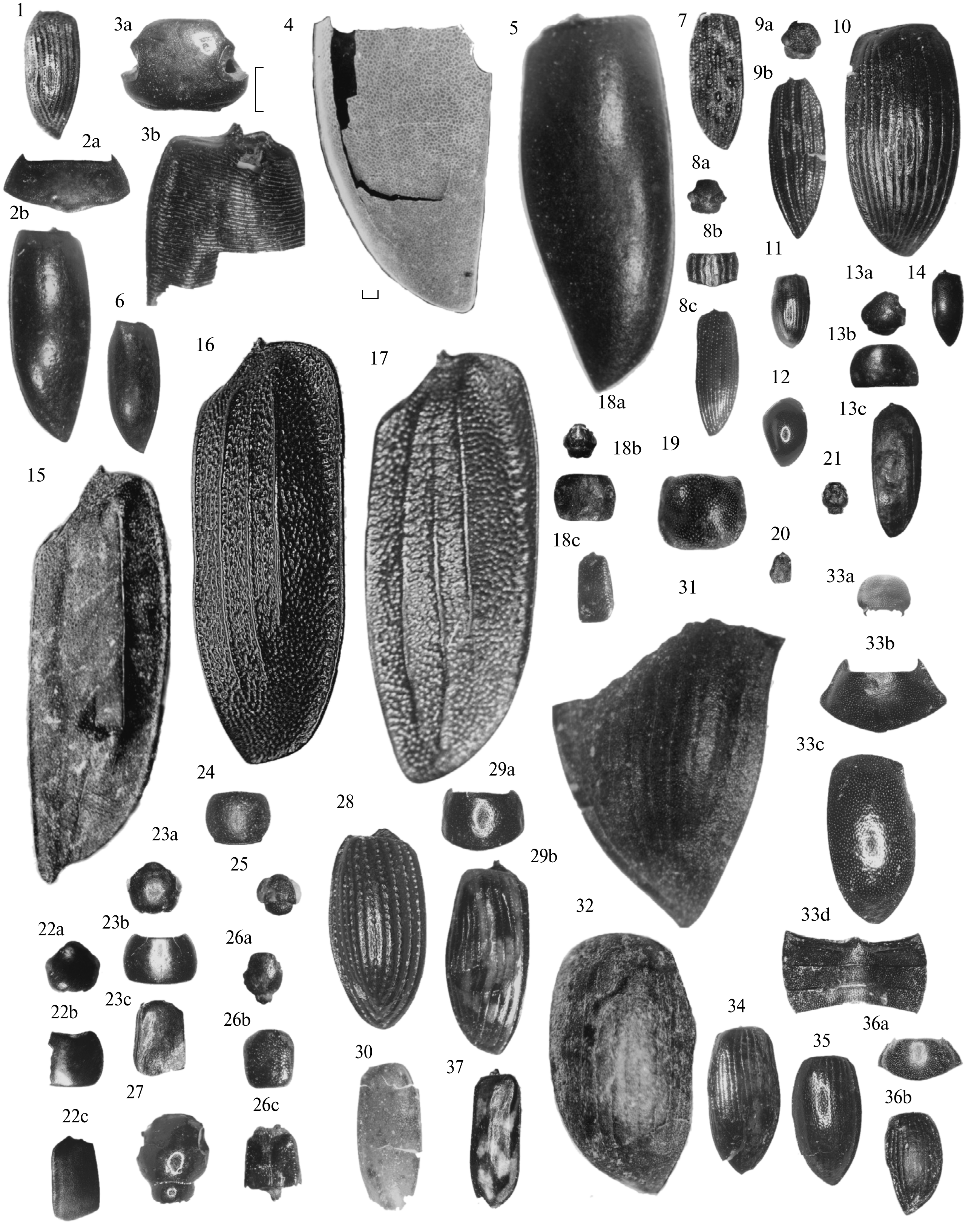

1
2a
2b
3a
3b
4
5
6
7
8a
8b
8c
9a
9b
10
11
12
13a
13b
13c
14
15
16
17
18a
18b
18c
19
20
21
22a
22b
22c
23a
23b
23c
24
25
26a
26b
26c
27
28
29a
29b
30
31
32
33a
33b
33c
33d
34
35
36a
36b
37

Fig. 36. Families Gyrinidae, Trachypachidae, and Carabidae (Nebriinae, Carabinae, Elaphrinae, Scaritinae, Trechinae, Patrobinae): (1) *Gyrinus opacus,* left elytron, Khomus-Yuryakh, sample 88-5; (2) *Trachypachus zetterstedti,* left elytron, Khomus-Yuryakh, sample 83-25; (3) *Nebria frigida*, pronotum, Lyakhovskii, sample LL-14-B17; (4) *Notiophilus sylvaticus*, left elytron, Buor-Khaya, sample BKh-02-7; (5) *N. aquaticus:* (5a) head, (5b) pronotum, (5c) right elytron, Main River, sample ChM-B26; (6) *Pelophila borealis* pronotum, Lyakhovskii, sample LL-14-B17; (7) *Carabus arvensis,* left elytron (without top), Alazeya River, sample 203-6; (8) *C. canaliculatus* Adams, left elytron (without top), Alazeya River, sample 203-6; (9) *C. kolymensis,* right elytron (without top) Buor-Khaya, sample BKh-13; (10) *C. odoratus,* right elytron (without top), Alazeya River, sample 66.1; (11) *C. shilenkovi,* right elytron (without top), Lyakhovskii, sample LL-14-B17; (12) *C. sibiricus:* (12a) pronotum, (12b) right elytron (without top), Buor-Khaya, sample BKh-13; (13) *C. truncaticollis,* right elytron, Main River, sample ChM-B17; (14) *C. vietinghoffii,* left elytron (without top), sample MKh-B-21; (15) *Blethisa catenaria,* right elytron, Alazeya River, sample 203.6; (16) *B. multipunctata,* left elytron, Khomus-Yuryakh, sample 83-25; (17) *Diacheila polita,* right elytron, Bykovsii, sample MKh-B-21; (18) *Elaphrus cupreus,* right elytron, Alazeya River, sample 203.5; (19) *E. lapponicus,* right elytron, Alazeya River, sample 203.5; (20) *E. riparius,* right elytron (without top), Alazeya River, sample 203.5; (21) *E. splendidus,* right elytron, Alazeya River, sample 203.5; (22) *Loricera pilicornis,* Bykovsii, sample B21; (23) *Dyschiriodes melancholicus,* right elytron, Alazeya River, sample 203.5; (24) *Bembidion varium:* (24a) pronotum, (b) right elytron, Oiagoss Yar, sample Oya-6-1; (25) *B. umiatense,* right elytron, Yana, sample Tums 1-11; (26) *B. lapponicum,* pronotum (half), Nagym, sample Nag-7+50 B-4; (27) *Bembidion (Plataphus)* sp., right elytron, Bykovsii, sample R-9; (28) *B. (Peryphanes) dauricum,* left elytron, Bykovsii, sample 2000-B2; (29) *Patrobus septentrionis,* left elytron, Anadyr, sample ChA-B-3.

Fig. 37. Family Carabidae (Harpalinae): **(**1) *Dicheirotrichus mannerheimi:* (1a) pronotum, Nagym, sample Nag-7+50 B-4, (1b) left elytron, Bykovsii, sample MKh-B-20; (2) *Harpalus amputatus,* pronotum, Oiagoss, sample Oya-6-1; (3) *H. vittatus kiselevi,* right elytron, Bykovsii, sample MKh-B-7; (4) *H. vittatus vittatus:* (34a) pronotum, (4b) left elytron, Yana, sample Tums-6.5; (5) *Cymindis arctica,* right elytron, Duvanny Yar, sample P-F1-1332s-1.2; (6) *C. vaporariorum,* left elytron, Nagym, sample Nag-7+50 B-3; (7) *Paradromius* sp., right elytron, Samoilov, sample Sam-2-B-6; (8) *Dromius quadraticollis*?, right elytron (without base), Buor-Khaya, sample BKh-B2; (9) *Agonum quinquepunctatum,* pronotum, Alazeya River, sample 203.5; (10) *Poecilus nearcticus:* (10a) pronotum, Yana, sample Tums-11, (10b) right elytron, Bykovsii, sample B-8; (11) *Pterostichus ventricosus:* (11a) pronotum, (11b) left elytron, Main River, sample ChM-B19a; (12) *P. brevicornis,* connected elytra, Bykovsii, sample MKh-B-21; (13) *P. pinguedineus,* pronotum, Main River, sample ChM-B1; (14) *P.* (*Cryobius*) sp.: (14a) pronotum, Main River, sample ChM-B29, (14b) connected elytra, sample ChM-B31b; (15) *P. agonus,* pronotum, Bykovsii, sample MKh-B-17; (16) *P. costatus,* left elytron, Bykovsii, sample MKh-R-13; (17) *P. vermiculosus*: (17a) pronotum, Bykovsii, sample Mkh-01-02, (17b) left elytron, Lyakhovskii, sample LL-14-B17; (18) *P. abnormis*: (18a) pronotum, Main River, sample ChM-B26, (18b) left elytron, Bykovsii, sample MKh-R-18; (19) *P. tundrae*, right elytron, Buor-Khaya, sample Bkh-02-B7; (20) *P.* (*Petrophilus*) *montanus,* left elytron, Bykovsii, sample MKh-R-5; (21) *P. sublaevis*, connected elytra, Bykovsii, sample MKh-B-24; (22) *Stereocerus haematopus*, right elytron, Main River, sample ChM-B26; (23) *Amara interstitialis,* left elytron, Bykovsii, sample MKh-B-2; (24) *A. glacialis:* (24a) pronotum, Main River, (24b) right elytron, sample ChM-B26; (25) *Curtonotus alpinus:* (25a) pronotum, (25b) right elytron, Oiagoss, sample Oya-6-1; (26) *C. bokori* pronotum, Main River, sample ChMB23a.

Fig. 38. Families Haliplidae, Dytiscidae Hydrophilidae, Leiodidae, Staphylinidae, Scarabaeidae, Scirtidae, Byrrhidae, Heteroceridae: (1) *Haliplus* sp., left elytron, Alazeya River, sample 203.5; (2) *Agabus moestus:* (2a) pronotum, Oiagoss, sample Oya-6-1, (2b) right elytron, Bykovsii, sample MKh-B4; (3) *Colymbetes dolabratus:* (3a) head, Oiagoss, sample Oya-6-1, (3b) left elytron (without top), Lyakhovskii, sample LL-14-B17; (4) *Dytiscus* sp., left elytron (top), Alazeya River, sample 203.5; (5) *Rhantus notatus,* right elytron, Anadyr, sample ChA-B-1; (6) *Hydroporus acutangulus?,* left elytron, Bykovsii, sample MKh-B20; (7) *Helophorus tuberculatus,* left elytron, Samoilov, sample Sam-2-B4; (8) *H. splendidus:* (8a) head, Oiagoss, sample Oya-6-1, (8b) pronotum, Nagym, Nag-7+50 B-7, (8c) right elytron, Oiagoss, sample Oya-6-1; (9) *H. sibiricus:* (9a) head, (9b) right elytron, Oiagoss, sample Oya-6-1; (10) *Hydrobius fuscipes,* left elytron, Bykovsii, sample Mkh-B20; (11) *Cercyon* sp., left elytron, Lyakhovskii, sample LL-14-B17; (12) *Cyrtoplastus irregularis?*, right elytron, Nagym, sample Nag-7-B-4; (13) *Cholevinus sibiricus:* (13a) head, (13b) pronotum, (13c) right elytron, Oiagoss, sample Oya-6-1; (14) *Colon* sp., right elytron, Oiagoss, sample Oya-6-1; (15) *Aclypea opaca,* right elytron, Alazeya River, sample 203-6; (16) *Phosphuga atrata,* right elytron, Bykovsii, sample MKh-01-01; (17) *Thanatophilus dispar,* right elytron, Alazeya River, sample 203-6; (18) *Eucnecosum tenue:* (18a) head, (18b) pronotum, (18c) left elytron, Oiagoss, sample Oya-6-1; (19) *Olophrum rotundicolle,* pronotum, Anadyr, sample ChA-B-1; (20) *Micralymma brevilingue,* left elytron, Nagym, sample Nag-7-B-4; (21) *Holoboreaphilus nordenskioeldi,* head, Nagym, Bkh-02-B-1; (22) *Tachinus arcticus:* (22a) head, (22b) pronotum, (22c) left elytron, Yana, sample Tums-11; (23) *T. brevipennis:* (23a) head, (23b) pronotum, (23c) left elytron, Main River, sample ChM-B26; (24) *Bledius* sp., pronotum, Nagym, sample N7-B4; (25) *Stenus* sp., head, Bykovsii, sample MKh-B21; (26) *Lathrobium longulum:* (26a) head, (26b) pronotum, (26c) connected elytra, Oiagoss, sample Oya-6-1; (27) *Quedius* sp., head, Lyakhovskii, sample LL-14-B17; (28) *Aegalia kamtschatica,* left elytron, Buor-Khaya, sample BKh-B2; (29) *Aphodius* sp.: (29a) pronotum, Main River, sample ChM-B27, (29b) left elytron, Buor-Khaya, sample BKh-B13; (30) *Cyphon* sp., left elytron, Anadyr, sample ChA-B-2; (31) *Byrrhus fasciatus,* right elytron (top), Buor-Khaya, sample BKh-02-B1; (32) *Cytilus sericeus,* right elytron, Alazeya River, sample 203-6; (33) *Morychus viridis|:* (33a) head, Bykovsii, sample MKh-R7, (33b) pronotum, (33c) right elytron, (33d) abdomen, Main River, sample ChM-B32; (34) *Simplocaria elongata,* left elytron, Oiagoss, sample Oya-6-1; (35) *S. semistriata,* left elytron, Nagym, sample Nag-4-B8; (36) *Curimopsis cyclolepidia:* (36a) pronotum, (36b) left elytron, Main River, sample ChM-B26; (37) *Heterocerus* sp., right elytron, Alazeya River, sample 203-7.

Table 41. Common fossil insect species of western Beringia (a total of 683 assemblages): number of records from QUINSIB database (Kuzmina, 2014)

Family	Species	Number of records, sum = 683	Average, %
Carabidae	*Pterostichus* (*Cryobius*) spp., including *P. ventricosus* Esch., *P. brevicornis* (Kby.), *P. pinguedineus* Esch.	643	12.6
Carabidae	*Curtonotus alpinus* Payk.	516	10.8
Byrrhidae	*Morychus viridis* Kuzm. et Kor.	492	22.2
Staphylinidae	*Tachinus arcticus* Motsch.	306	8.0
Curculionidae	*Lepyrus nordenskioeldi* Faust	298	3.7
Curculionidae	*Hypera ornata* Cap.	290	3.8
Carabidae	*Poecilus* (*Derus*) *nearcticus* Lth.	271	4.4
Leiodidae	*Cholevinus sibiricus* (Jean.)	248	4.1
Carabidae	*Pterostichus* (*Tundraphilus*) *sublaevis* Sahlb.	234	2.7
Curculionidae	*Sitona borealis* Kor.	224	2.7
Curculionidae	*Stephanocleonus eruditus* Faust	221	4.0
Carabidae	*Pterostichus* (*Lenapterus*) *costatus* Men.	199	2.6
Curculionidae	*Isochnus arcticus* Kor.	188	11.2
Curculionidae	*Phyllobius kolymensis* Kor. et Egorov	173	8.6
Curculionidae	*Notaris bimaculatus* F.	173	3.3
Curculionidae	*Coniocleonus ferrugineus* Fahr.	157	2.6
Chrysomelidae	*Chrysolina subsulcata* Mnnh.	142	3.0
Carabidae	*Dicheirotrichus mannerheimi* Sahlb.	140	3.1
Carabidae	*Stereocerus haematopus* (Dej.)	138	2.2
Carabidae	*Harpalus vittatus kiselevi* Kat. et Shil.	138	2.6
Hydrophilidae	*Helophorus splendidus* Sahlb.	138	2.6
Chrysomelidae	*Chrysolina tolli* Jac.	134	3.6
Chrysomelidae	*Chrysolina septentrionalis* Men.	124	2.6
Carabidae	*Diacheila polita* Fald.	116	2.1
Carabidae	*Notiophilus aquaticus* L.	109	2.6
Melyridae	*Troglocollops arcticus* L. Medv.	100	2.2

The list of host plants includes moss, grasses, sedges, *Artemisia*, herbs, and shrubs. At first glance, this is a usual tundra vegetation, but thorough analysis displays some specific features.

Moss is the most common group of tundra vegetation, but it plays only a minor role as food source for tundra animals. Indeed, very rare animals including insects are specialized on moss feeding, the members of Byrrhidae famile are quite unique exception. We can hardly collect numerous moss eaters in the modern environment, but not in the past. We indicate here (Table 42) the moss *Polytrichum piliferum*, as a host plant of one of the most popular Pleistocene beetle *Morychus viridis*. This moss, unlike other well-known species of the genus *Polytrichum* prefers dry sandy habitats (Abramova et al., 1961); on the driest soil, the moss usually appears as a tiny, short stem clump. In contrast to other tundra mosses, this moss cannot accumulate moisture. Such an accurate species identification prevents reconstruction of the typical tundra moss cover. We can make incorrect conclusion being restricted to only the palynological method, which allows identification only to the level "green moss spores."

In regard to grassy vegetation, the most common Pleistocene beetles are indicative of a great role of xerophilous sedges (*Carex argunensis, C. duriuscula*) and herbs (*Poa, Alopecurus, Agropyron*). The presence of a significant percentage of "Cyperaceae and Poaceae" spores in the palynological spectrum is probably evidence of wet tundra or boggy environment, but our host plants allow steppe-like and meadow vegetation to be reconstructed. Another feature of the insect-based vegetation reconstruction is a notable role of legumes (*Hedusarum, Oxytropus, Astragalus*), *Artemisia,* and various herbs. These plants could fit equally to dry grassy tundra or steppe communities.

Some host plants, however, verify tundra-like and wet habitats. The weevil *Isochnus arcticus* Kor., a usual Pleistocene beetle, is strongly associated with dwarf Arctic willows. Weevil was found in many samples, but its role increases dramatically during the last glacial maximum (Sher et al., 2005; Kuzmina et al., 2011).

Table 42. Some common beetle species from the Pleistocene of western Beringia, their host plants and environments

Species	Host plant, plant community	Reference
Curtonotus alpinus Payk.	Feeds on flowering shoots and young grass seeds, particularly, *Poa,* and *Alopecurus*.	Chernov, 1980
Morychus viridis Kuzm. et Kor.	Feeds on *Polytrichum piliferum* Hedw., in association with xerophilous sedge *Carex argunensis* Turcz.	Berman et al., 2001a
Lepyrus nordenskioeldi Faust	Willows, rarely, birch and alder	Chernov, 1980
Hypera ornata Cap.	Legumes (*Astragalus, Oxytropus*)	Chernov, 1980, Khruleva and Korotyaev, 1999
Sitona borealis Kor.	Legumes (*Hedusarum, Oxytropus*)	Chernov, 1980, Khruleva and Korotyaev, 1999
Stephanocleonus eruditus Faust	Mountain steppe and relict steppe patches in Yakutia (plant association with *Carex duriuscula* C.A. Meyer, *Agropyron, Artemisia pubescens* Ledeb., probably, *Artemisia*)	Berman et al., 2001
Isochnus arcticus Kor.	Arctic willows, including *Salix arctica* Pall., *S. glauca* L., *S. pulchra* Cham., *S. reptans* Rupr.	Khruleva and Korotyaev, 1999
Phyllobius kolymensis Kor. et Egorov	Steppe slopes and sand dunes with wild rose and willow	Berman et al., 2001a
Notaris bimaculatus F.	Sedge and reed (*Typha latifolia* L., *Phragmites australis* (Cav.), *Phalaroides arundinacea* L.)	Hoffmann, 1958
Coniocleonus ferrugineus Fahr.	Mountain steppe and relict steppe patches in Yakutia (plant association with *Carex duriuscula* C.A. Meyer, *Agropyron, Artemisia pubescens* Ledeb., probably, *Artemisia*)	Berman et al., 2001a
Chrysolina subsulcata Mnnh.	Polyphagous; commonly *Carex* (*Carex lugens* Holm.) and other plants (*Salix polaris* Wahlenb., *Stellaria, Minuartia, Parrya, Senecia, Petasites, Oxytropis*)	Silfverberg, 1994; Medvedev, 1996
Chrysolina tolli Jac.	Cruciferous plants (*Parrya*)	Medvedev, 1996
Chrysolina septentrionalis Men.	Polyphagous, commonly on Ranunculaceae (*Ranunculus, Delphinium*) and other plants (*Myosotis, Pedicularis, Silene repens* Patrin, *Cerastium arvense* L., *Minuartia*)	Chernov, 1980, Medvedev, 1996, Silfverberg, 1994, Makarova et al., 2007

Table 43. Occurrence of different types of tundra and steppe–tundra insect assemblages in the Pleistocene of western Beringia

Type	**TU/TU**	**TU/XE**	**TU/S-T**	**S-T/S-T**	**S-T/SS**	**S-T/MS**	**S-T/S-T**	Total
	16	96	107	138	50	11	11	429

Dwarf willows, especially low-stem *Salix arctica* could survive under very severe condition, but on the other hand, dwarf willows are also widespread in tundra shrubs. The weevil *Lepyrus nordenskioeldi,* another popular phytophage, is associated with medium-sized and tall willows. Other shrub-related insects are very rare in Pleistocene communities, becoming more common in the Holocene.

The last significant host plant is probably the *Phalaroides arundinacea* (two other species are not recorded in northeastern Siberia), which is related to the weevil *Notaris bimaculatus*. This is a tall riparian grass, which could grow in wet depressions of steppe–tundra.

Thus, we have two groups of host plants; the first is indicative of dry grassy–herbaceous habitats and the second corresponds to wet tundra-like and riparian environments. Insect species associated with dry grassy–herbaceous plants prevail in steppe–tundra assemblages.

Different types of steppe–tundra insect faunas reflect climate, soil, grazing influence, and other factors. The most popular types are the moderate steppe–tundra **S-T/S-T** and **TU/S-T** (Tables 42, 43). The third place belongs to the weak steppe–tundra type **TU/XE** (without thermophilous steppe insects); strong steppe tundra types are less common.

Table 43 gives only a rough picture, because we combined the data on different ages and different regions, but anyway, it reflects the current level of study of the region, which is quite detailed. The most common type **S-T/S-T** type is characterized by the absence of clear dominant species and a high role of members of three major ecological groups: wet and dry tundra (**mt, dt**) and sedge steppe (**ss**). Without significant presentation of steppe or arctic species, members of these three groups produce the type **S-T/S-T**. The most common fossils here are the ground beetles *Pterostichus* (*Cryobius*) spp. (**mt**), *Curtonotus alpinus* (**dt**), and the pill beetle *Morychus viridis* (**ss**).

Ground beetles of the subgenus *Cryobius* are common in modern tundra inhabitants. This is a very diverse group, sometimes with hardly recognizable species (especially fossils). The beetles live in modern boggy areas in taiga, near water, under shrub leaves. In our research, we collected many beetles (mostly *Pterostichus* (*Cryobius*) *brevicornis*, *P.* (*Cryobius*) *pinguedineus,* and *P.* (*Cryobius*) *ventricosus*) on the old part of Quaternary outcrops covered by vegetation. These species can live on disturbed land or in riparian habitats; thus, they are not undoubted tundra indicators. In the steppe–tundra environment, *Pterostichus* (*Cryobius*) spp. could live in wet depressions, which are widespread in the permafrost regions.

The ground beetle *Curtonotus alpinus* is an ecologically flexible species; it sometimes co-occurred with *Pterostichus* (*Cryobius*) spp. on disturbed land or under shrub leaves, but its main habitats in tundra is grassy meadow. Such meadows usually occupy drained thermokarst lakes. In the steppe–tundra environment, *Curtonotus alpinus* could live on grasses in moderately dry steppe patches.

The third species is the pill beetle *Morychus viridis*. We have discussed the ecology of this beetle above. At present, the habitats with tiny moss and xerophilous sedges are affected by strong ecological competition. In the Upper Kolyma region (Berman et al., 2001a), these sedge steppe patches occupy the tops of hills up to 600–800 m high, sometimes up to 1400 m high, or slope bends in windy valleys. The wind is critical for the sedge steppe association; it removes almost all snow cover, dries up the soil, and prevents lichen spread. Snow is gone by the second part of March here, so that the vegetative season starts somewhat earlier. Low or absent snow cover keeps soils as cold as the air in the winter, down to –40°–50°C. In the summer, the soil accepts high warm supply because of the early snow free, treeless, local continental climate with warm sunny summer and long sun day in the north. The soil temperature on the surface reaches +42°–45°C; at a depth of 5 cm; it decreases to 23°–25°C. These dramatic changes are a distinctive feature of sedge steppe with a dense root mat.

The sedge *Carex argunensis* is often a member of pioneering vegetative community. This sedge grows on after fire gravel ground in the Upper Kolyma region; sedge vegetation is replaced by mountain pine quite soon. Long existence of the sedge areas is only possible under certain circumstances which prevent natural succession. As an element of xerophilous sedge community, the pill beetle *Morychus viridis* is also a pioneering species. The number of the beetle larvae could be very large, up to 100 specimens per square meter. Such a high accumulation is attributable to the huge proportion of beetles in fossil assemblages, but we have to admit permanent existence of sedge communities. Today, hemicryoxerophilous steppes occupy only restricted areas with unique combination of different factors.

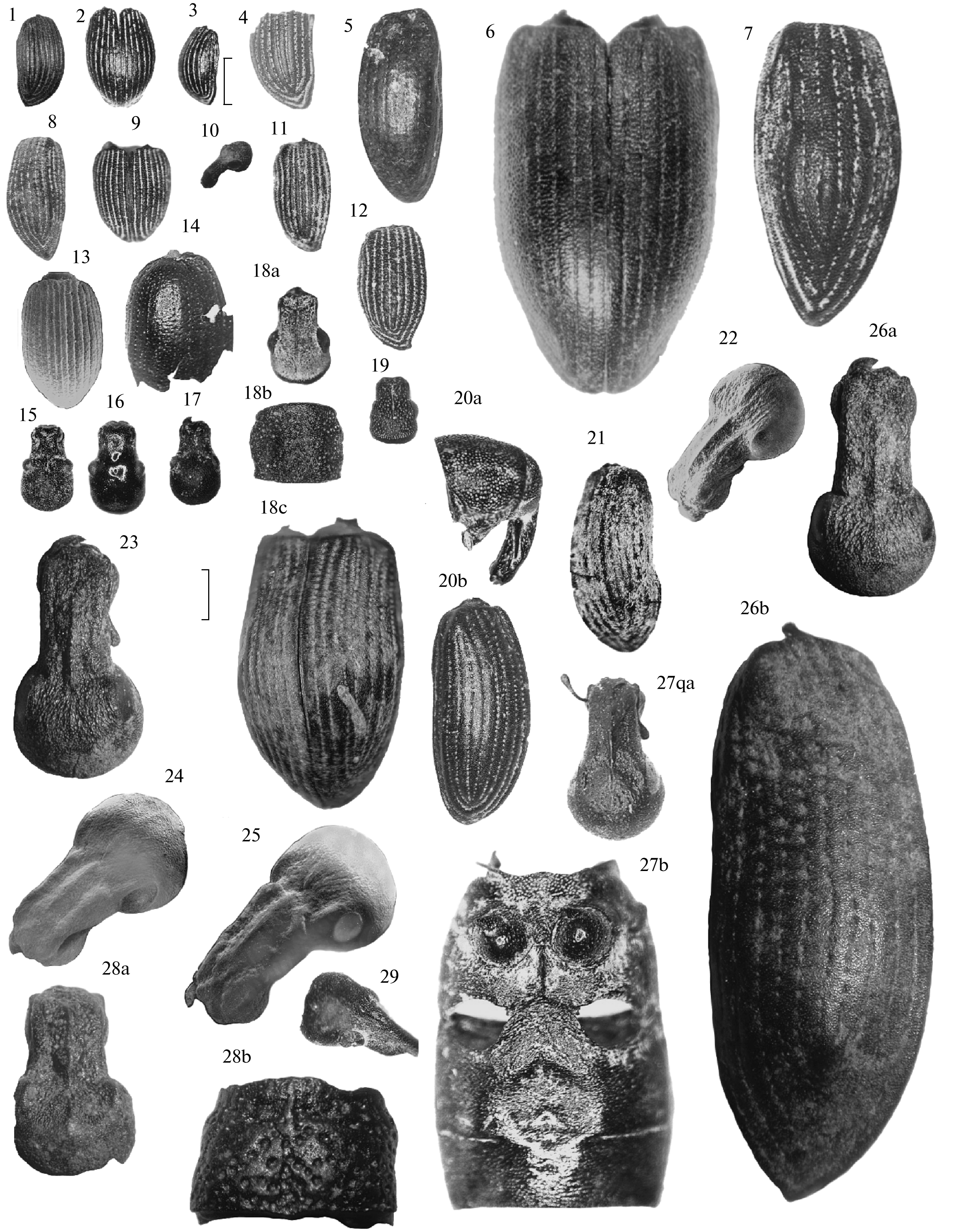
It is doubtless that sedge steppes were much more widespread in the past, but the question is how far the modern conditions necessary for the existence of this community correlate with the past ones. D.I. Berman considers that, in the past, the factors favorable for sedge were similar to the modern ones: continental climate, low moisture, and a lack of snow as a result of strong wind. This combination explains the survival of the pioneering sedge stage in some localities, but not everywhere in western Beringia. Strong wind contradicts large mammal requirements for winter survival at low temperatures.

We can take into account various factors that cut off a succession and support the pioneering stage. In addition to the wind, a number of other factors play certain role. One of them is soil. In western Beringia, a specific soil type (cryopedolith) was widespread during the cold stages of the Pleistocene (Gubin, 1984, 1997, 1999). Cryopedolith was not a completely developed soil, it lacked an organic horizon. Low temperatures caused by permafrost in the lower horizons prevent microbial activity and preserve dead roots and plant debris. This soil became warm in the summer and had a good aeration, supporting dry sedge community. Another presently absent factor is mammal trampling. Grazing mammals considerably affected the Pleistocene environment in the north (Zimov et al., 1995; Zimov, 2005; Blinnikov et al., 2011). Impoverished sedge community could have resulted from overgrazing or some other surprising, presently absent impacts. Diversity of fossil Quaternary insects (see Figs. 36–40).

5.4. Mosaic Environment

The mosaic structure of steppe–tundra community is the most popular point of view (Guthrie, 1968, 1984; Yurtsev, 1974, 1976, 2001; Matthews, 1982; Schweger, 1997). Steppe and tundra vegetation coexist, occupying different parts of the landscape. Following the succession theory developed by Razumovsky (1981), the mosaic could be explained by hydro- and xeroseries of the single succession line. The modern tundra fits to a hydroseries of the past steppe–tundra ecosystem, the xeroseries of which has been reduced to a critical size and has little chances to recover without grazing mammals. Accepting this point of view, we


1
2
3
4
5
6a
6b
6c
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22a
22b
23
24
25
26
27
28
29
30


1
2
3
4
5
6
7
8
9
10
11
12
13
14
18a
15
16
17
18b
19
20a
21
22
26a
18c
23
20b
26b
27qa
24
25
27b
28a
29
28b

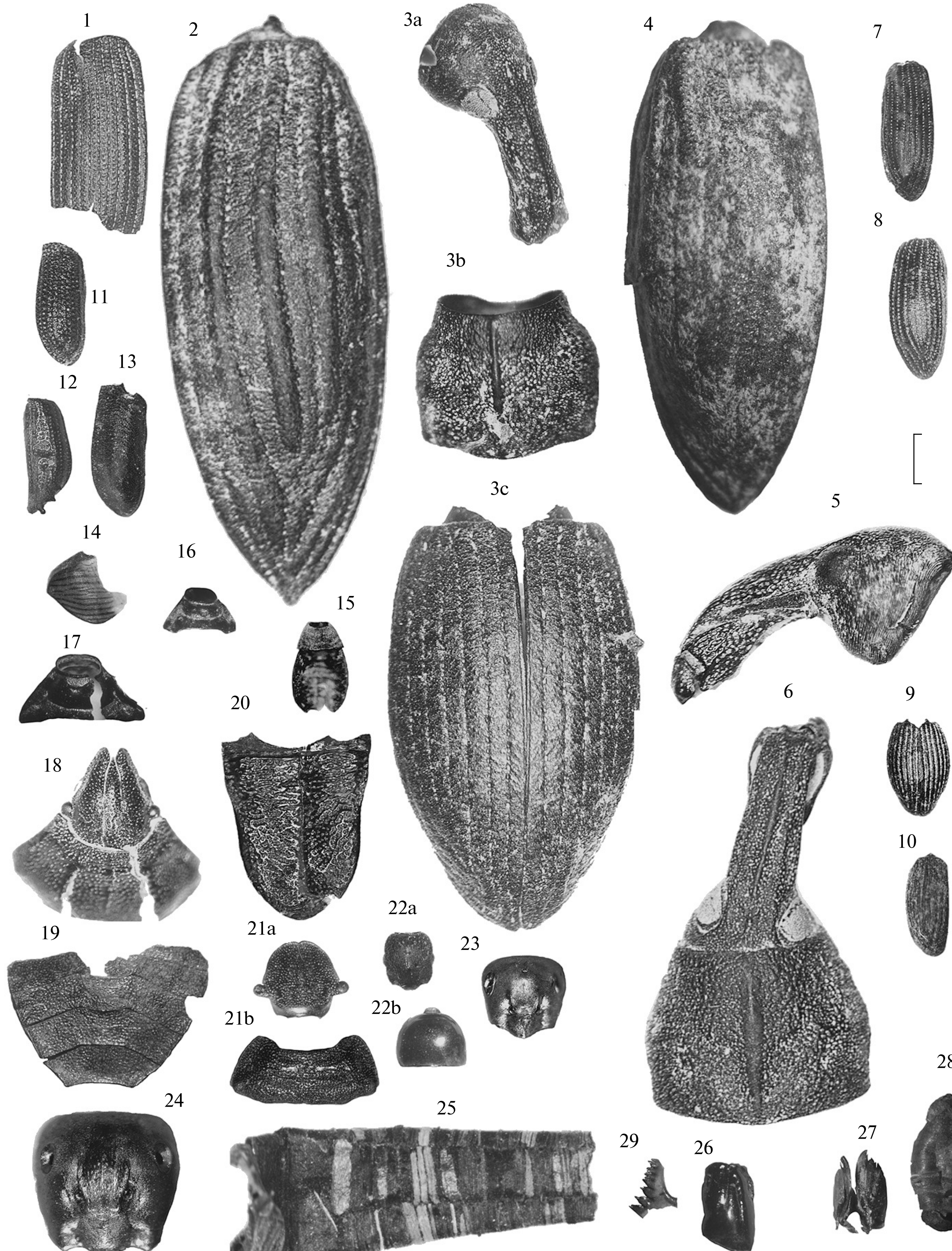

1
2
3a
4
7
8
11
3b
12
13
3c
5
14
16
15
17
20
6
9
18
10
22a
21a
23
19
21b
22b
28
24
25
29
26
27

Fig. 39. Families Elateridae, Anobiidae, Melyridae, Coccinellidae, Lathridiidae, Tenebrionidae, Chrysomelidae: (1) *Denticollis varians,* pronotum, Alazeya River, sample 662; (2) *Caenocara bovistae,* right elytron, Oiagoss, sample Oya-6-1; (3) *Troglocollops arcticus*, left elytron, Khomus-Yuryakh, sample 83-25; (4) *Anisosticta bitriangularis,* base of left elytron, Alazeya River, sample 203-7; (5) *Coccinella fulgida,* left elytron, Main River, sample ChM-B3; (6) *C. transversoguttata:* (6a) pronotum, (6b) metathorax, (6c) right elytron, Main River, sample ChM-B31b; (7) *Hippodamia arctica,* left elytron, Alazeya River, sample 203-1; (8) *Corticaria* sp., left elytron, Nagym, sample Nag-B4; (9) *Stephostethus* sp., left elytron, Nagym, sample Nag-7-B4; (10) *Upis ceramboides,* pronotum, Alazeya River, sample 661; (11) *Donacia* sp., right elytron, Alazeya River, sample 203-6; (12) *Cassida* sp., left elytron, Khomus-Yuryakh, sample 83-25; (13) *Chrysolina brunnicornis bermani,* left elytron, Khomus-Yuryakh, sample 83-25; (14) *Ch. brunnicornis wrangeliana,* left elytron, Khomus-Yuryakh, sample 83-25; (15) *Ch. tolli,* left elytron, Bykovsii, sample MkH-R16; (16) *Ch. subsulcata,* right elytron, Bykovsii, sample MkH-B16; (17) *Chrysolina* sp., right elytron, Khomus-Yuryakh, sample 83-25; (18) *Chrysomela blaisdelli,* right elytron, Khomus-Yuryakh, sample 83-25; (19) *Colaphellus alpinus,* head and pronotum, Khomus-Yuryakh, sample 83-25; (20) *Gastrolina peltoidea,* left elytron, Buor-Khaya, sample BKh-B2; (21) *Gonioctena affinis,* base of left elytron, Oiagoss, sample Oya-6-1; (22) *Hydrothassa hannoverana,* (22a) head, (22b) pronotum, Oiagoss, sample Oya-6-1; (23) *Phratora vulgatissima,* left elytron, Lena delta, sample BKh-B2; (24) *Plagiodera versicolora,* left elytron, Anadyr, sample ChA-B1; (25) *Prasocuris phellandrii,* right elytron, Buor-Khaya, sample BKh-B2; (26) *Hippuriphila modeeri,* left elytron, Nagym, sample Nag-4-B8 30; (27) *Galerucella grisescens,* head, Bykovsii, sample 99-3ac; (28) *Chaetocnema* sp., left elytron, Nagym, sample Nag-4-B8; (29) *Galeruca interrupta circumdata,* base of left elytron, Bykovsii, sample MkH-B28; (30) *Bromius obscurus,* right elytron, Alazeya River, sample 73.6.

Fig. 40. Families Brentidae, Brachyceridae, Curculionidae: (1) *Pseudoprotapion astragali,* left elytron, Yana, sample Tums1-8,5; (2) *Mesotrichapion wrangelianum,* connected elytra, Main River, sample ChM-B26; (3) *Hemitrichapion tschernovi,* right elytron, Main River, sample ChM-B26; (4) *Apion arcticum,* top of right elytron, Lyakhovskii, L-0-B25; (5) *Notaris eversmanni,* right elytron, Nagym, sample Nag-7-B4; (6) *N. bimaculatus,* connected elytra, Anadyr, ChA-B1; (7) *Grypus equiseti,* left elytron, Khomus-Yuryakh, sample 83-25; (8) *Bagous limosus,* right elytron, Nagym, sample Nag-7-B4; (9) *Ceutorhynchus* sp. nov., connected elytra, Khomus-Yuryakh, sample 83-25; (10) *Pelenomus velaris?,* head, Oiagoss, sample Oya-6-1; (11) *Phytobius leucogaster,* left elytron, Khomus-Yuryakh, sample 83-25; (12) *Zacladus radulata,* left elytron, Nagym, sample Nag-7-B4; (13) *Lepidophorus thulius,* connected elytra, Khomus-Yuryakh, sample 83-25; (14) *Otiorhynchus cribrosicollis,* base of left elytron, Nagym, sample Nag-7-B4; (15) *Phyllobius kolymensis,* head, Khomus-Yuryakh, sample 83-25; (16) *Phyllobius* sp. nov. 1, head, Khomus-Yuryakh, sample 83-25; (17) *Phyllobius* sp. nov. 2, head, Khomus-Yuryakh, sample 83-25; (18) *Sitona borealis:* (18a) head, (18b) pronotum, Bykovsii, sample MkH-B17, (18c) connected elytra, Yana, sample Tums1-8,5; (19) *S. lineellus,* head, Arga-Bilir-Aryta Island, BkH-B2; (20) *Hypera diversipunctata:* (20a) head and pronotum, (20b) left elytron, Main River, sample ChM-B26; (21) *H. ornata,* right elytron, Main River, sample ChM-B26; (22) *Coniocleonus astragali,* head, Khomus-Yuryakh, sample 83-25; (23) *C. cinerascens,* head, Duvanny Yar, sample P-1332s-2; (24) *C. ferrugineus,* head, Khomus-Yuryakh, sample 83-25; (25) *C. vinokurovi,* head, Khomus-Yuryakh, sample 83-25; (26) *C. zherichini:* (26a) head, (26b) left elytron; Stanchikovskii Yar, sample P-08-03; (27) *Stephanocleonus eruditus:* (27a) head, (27b) thorax and abdomen, Bykovsii, sample MkH-B17; (28) *S. fossulatus:* (28a) head, (28b) pronotum, Duvanny Yar, sample P-1332s-2; (29) *Lixus paraplecticus,* head, Buor-Khaya, sample BKh-B2.

Fig. 41. Family Curculionidae; Orders Heteroptera, Hymenoptera, Trichoptera, Megaloptera, Diptera: (1) *Magdalis duplicata*, left elytron, Nagym, sample Nag-7-B4; (2) *Lepyrus gemellus*, right elytron, Main River, sample ChM-B-21; (3) *L. nordenskioeldi:* (3a) head, (3b) pronotum, (3c) connected elytra, Main River, sample ChM-B26; (4) *L. volgensis*, left elytron, Main River, sample ChM-B1; (5) *Lepyrus* sp. nov., head, Khomus-Yuryakh, sample 83-25; (6) *Lepyrus* sp. nov. 2, head, Khomus-Yuryakh, sample 83-25; (7) *Dorytomus imbecillus,* left elytron, Nagym, sample Nag-7-B4; (8) *D. rufulus*, right elytron, Alazeya River, sample 203-5; (9) *Isochnus arcticus,* connected elytra, Buor-Khaya, sample Bkh-02-B13; (10) *I. flagellum,* left elytron, Buor-Khaya, sample Bkh-02-B5; (11) *Phloeotribus spinulosus,* right elytron, Nagym, sample Nag-7-B4; (12) *Ips cembrae,* left elytron, Nagym, sample Nag-R2; (13) *Polygraphu*s sp., right elytron, Nagym, sample Nag-R2; (14) *Sigara* sp., pronotum, Alazeya River, sample 77.6.2; (15) *Microvelia umbricola,* abdomen, Alazeya River, sample 203-5; (16) *Salda littoralis?,* pronotum, Oiagoss, sample Oya-6-1 (17) *Saldula pallipes,* pronotum, Oiagoss, sample Oya-6-1; (18) *Aelia frigida,* head and pronotum, Alazeya River, sample 77.2.2; (19) Pentatomidae gen. indet., abdomen, Duvanny Yar, sample P-F1-1332s-1,2; (20) *Neottiglossa metallica,* Alazeya River, sample 70-1+3; (21) *Sciocoris microphthalmus:* (21a) head, (21b) pronotum, Oiagoss, sample Oya-6-1; (22) *Leptothorax acervorum:* (22a) head, (22b) abdomen, Oiagoss, sample Oya-6-1; (23) *Formica gagatoides,* head, Alazeya River, sample 70.1; (24) *Camponotus herculeanus,* head, Alazeya River, sample 203-5; (25) Trichoptera larvae case, Samoilov, sample Sam-B3; (26) Sialidae larvae, head, Oiagoss, sample Oya-6-1; (27) Tipulidae, larvae, head, Oiagoss, sample Oya-6-1; (28) Diptera, pseudopupia, Oiagoss, sample Oya-6-1. Scale bar, 1 mm. (29) Branchiopoda mandible, Oiagoss, sample Oya-6-1.

can operate with specific steppe–tundra environment as an integrated structure.

During more than a million years, steppe–tundra was only temporary and locally replaced by the forest, the final succession stage. This treeless ecosystem seems a good example of a long-lived subclimax community, which is supported by the combination of the biotic (mammal activity) and abiotic (preservation of organic matter in the soil by permafrost) factors.

The landscape diversity was rather low in the northern plains. There was a lack of mountains and even hills, only extensive river valleys cut significantly the land. The permafrost, as a stable source of moisture probably increased the role of small depressions, which provided wet environment for tundra-like vegetation. The drained areas were covered with low and high steppe grasses.

Shrub beetles are common in steppe–tundra assemblages. The most popular species is *Lepyrus nordenskioeldi,* which lives on tall willows (Table 42); we also recorded a couple of other *Lepyrus* species, other weevils, and some shrub leaf beetles. Shrub vegetation was an important and permanent part of mosaic steppe–tundra environment. Forest insects are rare, but individual species occur even in true steppe–tundra assemblages. We recorded indirect forest indicators, such as ants and tree-related species, for example, the weevil *Pissodes*. Trees (probably larch) apparently occupied local depressions protected from wind, but forest islands were small and isolated.

5.5. Temperature Reconstruction, MCR

The presence of steppe weevils (genus *Stephanocleonus*) in Pleistocene fossil assemblages suggests that the summer temperature was rather high (Berman and Alfimov, 1998). Modern insect community of relict Yakutian steppe is dominated by two species, *Stephanocleonus eruditus* and *S. fossulatus* their main area is situated even far in south-southern Siberia, Mongolia, and Transbaikalia. These weevils require 2200°–2400°C of total temperature for normal larval development in the soil. This total temperature is associated with the mean July temperature of 22°–23°C, but in some regions with high air clarity and low moisture, the upper 5 cm of soil can reach required total temperature at 12°–14°C of mean July temperature. In the Arctic and Subarctic regions, the total temperature increases due to night sunshine in the summer.

Calculations (Berman and Alfimov, 1998) show that necessary mean air temperature in July that allowed *Stephanocleonus eruditus* and *S. fossulatus* to live on the plain was 12°–13°C; for the south facing slopes, only 12°–13°C. Soil moisture was at least 5–6%, that is less than that of the driest tundra soil (9–10%).

This reconstruction of the summer temperature (higher than at present) seems surprising for cold intervals, but it is also possible to take into account a number of additional factors. Modern cold and wet tundra is mostly the coastal zone. The sections under study were situated far more inland in the Pleistocene and even Early Holocene (Bauch et al., 2001).

A popular method of temperature reconstruction using fossil beetles is the Mutual Climatic Range (MCR). MCR is widely used in Europe (Atkinson et al., 1986) and North America (Elias et al., 1996; Elias, 2001; Elias, and Matthews, 2002). The first attempt to use MCR in western Beringia was made by D.I. Berman, A.V. Alfimov, and A.V. Sher (Alfimov et al., 2003) with reference to two sections in the Kolyma Lowland (Duvanny Yar and Aleshkina Zaimka). The temperature ranges of thermophilous (such as *Stephanocleonus eruditus*) and cold resistant species (such as *Chrysolina subsulcata*) overlap only slightly, if at all. The mean July temperature of 12–13°C is the only interval that satisfies both ranges. This method was developed on the analogy with modern taxa ranges; it is difficult to introduce corrections for the Pleistocene nonanalogue environment, where a number of cold resistant species could survive under a higher summer temperature, because they lived in a treeless landscape and avoided competition with thermophilous forest and meadow species. In some areas of western Beringia, true mean July temperature was probably even higher than the estimate of 12–13°C.

5.6. Extinct Species

Most of the fossils in question belong to modern species (Kiselev, 1981; Kiselev and Nazarov, 2009). In the modern fauna, some species (*Poecilus nearcticus, Lepidophorus thulius*) became extremely rare, some (*Morychus viridis*) decreased dramatically in geographical range, and some (*Stephanocleonus*) disappeared in the north, but survived in the south. In addition, some actually extinct species have been recorded (Kuzmina, 2001). Available data are based mostly on a unique large fossil insect assemblage from the Khomus-Yuryakh site, sample 83-25 (Table 7). We found two new species of the genus *Lepyrus*, one *Ceuthorynchus*, two *Phyllobius*, and one problematic *Chrysolina* or close genus of Chrysomelidae. Quaternary beetles are similar in preservation to modern taxa, but without some important features, so that it is not easy to describe new species, using such material. It has been established with certainty that extinct species were inhabitants of the steppe–tundra environment. This fact confirms the unique character of the steppe–tundra environment.

5.7. Steppe–Tundra As a Unique Nonanalogue Environment

We can describe numerous differences between modern tundra and modern steppe and the Pleistocene steppe–tundra. Even insect community from the relict steppe areas in central Yakutia (Berman et al., 2001a), which is the closest one to the Pleistocene steppe–tundra, shows a number of significant differences.

Steppe–tundra insect assemblages contain a very few necrophilous and coprophilous beetles. Silphidae beetles, which are common in modern tundra and forest, were almost absent in steppe–tundra, while abundant mammoth fauna seems to provide good food source for them. The main role in the dead body utilization probably belonged to dipterans. The beetle *Cholevinus sibiricus* (Leiodidae), which is presently an unspecialized detritophage, was probably partly necrophage in the Pleistocene (Kuzmina and Perkovsky, 2002).

Coprophage beetles, which are presently very common in steppes, played a less important role in Pleistocene steppe–tundra. Only dung beetles of the genus *Aphodius*, one or two species, were recorded in the Pleistocene. A greater abundance of *Aphodius* is correlated with the strong steppe–tundra type **S-T/ST.**

These examples show that the insect fauna of the severe steppe–tundra environment was poorer than that of ordinary steppe. A lack of necro- and coprophagous beetles is probably accounted for by the mountain origin of steppe species, since most of steppe beetles from Pleistocene steppe–tundra community presently live in mountain steppes.

Fossil Orthoptera have never been found in western Beringia. These insects are very common in steppes, including northern steppes; eight species were found in relict steppes of Yakutia (Berman et al., 2001). Grasshoppers are usually well preservation and the absence of this group in the fossil record suggests that it was actually absent in the Pleistocene.

A careful comparison of the species lists from the relict steppe areas of Yakutia and fossil record (Berman et al., 2011) shows that the weevil fauna is more or less uniform, the leaf beetle fauna has moderate differences, but ground beetles are substantially different. In addition, steppe and tundra species are strictly separated in the modern environment; the floodplain terraces and mountain tundra, even local wet depressions in the modern steppe patches have yielded nonsteppe beetle species. Pleistocene steppe–tundra landscapes had a considerably less opportunity for such physical separation; steppe and tundra species often had to share the same habitats, such as the south faced slopes or plain grassland.

Most of plant and insect species from steppe–tundra community survived environmental changes in the Holocene. Some species survived in zonal tundra, others live in zonal steppe or relict steppes inside the forest zone. A unique feature of Pleistocene steppe–tundra was the combination of these presently disconnected elements in the same environment, which existed with moderate variations for more than million years and was completely disrupted during the last dramatic climatic change.

CHAPTER 6. DISTINCTIVE FEATURES OF INSECT FAUNAS OF WESTERN AND EASTERN BERINGIA

Beringia was an integrated large region of ice-free land, including western Beringia (northeastern Asia), eastern Beringia (northwestern North America), and the Bering Bridge. The three regions are distinguished by the climate and environmental features. The Bering Bridge was situated in place of the modern Bering Strait and adjacent shelf. Fossil insects from this area have only been studied in small ice core samples provided by sea drilling (Elias et al., 1992, 1996, 1997; Elias, 1996); fossil insects are mostly indicative of wet tundra environments.

Insects from western Beringia (as shows the present study), eastern Beringia (see review in Morgan et al., 1983; Elias, 1994; Matthew and Telka, 1997), and both parts are well studied (Elias et al., 2000).

The list of all presently known data on eastern and western Beringia has been published by Kuzmina and Matthews (2012). This list shows that Pleistocene faunas from of these areas are rather different; only one-fifth of the list is identical. Fossil ground beetles and rove beetles are better presented in eastern Beringia, while weevils are more abundant in western Beringia.

Fossil insect faunas of western and eastern Beringia are dominated by different species. Steppe–tundra faunas of eastern Beringia are usually dominated by *Lepidophorus lineaticollis*, whereas steppe–tundra faunas of western Beringia are often dominated by *Morychus viridis*. The only habitats where pill beetles, such as *Morychus viridis,* prevail are areas of relict steppe, such as hemicryophytic steppe. In the Pleistocene, this species was a superdominant in west Beringian steppe–tundra assemblages, often comprising 90% of the total number of individuals in particular faunas (Kiselev, 1981; Kiselev and Nazarov, 2009).

In eastern Beringia, another *Morychus* species, *M.* aff. *aeneolus* (certainly different than Asiatic *M. viridis* and somewhat different than *M. aeneolus,* currently occurring in Alaska and Yukon), was often rather frequent, but it is rarely accounted for more than 10% of specimens in fossil assemblages (Berman et al., 2011).

The weevil *Lepidophorus lineaticollis* is a very common beetle in eastern Beringia; it prevails in many fossil assemblages (Matthews, 1983; Matthews and Telka, 1997). *L. lineaticollis* is presently widespread in Alaska, the Yukon, western Northwest Territories, and northern British Columbia. In the Yukon, this species mostly occurs in the steppe areas, but it is also widespread in tundra, where it can inhabit environments ranging from dry to wet and it is common on disturbed ground in the forest (Berman et al., 2011).

The fossil record of *Lepidophorus lineaticollis* in western Beringia is particularly interesting, as it is only known from Miocene faunas of the Ary-Mas section (identification needs verification), in the western part of the region (Elias et al., 2006; Kiselev and Nazarov, 2009). It has not been found in Pleistocene or Holocene faunas, even in the eastern parts of the Chukotka Peninsula, even though it lives there today. Perhaps, this species was accidentally introduced by man in recent years. The modern ecology and distribution of *L. lineaticollis* shows that this species is tolerant of various conditions. The reasons why it is absent in the western Beringian Pleistocene–Holocene record remains uncertain.

Another species, *Lepidophorus thulius* has been found in both Late Pliocene and Early Pleistocene faunal assemblages from the Kolyma and Anadyr basins as well as in fossil assemblages from Alaska and the Yukon, but it has not been found in the modern Asiatic fauna.

The weevil *Connatichela artemisiae* (presently endemic to steppe area of Yukon) has never been found in the past or present Asia. This strictly xerophilous species presently endemic to the Yukon Territory and adjacent regions of Alaska is commonly found in Pleistocene faunal assemblages of eastern Beringia (Anderson, 1984; Matthews and Telka 1997; Zazula et al., 2006). It is evident that *C. artemisiae* was more widespread in the Pleistocene than today, but its range probably did not reach the Bering Bridge. *C. artemisiae* has not been found in the areas close to the Bering Bridge, such as the Seward Peninsula (Matthews, 1974; Matthews and Telka, 1997; Kuzmina et al., 2008).

The Eurasian weevil genus *Phyllobius* is virtually absent in fossil assemblages of North America. The only specimen was recorded in the Pliocene of Alaska (Matthews and Telka, 1997) and this requires verification. Perhaps, it only recently penetrated into America (Bousquet, 1991). In western Beringia, fossil *Phyllobius* are common. The most common species *Phyllobius kolymensis* is only known from fossil faunas associated with xerophilous landscapes in the upper reaches of the Kolyma River (Kiselev, 1981; Kiselev and Nazarov, 2009).

Only one Asian species Cleonini , *Coniocleonus zherichini*, penetrated into Nearctic. *C. zherichini* is known from northeastern Palearctic (Korotyaev, 1980; Ter-Minasyan, 1988); it was recorded from the Yukon Territory as *Stephanocleonus stenothorax*, but later synonymized under *Stephanocleonus zherichini* (Anderson, 1997) (*Coniocleonus zherichini* in this paper). In the Chukotka Peninsula, this species is only found in relict hemicryophytic steppe or steppe–tundra. Based on its habitat requirements, this is a cryoxerophilous species. It is rare in fossil assemblages from western Beringia (Kiselev and Nazarov, 2009), but more or less common in eastern Beringian. *C. zherichini* has been found in many fossil samples of Klondike and Old Crow (Kuzmina et al., 2014, and unpublished data).

Other species of the tribe Cleonini are different. West Beringia species belong to two groups, *Stephanocleonus* and *Coniocleonus*. *Stephanocleonus* sensu stricto is absent in eastern Beringia in the Pleistocene and at present. In his revision of Cleonini, Anderson (1989) described *Coniocleonus* as a junior synonym of the genus *Stephanocleonus*. This decision is doubtful (Korothyaev in Berman et al., 2001b) and confuses zoogeographical discussion. In fact, the Nearctic fauna includes only *Coniocleonus* weevils.

The traditional view is that the Bering Land Bridge acted as a migrational filter (Elias et al., 1996, 1997; Guthrie, 2001; Elias and Crocker, 2008), because its climate was more humid than that of western and eastern Beringia. Reconstruction of the summer temperature regime and aridity in the Pleistocene of western Beringia (Alfimov and Berman, 2004) suggests that tundra–steppes with Asian steppe species never expanded as far east as the Anadyr River basin, remaining in the Chukotka Peninsula alone. This conclusion is confirmed by the fossil record of Chukotka (Amguema and Main rivers), where thermophilous steppe insects are extremely rare. This wide transition area was occupied by weak steppe–tundra communities with only one index species, *Morychus viridis*. The boundary between two closest species, *M. viridis* in Asia and *M.* aff. *aeneolus* in North America, lies exactly between continents. The limited faunal exchange could have been caused by the fact that respective ecological niches were already occupied by indigenous species (Sher, 1971). This possibly explains the persistence of different *Morychus* species on different sides of the Bering Strait.

CONCLUSIONS

(1) Quaternary fossil insects are very common in the permafrost regions of northeastern Asia. Excellent preservation and high concentration allows identification to species and accurate correlation of different assemblages. The Quaternary insect method is a very sensitive tool for environmental and climatic reconstructions.

(2) A large ice-free land situated in northeastern Asia and northwestern North America, including the drained Arctic sea shelf, provided specific conditions for permanent existence of various types of steppe–tundra environment during the Pleistocene and Early Holocene.

(3) The insect fauna reflects moderate environmental changes within the main ecosystem (steppe–tundra). Assemblages with a high proportion of thermophilous steppe insects were recorded in all main Pleistocene climatic cycles, but became more common in the Late Pleistocene.

(4) Most developed steppe–tundra communities were located in the Kolyma Lowland. The northern (Laptev Sea region) and eastern areas (eastern Chukotka) were occupied by more tundra-like vegetation.

(5) Fossil insects allow the recognition of the last glacial maximum (MIS2) and reconstruct environmental changes during this cold time. A detailed investigation of the Bykovsii section shows that MIS2 includes two substages: the first, cold (25–18 ka) and the second, relatively warm time.

(6) Insects confirm that steppe–tundra was a unique nonanalogue landscape.

(7) The study of extant beetles from relict steppes provides the basis for reconstructions of the past environment and temperature. The presence of *Stephanocleonus eruditus* and *S. fossulatus* in the fossil assemblage means that the mean July temperature for the coldest Pleistocene intervals was not lower than 11–12°C, with a low level of precipitation and high air clarity. The climate was high continental with cold winter and relatively warm summer (warmer than now), while average annual temperature could have been lower than now.

(8) Steppe–tundra insect faunas of western and eastern Beringia were formed in separate resources. Transberingian migrations were restricted, especially

for xerophilous species. A trend towards xerophilous insect fauna impoverishment in modern steppes from Indigirka to Chukotka, along with a similar trend in fossil communities give additional explanation of restricted migrations between western and eastern Beringia. The dissociation of insect steppe communities in Asia and America could be caused not only by unsuitable climate of the Bering Bridge, but, what is more important, by a barrier of Chukotka, a waste area occupied mostly by tundra-like and meadow-like communities.

(9) Elements of the Pleistocene steppe–tundra insect fauna survived dramatic environmental changes at the Pleistocene–Holocene boundary. Complete disruption of the steppe–tundra fauna was correlated with the Holocene Boreal warming (average annual temperature higher than now); an important factor was forest expansion from the south. The latest refuges of the steppe–tundra biota remained in the northern, still treeless areas.

ACKNOWLEDGMENTS

This work is a result of the long-term study of Quaternary insects. I am thankful to all people who support this research, in particular, my teacher in Quaternary insects S.V. Kiselev, long time team leader A.V. Sher, my supervisor in PhD dissertation A.G. Ponomarenko, my field teacher S.F. Kolesnikov, my supervisors from the Paleontological Department of Moscow State University I.S. Barskov, and A.S. Alekseev, who understood the importance of this exotic for traditional paleontology subject.

I thank researchers who worked with me in the field, or collected fossil and modern insects in their field works: I.R. Plakht, S.V. Gubin, D.A. Gilichinsky, O.G. Zanina, P.A. Nikolsky, T.V. Kuznetsova, V.N. Tumskoi, D.Yu. Bolshiyanov, K. Ziegert, L. Shirrmeister, F. Kienast, S. Wetterich, D. Froese, and many others. I am grateful to many entomologists for help in fossil insect identification: B.A. Korotyaev, B.M. Kataev, O.A. Benkovsky, G.M. Dlussky, E.E. Perkovsky, V.G. Shilenkov, K.V. Makarov, N.N. Vinokurov, A.E. Brinevsky, R.R. Petrov, and N.B. Nikitsky. I am thankful to V.V. Zherikhin, D.I. Berman, A.V. Alfimov, A.P. Rasnitsyn, and G. Zazula for interesting and productive discussions about features of the steppe–tundra environment.

The study was performed in the Borissiak Paleontological Institute of the Russian Academy of Sciences. This research was supported by the Russian Foundation for Basic Research (project nos. 98-04-48084, 01-04-48930); Otto Schmidt Laboratory, St. Petersburg; and Alfred Wegener Institute for Polar and Marine Research, Potsdam. The final support was made by F.K. Shidlovsky from the Ice Age Museum, Moscow.

REFERENCES

Abramova, A.L., Savich-Lyubitskaya, L.I., Smirnova, Z.N., *Opredelitel' listostebel'nykh mkhov Arktiki SSSR* (Key to Leafy Mosses of Arctic of the USSR). Moscow–Leningrad: Akad. Nauk SSSR, 1961.

Alekseev, M.N., Some features of Pleistocene deposition in the Lena–Kolyma Region of the Arctic Basin, in *Severnyi Ledovityi okean i ego poberezh'e v kainozoe* (Arctic Ocean and Its Surround in the Cenozoic), Tolmachev, A.I., Ed., Leningrad, Gosmeteoizdat, 1970, pp. 480–484.

Alekseev, M.N., *Antropogen Vostochnoi Azii* (Anthropogenic of Eastern Asia), Moscow: Nauka, 1978.

Alekseev, M.N., Stratigraphy of the Quaternary deposits of the Novosibirskie Islands, in *Chetvertichnyi period. Stratigrafiya* (Quaternary Period: Stratigraphy), Alekseev, M.N. and Nikiforova, K.V., Eds., Moscow: Nauka, 1989, pp. 159–167.

Alfimov, A.V. and Berman, D.I., Climate of Bering Land in the Late Pleistocene and Holocene, *Quat. Sci. Rev.,* 2001, vol. 20, no. 1, pp. 127–134.

Alfimov, A.V. and Berman, D.I., Distribution of thermophytic tundra–steppe and the climate of the Last Glacial Maximum in northeastern Asia, *Kriosf. Zemli,* 2004, vol. 8, no. 4, pp. 78–87.

Alfimov, A.V., Berman, D.I., and Sher, A.V., Tundra–steppe assemblages of insects and climatic reconstructions for the lower Kolyma River in the Late Pleistocene, *Zool. Zh.,* 2003, vol. 82, no. 2, pp. 281–300.

Anderson, P.M. and Lozhkin, A.V., Eds., *Pozdnechetvertichnaya rastitel'nost' i klimat Sibiri i Dal'nego Vostoka Rossii (Palinologicheskaya i radiouglerodnaya baza dannykh)* (Late Quaternary Vegetation and Climate of Siberia and the Russian Far East: Palynological and Radiocarbon Database), Magadan: Severo-Vost. Kompl. Nauchno-Issled. Inst. Dal'nevost. Otd. Ross. Akad. Nauk, 2002.

Anderson, R.S., *Connatichela artemisiae*, a new genus and species of weevil from the Yukon Territory (Coleoptera: Curculionidae; Leptopiinae): Taxonomy, paleontology and biogeography, *Can. Entomol.,* 1984, vol. 116, pp. 1571–1580.

Anderson, R.S., New synonymy in North American *Stephanocleonus* Motschulsky (Coleoptera: Curculionidae), *Coleopt. Bull.,* 1989, vol. 43, pp. 93.

Anderson, R.S., Weevils (Coleoptera: Curculionoidea, Excluding Scolytinae and Platypodinae) of the Yukon, in *Insects of the Yukon: Biological Survey of Canada* (*Terrestrial Arthropods*), Danks, H.V. and Downes, J.A., Eds., Ottawa, 1997, pp. 523–562.

Andreev, A.A., Grosse, G., Schirrmeister, L., Kuzmina, S.A., Novenko, E. Yu., Bobrov, A.A., Tarasov, P.E., Kuznetsova, T.V., Krbetschek, M., Meyer, H., and Kunitsky, V.V., Late Saalian and Eemian palaeoenvironmental history of the Bol'shoy Lyakhovskii Island (Laptev Sea region, Arctic Siberia), *Boreas,* 2004, vol. 33, no. 4, pp. 319–348.

Andreev, A.A., Grosse, G., Schirrmeister, L., Kuznetsova, T.V., Kuzmina, S.A., Bobrov, A.A., Tarasov, P.E., Novenko, E.Y., Meyer, H., Derevyagin, A.Y., Kienast, F., Bryantseva, A., and Kunitsky, V.V., Weichselian and Holocene palaeoenvironmental history of the Bol'shoi Lyakhovskii Island, New Siberian Archipelago, Arctic Siberia, *Boreas*, 2009, vol. 38, no. 1, pp. 72–110.

Andreev, A.A., Schirrmeister, L., Siegert, Ch., Bobrov, A.A., Demske, D., Seiffert, D., and Hubberten, H.-W., Paleoenvironmental changes in northeastern Siberia during the Late Quaternary—evidence from pollen records of the Bykovsii Peninsula, *Polarforschung,* 2002, vol. 70, pp. 13–25.

Arkhangelov, A.A., Underground glaciation in the northern Kolyma Lowland in the Late Cenozoic, *Probl. Kriolitol.,* 1977, no. 6, pp. 26–57.

Arkhangelov, A.A., Kartasheva, G.G., Kovalenko, F.Ya., Plakht, I.R., Ter-Grigorian, E.V., and Fishkin, O.N., Paleogene and Neogene of the northern coastline of the Chukotka Peninsula, in *Kontinental'nye tretichnye tolshchi Severo-Vostochnoi Azii* (Tertiary Continental Deposits of Northeastern Asia), Novosibirsk: Nauka, 1979, pp. 40–52.

Arkhangelov, A.A., Kuznetsova, T.P., Popov, A.I., and Rozembaum, G.E., On the question of the Edoma genesis in the coastal plains of northern Yakutia, *Probl. Kriolitol.,* 1983, vol. 11, pp. 87–98.

Arkhangelov, A.A., Mikhalev, D.V., and Nikolaev, V.I., On the early epochs of permafrost formation in northern Yakutia and age of ancient relicts of underground glaciation, in *Razvitie oblasti mnogoletnei merzloty i periglyatsial'noi zony Severnoi Evrazii i usloviya rasseleniya drevnego cheloveka* (Development of the Permafrost Area and Periglacial Zone of the Northern Eurasia and Environment of Ancient Men Spreading), Velichko, A.A., Arkhangelov, A.A., Borisova, O.K., Gribchenko, Yu.N., Drenova, A.N., Zelikson, E.M., Kurenkova, E.N., Mikhalev, D.V., Nikolaev, V.I., Novenko, E.Yu., and Timireva, S.A., Eds., Moscow: Inst. Geogr. Ross. Akad. Nauk, 1996, pp. 102–109.

Atkinson, T.C., Briffa, K.R., Coope, G.R., Joachim, M., and Perry, D., Climatic calibration of coleopteran data, in *Handbook of Holocene Paleoecology and Paleohydrology*, Berglund, B.E., Ed., New York: Wiley, 1986, pp. 851–858.

Baranova, Yu.P., Geomorphological sketch of the eastern part of the Kolyma Lowland, in *Materialy po geologii i poleznym iskopaemym Severo-Vostoka SSSR* (Materials of Geology and Minerals of the Northeastern USSR), Magadan: Magad. Izd–vo, 1957, vol. 11, pp. 208–222.

Baranova, Yu.P. and Biske, S.F., *Istoriya razvitiya rel'efa Sibiri i Dal'nego Vostoka. Severo-Vostok SSSR* (History of Relief Development in Siberia and the Far East: Northeastern USSR), Moscow: Nauka, 1964.

Bashlavin, D.K., Zhigulevtseva, S.N., and Ovander, M.G., Pliocene–Pleistocene deposits of the eastern Yana–Indigirka Lowland, *Tr. Akad. Nauk SSSR, Ser. Geol.,* 1986, vol. 10, pp. 130–135.

Bashlavin, D.K., Zhigulevtseva, S.N., and Ovander, M.G., The Keremesit River section, the type for the Middle Pleistocene of the Yana–Indigirka Lowland, in *Chetvertichnyi period Severo-Vostoka Azii* (Quaternary Period in Northeastern Asia), Pokhialainen, V.P., Ed., Magadan: Akad. Nauk Dal'nevost. Otd., 1987, pp. 110–118.

Bauch, H.A., Mueller–Lupp, T., Taldenkova, E., Spielhagen, R.F., Kassens, H., and Grootes, P.M., Chronology of the Holocene transgression at the North Siberian margin, in *Global and Planetary Changes*, Elsevier, 2001, pp. 125–139.

Berman, D.I., Alfimov, A.V., Reconstruction of the Late Pleistocene climate of Asian and Central Bering Land based on entomological data, *Vest. Dal'nevost. Otd. Ross. Akad. Nauk,* 1998, vol. 1, pp. 27–34

Berman, D.I., Alfimov, A.V., and Kuzmina, S.A., Invertebrates of relict steppe ecosystems of Beringia and reconstruction of Pleistocene landscapes, *Quat. Sci. Rev.,* 2011, vol. 30, pp. 2200–2219.

Berman, D.I., Alfimov, A.V., Mazhitova, G.G., Grishkan, I.B., and Yurtsev, B.A., *Kholodnye stepi severo-vostochnoi Azii* (Cold Steppes of Northeastern Asia), Vladivostok: Dal'nauka, 2001a.

Berman, D.I., Korotyaev, B.A., and Alfimov, A.V., Contribution to the weevil fauna (Coleoptera: Apionidae, Curculionidae) of the mountain steppes in the Yukon Territory, Canada, with reference to the Pleistocene history of Beringia, *Entomol. Rev.,* 2001b, vol. 81, no. 8, pp. 2001 [Translated from *Zool. Zh.,* 2001, vol. 80, no. 11, pp. 993–998.

Bidashko, F.G., Integrated method of fossil insect sampling under kerosene flotation and some recommendations for the preparation of fossils for identification. *Zool. Zh.,* 1987, vol. 66, no. 7, pp. 1086–1089.

Biske, S.F., Quaternary deposits of the Kolyma Lowland, in *Materialy po geologii i poleznym iskopaemym Severo-Vostoka SSSR* (Materials of Geology and Minerals of the Northeastern USSR, 2), Magadan: Magadan. Izd–vo, 1957, vol. 11, pp. 68–81.

Blinnikov, M.S., Gaglioti, B.V., Walker, D.A., Wooller, M.J., and Zazula, G.D., Pleistocene graminoid-dominated ecosystems in the Arctic, *Quat. Sci. Rev.,* 2011, vol. 30, pp. 2906–2929.

Boeskorov, G., The north of Eastern Siberia: Refuge of the Mammoth Fauna in the Holocene, *Gondwana Res.,* 2004, vol. 7, no. 2, pp. 451–455.

Borisov, B.A., On the change of the lower boundary of the Quaternary System and elaboration of its main subdivisions, *Reg. Geol. Metallog.,* 2007, vol. 41, pp. 26–28.

Borisov, B.A., General stratigraphic chart of the Quaternary: Neopleistocene reference sections of European Russia, *Materialy VI Vserossiiskogo soveshchaniya po izucheniyu chetvertichnogo perioda* (Materials of VI All-Russia Meeting on the Quaternary Studies), Novosibirsk: Sib. Otd. Ross. Akad Nauk, 2009, pp. 84–88.

Bousquet, Y., Ed., *Checklist of Beetles of Canada and Alaska,* Ottawa: Res. Br. Agric. Can., 1991, publ. 1861/E.

Brauner, A.A., On "mixed" fossil faunas, *Priroda,* 1934, no. 11, pp. 92–93.

Chernov, Yu.I., *Zhizn' tundry* (The Life of Tundra), Moscow: Mysl', 1980.

Clark, S.H.E. and Edwards, K.J., Elm bark beetle in Holocene peat deposits and the northwest European elm decline, *J. Quat. Sci.,* 2004, vol. 19, pp. 525–528.

Colinvaux, P.A., Land bridge of Duvanny Yar: Early Americans, *Nature*, 1985, vol. 314, pp. 581–582.

Coope, G.R., The invasion of northern Europe during the Pleistocene by Mediterranean species of Coleoptera, in Biological Invasions in Europe and the Mediterranean Basin, Castri, F. di, Hansen, A.J., Debussche, M., Eds., the Netherlands, Dordrecht: Kluwer, 1990, pp. 203–215.

Coope, G.R., The response of insect faunas to glacial–interglacial climatic fluctuations, *Phil. Trans. R. Soc. London,* 1994, vol. 344, pp. 19–26.

Dort-Gol'ts, Yu.E., Features of the formation of the Late Pleistocene Edoma Assemblage of the southeastern Chukotka Peninsula, in *Merzlotno–geologicheskie protsessy i paleogeografiya nizmennostei Severo-Vostoka Azii* (Permafrost: Geological Processes and Paleogeography of the Northeastern Lowlands of Asia), Svitoch, A.A., Ed., Magadan: Severo-Vost. Kompl. Nauchno-Issled. Inst. Dal'nevost. Otd. Akad. Nauk SSSR, 1982, pp. 75–81.

Elias, S.A., *Quaternary Insects and Their Environments,* Washington, DC: Smiths. Inst., 1994.

Elias, S.A., Insect fossil evidence on late Wisconsin environments of the Bering Land Bridge: New data on the nature and timing of inundation, in American Beginnings: The Prehistory and Paleoecology of Beringia, West, F. H., Ed., Chicago: Univ. Chicago Press, 1996, pp. 110–119.

Elias, S.A., Mutual climatic range reconstructions of seasonal temperatures based on late Pleistocene fossil beetle assemblages in eastern Beringia, *Quat. Sci. Rev.,* 2001, vol. 20, pp. 77–91.

Elias, S.A., Anderson, K.H., and Andrews, J.T., Late Wisconsin climate in northeastern USA and southeastern Canada, reconstructed from fossil beetle assemblages, *J. Quat. Sci.,* 1996, vol. 11, pp. 417–421.

Elias, S.A., Berman, D., and Alfimov, A., Late Pleistocene beetle faunas of Beringia: Where east met west, *J. Biogeogr.,* 2000, vol. 27, pp. 1349–1364.

Elias, S.A. and Crocker, B., The Bering Land Bridge: A moisture barrier to the dispersal of steppe–tundra biota, *Quat. Sci. Rev.,* 2008, vol. 27, nos. 27–28, pp. 2473–2483.

Elias, S.A., Kuzmina, S., and Kiselev, S., Late Tertiary origins of the Arctic beetle fauna, *Palaeogeogr. Palaeoclimatol.. Palaeoecol.,* 2006, vol. 241, nos. 3–4, pp. 373–392.

Elias, S.A. and Matthews, J.V., jr., Arctic North American seasonal temperatures in the Pliocene and Early Pleistocene, based on mutual climatic range analysis of fossil beetle assemblages, *Can. J. Earth Sci.,* 2002, vol. 39, pp. 911–920.

Elias, S.A., Short, S.K., and Birks, H.H., Late Wisconsinian Environments of the Bering Land Bridge, *Palaeogeogr. Palaeoclimatol. Palaeoecol.,* 1997, vol. 136, pp. 293–308.

Elias, S.A., Short, S.K., Nelson, C.H., and Birks, H.H., The life and times of the Bering Land Bridge, *Nature,* 1996, vol. 382, pp. 60–63.

Elias, S.A., Short, S.K., and Philips, R.L., Paleoecology of late glacial peats from the Bering Land Bridge, Chukchi sea shelf region, Northwestern Alaska, *Quat. Res.,* 1992, vol. 38, pp. 371–378.

Galabala, R.O., New data on the structure of the Lena delta, in *Chetvertichnyi period Severo-Vostoka Azii* (Quaternary Period in Northeastern Asia), Pokhialainen, V.P., Ed., Magadan: Severo-Vost. Kompl. Nauchno-Issled. Inst. Dal'nevost. Otd. Akad. Nauk SSSR, 1987, pp. 152–171.

Gibbard, P. and Head, M.J., The definition of the Quaternary System/Era and the Pleistocene Series/Epoch, *Quaternaire,* 2009a, vol. 20, pp. 125–133.

Gibbard, P.L. and Head, M.J., IUGS ratification of the Quaternary System/Period and the Pleistocene Series/Epoch with a base at 2.58 Ma, *Quaternaire,* 2009b, vol. 20, pp. 411–412.

Gibbard, P.L. and Head, M.J., The newly ratified definition of the Quaternary System/Period and redefinition of the Pleistocene Series/Epoch, and comparison of proposals advanced prior to formal ratification, *Episodes,* 2010, vol. 33, pp. 152–158.

Giterman, R.E., Stages of the Quaternary vegetation develop in Yakutia and their importance for stratigraphy, *Tr. Geol. Inst. Akad. Nauk,* 1963, vol. 78, pp. 1–121.

Giterman, R.E., History of the vegetation of the northeastern USSR in the Pliocene and Pleistocene, *Tr. Geol. Inst. Akad. Nauk,* 1985, vol. 380, pp. 1–96.

Grichuk, V.P., Late Pleistocene vegetation history, in *Late Quaternary Environments of the Soviet Union,* Velichko, A.A., Ed., Minneapolis: Univ. Minnesota Press, 1984, pp. 155–178.

Grichuk, M.P. and Grichuk, V.P., On periglacial vegetation in the territory of the USSR, in *Tr. Geogr. Inst. Akad. Nauk SSSR,* 1960, vol. 80, pp. 66–100.

Grigoriev, M.N., *Kriomorfogenez ustevoi oblasti r. Lena* (Cryomorphogenesis of the Lena River Mouth Area), Yakutsk: Sib. Otd. Akad. Nauk SSSR, 1993.

Grinenko, O.V. and Minyuk, P.S., Paleomagnetism and stratification of the Upper Cenozoic deposits of the Alazeya River Basin (northern Yakutia), in *Paleomagnetizm i problemy stratigraficheskoi korrelyatsii* (Paleomagnetism and Problems of Stratigraphic Correlations), Goncharov, V.I., Ed., Magadan: Severo-Vost. Kompl. Nauchno-Issled. Inst. Dal'nevost. Nauchn. Tsentr Akad. Nauk SSSR, 1985, pp. 124–132.

Gubin, S.V., Paleopedological analysis of Late Pleistocene (Edoma) deposits in the Duvanny Yar exposure, *Byull. Chetvert. Komm. Izuch. Chetvert. Per.,* 1984, vol. 53, pp. 125–128.

Gubin, S.V., Soil structires at the final stage of loess–glacial deposits accumulation, in *Itogi fundamental'nykh issledovanii kriosfery Zemli v Arktike i Subarktike* (Results of Fundamental Studies of the Earth Cryosphere in the Arctic and Subarctic), Melnikov, E.S., Ed., Novosibirsk: Nauka, 1997, pp. 19–24.

Gubin, S.V., Late Pleistocene soil formation in ice–loess deposits of northeastern Eurasia, *Doctoral Dissertation in Soil Science,* Pushchino, 1999.

Gubin, S.V., Zanina, O.G., Maksimovich, S.V., Kuzmina, S.A., and Zazhigin, V.S., Reconstruction of ice complex sediment formation conditions based on the study of Late Pleistocene rodent burrows, *Kriosf. Zemli,* 2003, vol. 7, no. 3, pp. 13–22.

Guthrie, R.D., Paleoecology of the large mammal community in interior Alaska during the Late Pleistocene, *Am. Midl. Natur.,* 1968, vol. 79, pp. 346–363.

Guthrie, R.D., Environmental influences on body size, social organs, population parameters and extinction of Beringian mammals, in *Beringiya v kainozoe* (Bering Land in the Cenozoic), Kontrimavichus, V.L., Ed., Vladivostok, 1976, pp. 297–321.

Guthrie, R.D., Mammals of the mammoth steppe as paleoenvironmental indicators, in *Paleoecology of Beringia,* Hopkins, D.M., Matthews, J.V., Jr., Schweger, C.E., and Young, S.B., Eds., New York: Academic Press, 1982, pp. 307–326.

Guthrie, R.D., Mosaics, allelochemics, and nutrients: An ecological theory of Late Pleistocene megafaunal extinctions, in *Quaternary Extinctions,* Martin, P.S. and Klein, R.G., Eds., Tucson: Univ. Arizona Press, 1984, pp. 259–298.

Guthrie, R.D., Origin and causes of the mammoth steppe: A story of cloud cover, woolly mammal tooth pits, buckles, and inside–out Beringia. *Quat. Sci. Rev.*, 2001, vol. 20, pp. 549–574.

Hibbert, D., History of the steppe–tundra concept, in *Paleoecology of Beringia,* Hopkins, D.M., Matthews, J.V., Jr., Schweger, C.E., and Young, S.B., Eds., New York: Academic Press, 1982, pp. 153–156.

Hoffmann, A., Faune de France: 62, in *Coléoptères Curculionides (Troisième partie),* Lechavalier, P., Ed., Paris: Fédér. Fran. Soc. Sci. Natur, 1958, pp. 1209–1841.

Igarashi, Y., Fukuda, M., Nagaoka, D., and Saito, K., Vegetation and climate during accumulating period of Edoma, inferred from pollen records, in *Proceedings of the Third Symposium on the Joint Siberian Permafrost Studies between Japan and Russia in 1994, Tsukuba, Japan,* Takahashi, K., Osawa, A., and Kanazawa, Y., Eds., Tsukuba, 1995, pp. 139–147.

Ivanov, O.A., Stratigraphy and correlation of Neogene and Quaternary deposits in the subarctic plains of eastern Yakutia, in *Problemy izucheniya chetvertichnogo perioda* (Problems of Quaternary Research), Moscow: Nauka, 1972, pp. 202–211.

Kaplin, P.A., Ed., *Noveyshie otlozheniya i paleogeografiya pleistotsena Chukotki* (The Latest Deposits and Paleogeography of the Pleistocene in the Chukotka Peninsula), Moscow: Nauka. 1980.

Kaplina, T.N., History of permafrost sediments of northern Yakutia in the Late Cenozoic, in *Istoriya razvitiya mnogoletnemerzlykh porod Evrazii* (History of the Development of Permafrost Sediments of Eurasia), Dubikov, G.I. and Baulin, V.V., Eds., Moscow: Nauka, 1981, pp. 153–181.

Kaplina, T.N. and Giterman, R.E., Molotkovskii Kamen'—reference section of the Late Pleistocene deposits of the Kolyma Lowland, *Tr. Akad. Nauk SSSR, Ser. Geol.,* 1983, vol. 6, pp. 79–83

Kaplina, T. N., Giterman, R. E., Lakhtina, O. V., Abrashov, B.A., Kiselev, S. V., and Sher, A. V., Duvanny Yar—reference section of Late Pleistocene deposits in the Kolyma Lowland, *Byull. Komm. Izuch. Chetvert. Per.,* 1978, vol. 48, pp. 49–65.

Kaplina, T.N. and Kuznetsova, I.L., Geotemperature and climatic model of accumulation epoch of the Edoma Formation in the Yakut Coastal Lowland, in *Problemy paleogeografii lessovykh i periglyatsial'nykh oblastei* (Problems of Paleogeography of Loess and Periglacial Regions), Velichko, A.A., Ed., Moscow: Nauka, 1975, pp. 170–174.

Kaplina, T.N., Lakhtina, O.V., and Rybakova, N.O., Cenozoic deposits of the middle stream of the Alazeya River (Kolyma Lowland), *Tr. Akad. Nauk SSSR, Ser. Geol.,* 1981, no. 8, pp. 51–63.

Kaplina, T.N. and Lozhkin, A.V., Age of alas deposits of the coastal lowland of Yakutia, *Tr. Akad. Nauk SSSR, Ser. Geol.,* 1979, vol. 2, pp. 69–76.

Kaplina, T.N., Sher, A.V., Giterman, R.E., Zazhigin, V.S., Kiselev, S.V., Lozhkin, A.V., and Nikitin, V.P., The principal section of the Pleistocene deposits on the Allaikha River (low stream of the Indigirka River), *Byull. Komm. Izuch. Chetvert. Per.,* 1980, no. 50, pp. 73–95.

Kienast, F., Wetterich, S., Kuzmina, S., Schirrmeister, L., Andreev, A., Tarasov, P., Nazarova, L., Kossler, A., Frolova, A., and Kunitsky, V.V., Paleontological records indicate the occurrence of open woodlands in a dry inland climate at the present-day Arctic coast in western Beringia during the Last Interglacial. *Quat. Sci. Rev.,* 2011, vol. 17, pp. 2134–2159.

Kiselev, S.V., Outcrop of the Main River valley: Entomofauna analysis, in *Noveishie otlozheniya i paleogeografiya pleistotsena Chukotki* (The Latest Deposits and Paleogeography of the Pleistocene in the Chukotka Peninsula), Kaplin, P.A., Ed., Moscow: Nauka, 1980a, pp. 149–150.

Kiselev, S.V., Outcrop of Aion Island: Entomofauna analysis, in *Noveishie otlozheniya i paleogeografiya pleistotsena Chukotki* (The Latest Deposits and Paleogeography of the Pleistocene in the Chukotka Peninsula), Kaplin, P.A., Ed., Moscow: Nauka, 1980b, pp. 194–196.

Kiselev, S.V., *Pozdnekainozoiskie zhestkokrylye Severo-Vostoka Sibiri* (Late Cenozoic Coleoptera of Northeastern Siberia), Moscow: Nauka, 1981.

Kiselev, S.V., North Eurasian environments in the Pleistocene and Holocene (based on the study of Coleoptera), *Doctoral Dissertation in Biology,* Moscow: Mosk. Gos. Univ., 1995.

Kiselev, S.V. and Nazarov, V.I., Late Cenozoic Insects of Northern Eurasia, *Paleontol. J.,* 2009, vol. 43, no. 7, pp. 723–850.

Khruleva, O.A. and Korotyaev, B.A., Weevils (Coleoptera: Apionidae, Curculionidae) of Wrangel Island, *Entomol. Rev.,* 1999, vol. 78, no. 3, pp. 648–670.

Konishchev, V.N., Cryolithological evidence of heterogeneous structure of the "Ice Complex" deposits in the Duvanny Yar exposure, in *Problemy kriolitologii* (Problems of Cryolithology), Popov, A.I., Ed., Moscow: Mosk. Gos. Univ., 1983, vol. 11, pp. 56–64.

Korotyaev, B.A., Contribution to the weevil fauna (Coleoptera, Curculionidae) in the northeastern USSR, in *Issledovaniya po entomofaune Severo-Vostoka SSSR* (Research on the Insect Fauna of the Northeastern USSR), Medvedev, G.S. and Matis, E.G., Eds., Vladivostok: Dal'nevost. Nauchn. Tsentr Akad. Nauk SSSR, 1980, pp. 23–50.

Kotov, A.N., Polyfacies complex of the Late Pleistocene sin- and epicryogenic deposits of the Main River valley (Chukotka), in *Problemy kriolitologii* (Problems of Cryolithology), Melnikov, P.I., Ed., Moscow: Nauka, 1988, pp. 108–115.

Kotov, A.N., Environment of cryolithogenesis of the Ice Complex deposits of the Chukotka Peninsula in the Late Pleistocene, *Kriosf. Zem.,* 2002, vol. 6, no. 3, pp. 3–14.

Kotov, A.N. and Ryabchun, V.K., Cryolithological structure of the Ice Bluff exposure (Central Chukotka), in *Geokriologicheskie issledovaniya* (Geocryological Research), Ershov, E.D., Ed., Moscow: Mosk. Gos. Univ., 1986, pp. 114–120.

Kotov, A.N., Lozhkin, A.V., and Ryabchun, V.K., Permafrost—facial conditions of the Upper Pleistocene deposit creation of the Main River valley (Chukotka), in *Formirovanie rel'efa, korrelyatnykh otlozhenii i rossypei Severo-Vostoka SSSR* (Formation of Relief, Correlated Deposits, and Gravels of the Northeastern USSR), Ivanov, V.F. and Palymsky, B.F., Eds., Magadan: Severo-vost. Kompl. Nauchno-Issled. Inst. Dal'nevost. Otd. Ross. Akad. Nauk SSSR, 1989, pp. 117–131.

Krbetschek, M.R., Gonser, G., and Schwamborn, G., Luminescence dating results on sediment sequences of the Lena delta, *Polarforschung,* 2002, vol. 70, pp. 83–88.

Kryzhanovsky, O.L. and Emets, V.M., New ground beetle species of genus *Cymindis* (Coleoptera, Carabidae) from Yakutia, *Zool. J.,* 1979, vol. 58, no. 3, pp. 447–448.

Kunitsky, V.V., *Kriolitologiya nizov'ya Leny* (Cryolithology of the Lower Lena Region), Yakutsk: Inst. Merzlotoved. Sib. Otd. Akad. Nauk SSSR, 1989.

Kunitsky, V.V., Ice complex and cryoplanation terraces of the Bol'shoi Lyakhovskii Island, in *Problemy geokriologii* (Geocryology Problems). Yakutsk: Inst. Merzlotoved. Ross. Akad. Nauk, 1998, pp. 60–72.

Kuzmina, S.A., Holocene insects from a site in the middle stream of the Alazeya River (Kolyma Lowland), *Byull. Mosk. Ob-va Ispyt. Prir., Ser. Geol.,* 1986, vol. 61, no. 4, pp. 154–155

Kuzmina, S.A., Late Pleistocene insects from the Alazeya River (Kolyma Lowland)*, Byull. Mosk. Ob-va Ispyt. Prir., Ser. Geol.,* 1989, vol. 64, no. 4, pp. 42–55.

Kuzmina, S.A., Quaternary insects of the Coastal Lowlands of Yakutia, *Candidate's Dissertation in Biology,* Moscow: Paleontol. Inst. Ross. Akad. Nauk, 2001.

Kuzmina, S., New approach to the Quaternary studies: QINSIB—The database of Siberian fossil insects, *Quat. Int.,* 2014, vol. 341, pp. 283–293.

Kuzmina, S.A. and Bolshiyanov, D., Forest insect spectra in Late Holocene deposits of the Lena delta terrace, north of the actual tree line, *Polarforschung,* 2002, vol. 70, pp. 101–105.

Kuzmina, S. Froese, D., Jensen, B.J.L., Hall, E., and Zazula, G.D., Middle Pleistocene (MIS 7) to Holocene fossil insect assemblages from the Old Crow Basin, northern Yukon, Canada, *Quat. Int.,* 2014, vol. 341, pp. 216–242.

Kuzmina, S. and Kolesnikov, S., Insects from the Late Pleistocene and Holocene deposits of the Medvezhyi Islands (East Siberian Sea)*, Byull. Mosk. Ob-va Ispyt. Prir., Ser. Geol.,* 2000, vol. 75, no. 2, pp. 68–71.

Kuzmina, S.A. and Korotyaev, B.A., New species of the pill beetle genus *Morychus* Er. (Coleoptera, Byrrhidae) from the Northeastern USSR, *Entomol. Rev.,* 1987, vol. 66, no. 2, pp. 342–344.

Kuzmina, S.A. and Matthews, J.V., Late Cenozoic insects of Beringia, *Euroas. Entomol. J.,* 2012, vol. 11, suppl. no. 1, pp. 59–97.

Kuzmina, S. and Perkovsky, E., Environment of *Cholevinus sibiricus* (Jeannel) (Coleoptera: Leiodidae) in the Pleistocene, Dokl. Khar'k. Entomol. Ob–va. 2001, 2002, vol. 9, nos. 1–2, pp. 237–240.

Kuzmina, S.A. and Ponomarenko, A.G., Paleoentomological data on the environmental condition of mammoths, *Mamont i ego okruzhenie: 200 let izucheniya* (Mammoth and Its Environment: 200 Years of Investigations), Moscow, GEOS, 2001, pp. 279–286.

Kuzmina, S. and Sher, A., Some features of the Holocene insect faunas of northeastern Siberia, *Quat. Sci. Rev.*, 2006, vol. 25, nos. 15–16, pp. 1790–1820.

Kuzmina, S., Sher, A., Edwards, M., Haile, J., Yan, E., Kotov, A., and Willerslev, E., The Late Pleistocene environment of eastern West Beringia based on the principal section at the Main River, Chukotka, *Quat. Sci. Rev.*, 2011, vol. 30, pp. 17–18.

Kuznetsova, T.V., Kuzmina, S.A., Kunitsky, V.V., Schirrmeister, L., and Sher, A.V., The fauna of alas sequences in the Ice Complex area: The case of Mamontovyi Bysagasa northwest exposure, Bykovsii Peninsula, in *Fifth Workshop on Russian–German Cooperation: Laptev Sea System, 2000, November 26–28, St. Petersburg, Russia*, Koln: Terra Nostra Schriften der Alfred–Wegener–Stiftung, 1999, pp. 49–50.

Kuznetsov-Ugamsky, N.N., Regarding "mixed" fossil faunas, *Priroda,* 1934, no. 8, 73–74.

Laxton, N.F., Burn, C.F, and Smith, C.A.S., Productivity of loessal grasslands in the Kluane Lake region, Yukon Territory and Beringian "Production Paradox", *Arctic,* 1996, vol. 49, no. 2, pp. 129–140.

Lozhkin, A.V., Habitat conditions of the Berelekh mammoth population, *Tr. Zool. Inst. Akad. Nauk SSSR,* 1977, vol. 72 (Mammoth Fauna of the Russian Plain and Western Siberia), pp. 67–68.

Lozhkin, A.V. and Anderson, P.M., The last interglacial in northeastern Siberia, *Quat. Res.,* 1995, vol. 43, pp. 147–158.

Lozhkin, A.V., Kotov, A.V., and Ryabchun, V.K., Palynological and radiocarbon data of the Ledovyi Obryv exposure (southeastern Chukotka), in *Beringiya v chetvertichnyi period* (Quaternary Period of Beringia), Simakov, K.V., Ed., Magadan: Severo–Vost. Kompl. Nauchno-Issled. Inst. Dal'nevost. Otd. Ross. Akad. Nauk, 2000, pp. 53–75.

Lungersgauzen, G.F., Geological history of the middle Lena and some questions of Quaternary deposits stratigraphy in Eastern Siberia, in *Materialy Vsesoyusnogo Soveshchaniya po izucheniyu chetvertichnogo perioda, Moskva, 1957* (Contributions to All-Union Conference on the Study of the Quaternary Period, Moscow, 1957), Lungersgauzen, G.F. and Ravskii, E.I., Eds., Moscow: Akad. Nauk SSSR, 1961, vol. 3, pp. 209–217.

Makarova, O.L., Bieńkowski, A.O., Bulavintsev, V.I., and Sokolov, A.V., Beetles (Coleoptera) in Polar Deserts of the Severnaya Zemlya Archipelago, *Entomol. Rev.,* 2007, vol. 87, no. 9, pp. 1142–1154 [*Zool. Zh,*. 2007, vol. 86, no. 11, pp. 1303–1314.)

Matthews, J.V., East Beringia during Late Wisconsin time: A review of the biotic evidence, in *Paleoecology of Beringia,* Hopkins, D.M., Matthews, J.V. Jr., Schweger, C.E., and Young, S.B., Eds., New York: Academic Press, 1982, pp. 127–150.

Matthews, J.V., A method for comparison of northern fossil insect assemblages, *Géogr. Phys. Quarter.,* 1983, vol. 37, no. 3, pp. 297–306.

Matthews, J.V., Jr., Quaternary environments at Cape Deceit (Seward Peninsula, Alaska): Evolution of a tundra ecosystem, *Bull. Geol. Soc. Am.,* 1974, vol. 85, pp. 1357–1384.

Matthews, J.V., Jr. and Telka, A., Insect fossils from the Yukon, in *Insects of the Yukon,* Danks, H.V. and Downes, J.A., Eds., Ottawa: Biol. Surv. Can. Terr. Arthrop., 1997, pp. 911–962.

McDowell, P.F. and Edwards, M.E., Evidence of Quaternary climatic variations in a sequence of loess and related deposits at Birch Creek, Alaska: Implications for the Stage 5 climatic chronology, *Quat. Sci. Rev.,* 2001, vol. 20, pp. 63–76.

Medvedev, L.N., Leaf beetles in the Arctic, *Chrysomel. Biol.,* 1996, vol. 3, pp. 57–62.

Melnikova, T.V., Ed., *Spravochnik po klimatu SSSR* (Reference Book for Climate of the USSR), Leningrad: Gidrometeoizdat, 1965.

Meyer, H., Dereviagin, A., Siegert, Ch., and Hubberten, H.-W., Paleoclimate studies on the Bykovsii Peninsula, north Siberia—hydrogen and oxygen isotopes in ground ice, *Polarforschung,* 2002, vol. 70, pp. 37–51.

Morgan, A., The fossil occurrence of *Helophorus arcticus* Brown (Coleoptera Hydrophilidae) in Pleistocene deposits of the Scarborough Bluffs, Ontario, *Can. J. Zool.,* 1972, vol. 50, pp. 555–558.

Morgan, A.V., Morgan, A., Ashworth, A.C., and Matthews, J.V., Late Wisconsin fossil beetles in North America, in *Late Quaternary Environments of the United States,* Wright, H.E., Ed., London: Longman, 1983, pp. 354–363.

Morgan A.V., Morgan A., Nelson R.E., and Pilny, J.J., Current status of knowledge on the past and present distribution of the genus *Blethisa* (Coleoptera: Carabidae) in North America. *Coleopt. Bull.,* 1986, vol. 40, no. 2, pp. 105–115.

Morozova, T.D. and Velichko, A.A., Loess–ice formation in northeastern Asia, in *American Beginnings: The Prehistory and Paleoecology of Beringia,* West, C.F., Ed., Chicago–London: Univ. Chicago Press, 1996, pp. 52–57.

Muhs, D.R., Ager, T.A., Bettis, E.A., McGeehin, J., Been, J.M., Beget, J.E., Pavich, M.J., Stafford, T.W., and Stevens, D.S.P., Stratigraphy and paleoclimatic significance of Late Quaternary loess–paleosol sequences of the Last Interglacial–Glacial cycle in central Alaska, *Quat. Sci. Rev.*, 2003, vol. 22, pp. 1947–1986.

Nagaoka, D., Saijo, K., and Fukuda, M., Sedimental environment of the Edoma in high Arctic eastern Siberia, in *Proceedings of the 3rd Symposium on the Joint Siberian Permafrost Studies between Japan and Russia in 1994,* Sapporo, Japan: Hokkaido Univ. Press, 1995, pp. 8–13.

Nehring, A., Übersicht uber vierundzwanzig mitteleuropaische Quartar-Faunen, *Z. Deutsch. Geol. Gesell.,* 1880, vol. 32, pp. 468–509.

Nelson, R.E. and Carter, L.D., Paleoenvironmental analysis of insects and extralimital *Populus* from an Early Holocene site on the Arctic slope of Alaska, USA, *Arc. Alp. Res.,* 1987, vol. 19, pp. 230–241.

Ovander, M.G. and Rybakova, N.O., Sections of the Paleogene and Neogene of the Dzhelon–Sise Upland (lower Indigirka River Basin), *Dokl. Akad. Nauk SSSR,* 1985, vol. 282, no. 2, pp. 412–416.

Pavlova, E.Y. and Dorozhkina, M.V., The Holocene alluvial delta relief complex and hydrological regime of the Lena River Delta, *Polarforschung,* 2000, vol. 70, pp. 89–100.

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

Pitulko, V.V. and Pavlova, E.Yu., Age of the Paleolithic relics of the Yana–Indigirka Lowland and features of the radiocarbon dating of the Ice Complex deposit, in *Vozrast pamyatnikov paleolita Yano–Indigirskoi nizmennosti i osobennosti radiouglerodnogo datirovaniya otlozhenii ledovogo kompleksa. Radiouglerod v arkheologicheskikh i paleontologicheskikh issledovaniyakh. Materialy konferentsii posvyashchennoi 50-letiyu Radiouglerodnoi laboratorii IIMK RAN, 9–12 aprelya 2007 g., Sankt-Peterburg* (Age of Paleolithic Sites in the Yana–Indigirka Lowland and Features of Radiocarbon Dating the Ice Complex: Radiocarbon in Archeological and Paleontological Research: Materials of the Meeting in Honor of 50th Anniversary of Radiocarbon Laboratory of IIMK of the Russian Academy of Sciences, St. Petersburg, April 9–12, 2007), St. Petersburg, 2007, pp. 155–161.

Pitulko, V.V., Pavlova, E.Yu., Kuzmina, S.A., Nikolsky, P.A., Basilyan, A.E., Tumskoi, V.E., and Anisimov, M.A., Natural climatic changes in the Yana–Indigirka Lowland during the terminal Karginian Time and habitat of Late Paleolithic man in the northern part of Eastern Siberia, *Dokl. Akad. Nauk,* 2007, vol. 417, no. 1, pp. 103–108.

Polevoi, P.I., Anadyr Region, in *Doklady Geologicheskoi Kommissii, Novaya Seriya* (Reports of Geological Commission, New Series), Petrograd, 1915.

Popov, A.I., On the condition of deposits of the cryogenetic (Edoma) complex in the Pleistocene of the coastal plains of Subarctic, *Probl. Kriolitol.,* 1983, vol. 11, pp. 19–37.

Razumovsky, S.M., *Zakonomernosti dinamiki biotsenozov* (Patterns of the Biocoenosis Dynamics), Moscow: Nauka, 1981.

Roberts, H.M., Muhs, D.R., and Bettis, III, E.A., Loess Records of North America, in *Encyclopedia of Quaternary Science,* Elias, S., Ed., Amsterdam: Elsevier, 2007, pp. 1456–1466.

Romanovskii, N.N., New data on Quaternary deposits structure on Bol'shoi Lyakhovskii Island (Novosibirskie Islands), *Izv. Akad. Nauk Ser. Geol.,* 1958a, vol. 2, pp. 243–248.

Romanovskii, N.N., Paleogeographical conditions of the formation of Quaternary deposits on Bol'shoi Lyakhovskii Island (Novosibirskie Islands), in *Voprosy fizicheskoi geografii polyarnykh stran* (Problems of Physical Geography of Polar Countries), Bogorov, V.G., Ed., Moscow: Mosk. Gos. Univ., 1958b, vol. 1, pp. 80–88.

Rybakova, N.O. and Chernyshova, M.B., New data on the Holocene flora in Yakutia, *Byull. Mosk. Ob–va Ispyt. Prir., Ser. Geol. Geofiz.,* 1979, vol. 54, no. 4, pp. 125–131.

Sanborn, P.T., Smith, C.A.S., Froese, D.G., Zazula, G.D., and Westgate, J.A., Full-glacial paleosols in perennially frozen loess sequences, Klondike goldfields, Yukon Territory, *Can. Quat. Res.,* 2006, vol. 66, pp. 147–157.

Schirrmeister, L., Grosse, G., Schnelle, M., Fuchs, M., Krbetschek, M., Ulrich, M., Kunitsky, V., Grigoriev, M.M., Andreev, A., Kienast, F., Meyer, H., Babii, O., Klimova, I., Bobrov, A., Wetterich, S., and Schwamborn, G., Late Quaternary paleoenvironmental records from the western Lena delta, Arctic Siberia, *Palaeogeogr. Palaeoclimatol. Palaeoecol.,* 2011, vol. 299, pp. 175–196.

Schirrmeister, L., Kunitsky, V.V., Grosse, G., Schwamborn, G., Andreev, A.A., Meyer, H., Kuznetsova, T., Bobrov, A., and Oezen, D., Late Quaternary history of the accumulation plain north of the Chekanovsky Ridge (Lena delta, Russia)—a multidisciplinary approach, *Polar. Geogr.,* 2003, vol. 27, pp. 277–319.

Schirrmeister, L., Oezen, D., and Geyh, M.A., 230Th/U dating of frozen peat, Bol'shoi Lyakhovskii Island (North Siberia), *Quat. Res.,* 2002a, vol. 57, pp. 253–258.

Schirrmeister, L., Siegert, C., Kunitsky, V.V., Grootes, P., and Erlenkeuser, H., Late Quaternary ice-rich permafrost sequences as an archive for the Laptev Sea environment, *Int. J. Geosci. (Geologische Rundschau),* 2002b, vol. 91, pp. 154–167.

Schirrmeister, L., Siegert, C., Kuznetsova, T., Kuzmina, S., Andreev, A.A., Kienast, F., Meyer, H., and Bobrov, A., Paleoenvironmental and paleoclimatic records from permafrost deposits in the Arctic region of northern Siberia, *Quat. Int.,* 2002c, vol. 89, pp. 97–118.

Schwamborn, G., Rachold, V., and Grigoriev, M.N., Late Quaternary sedimentation history of the Lena delta, *Quat. Int.,* 2002, vol. 89, pp. 119–134.

Schweger, C.E., Late Quaternary paleoecology of the Yukon: A Review, in Insects of Yukon, Danks, H.V. and Downes, J.A., Eds., Ottawa: Biol. Surv. Can. Terr. Arthrop., 1997, pp. 59–72.

Sher, A.V., Fossil saiga in northeastern Siberia and Alaska, *Byull. Komm. Izuch. Chetvert. Per. Akad. Nauk SSSR,* 1967, vol. 33, pp. 97–112.

Sher, A.V., *Mlekopitayushchie i stratigrafiya pozdnego pleistotsena krainego Severo-Vostoka SSSR i Severnoi Ameriki* (Mammals and Stratigraphy of the Late Pleistocene of the Extreme Northeastern USSR and North America), Moscow: Nauka, 1971 [English translation: Pleistocene mammals and stratigraphy of the Far Northeast USSR and North America, *Int. Geol. Rev.,* 1974, vol. 16, nos. 7–10].

Sher, A.V., The role of Bering Land in the development of the Holarctic mammalian fauna in the Late Cenozoic, in *Beringiya v kainozoe* (Bering Land in the Cenozoic), Kontrimavichus, V.L., Ed., Vladivostok: Akad. Nauk SSSR, 1976, pp. 227–24.

Sher, A.V., On some stratigraphic boundaries of the Upper Cenozoic of the northeastern USSR, in *14th Tikhookeanskii nauchnyi kongress, Khabarovsk, avgust 1979 g.* (14th Pacific Scientific Congress, Khabarovsk, August 1979), Moscow: Vses. Inst. Nauchn. Tekhnich. Inform., 1979, pp. 138–139.

Sher, A.V., On the history of the mammal fauna of Beringida, *Mlekopitayushchie SSSR. Tezisy dokladov III S'ezd Vsesoyuznogo Teriologicheskogo obshchestva. Moskva, 1–5 fevralya, 1982 g.,* (Mammals of the USSR: Reports of the III Congress of All-Union Theriological Society, Moscow, 1–5 February, 1982), Moscow, 1982, pp. 89–90.

Sher, A.V, Age of Quaternary deposits of the Yana–Kolyma Lowland and its mountain border, *Dokl. Akad. Nauk SSSR,* 1984, vol. 278, no. 3, pp. 708–713.

Sher, A.V., Problems of ecology of Pleistocene mammals, in *Aktual'nye problemy morfologii i ekologii vysshikh pozvonochnykh* (Actual Problems of Morphology and Ecology of Higher Vertebrates), Moscow: Ist. Evol. Morfol. Ekol. Zhiv. Akad. Nauk SSSR, 1988, part 2, pp. 432–464.

Sher, A.V., Actualism and disconformism in the studies of Pleistocene mammal ecology, *Zh. Obshch. Biol.,* 1990, vol. 51, no. 2, pp. 163–177.

Sher, A.V., A brief overview of the Late Cenozoic history of the western Beringian Lowland, in *Terrestrial Paleoenvironmental Studies in Beringia*, Edwards, M. E., Sher, A.V., and Guthrie, R. D., Eds., Fairbanks: Univ. Alaska Mus., 1997a, pp. 3–6.

Sher, A.V., Edoma as a store of paleoenvironmental records in Beringida, in *Beringian Paleoenvironments workshop, September 20–23, 1997*, Colorado: Florissant, 1997b, pp. 140–144.

Sher, A.V., Nature restructuring in the East Siberian Arctic at the Pleistocene–Holocene boundary and its role in mammal extinction and emergence of modern ecosystems: Communication 1, *Kroiosf. Zemli,* 1997c, vol. 1, np. 1, pp. 21–29.

Sher, A.V., Nature restructuring in the East Siberian Arctic at the Pleistocene–Holocene boundary and its role in mammal extinction and emerging of modern ecosystems: Communication 2, *Kroiosf. Zemli,* 1997d, vol. 1, no. 2, pp. 3–11.

Sher, A.V., Kaplina, T.N., Giterman, R.E., Lozhkin, A.V., Arkhangelov, A.A., Kiselev, S.V., Kuznetsov, Y.V., Virina, E.I., and Zazhigin, V.S., Late Cenozoic of the Kolyma Lowland, in *14th Tikhookeanskii nauchnyi kongress, Khabarovsk, avgust 1979 g.* (14th Pacific Scientific Congress, Khabarovsk, August 1979), Moscow: Vses. Inst. Nauchn. Tekhnich. Inform., 1979, pp. 1–116.

Sher, A.V., Kaplina, T.N., and Ovander, M.G., Unified Regional Stratigraphic Chart for the Quaternary deposits in the Yana–Kolyma Lowland and its mountainous surroundings: Explanatory notes, in *Resheniya Mezhvedomstvennogo stratigraficheskogo soveshchaniya po chetvertichnoi systeme Vostoka SSSR, Magadan, 1982. Ob"yasnitel'naya zapiska k regional'nym stratigraficheskim skhemam chetvertichnykh otlozhenii vostoka SSSR* (Resolutions of Interdepartmental Conference on Quaternary Stratigraphy of the Eastern USSR, Magadan, 1982. Explanatory Notes for the Regional Stratigraphic Schemes of the Quaternary Deposits of the Eastern USSR), Shilo, N.A., Ed., Magadan: Severo-Vost. Kompl. Nauchno-Issled. Inst. Dal'nevost. Otd. Akad. Nauk SSSR, 1987, pp. 43–88.

Sher, A.V., Kuzmina, S.A., Kuznetsova, T.V., and Sulerzhitsky, L.D., New insights into the Weichselian environment and climate of the East Siberian Arctic, derived from fossil insects, plants, and mammals. *Quat. Sci. Rev.,* 2005, vol. 24, nos. 5–6, pp. 533–569.

Sher, A.V., Virina, E.I., and Zazhigin, V.S., Stratigraphy, paleomagnetism, and mammal fauna of the Pliocene–Pleistocene deposits of the Lower Kolyma River, *Dokl. Akad. Nauk SSSR,* 1977, vol. 234, no. 5, pp. 1171–1175.

Shilo, N.A., Ed., *Resheniya Mezhvedomstvennogo stratigraficheskogo soveshchaniya po chetvertichnoi systeme Vostoka SSSR, Magadan, 1982. Ob"yasnitel'naya zapiska k regional'nym stratigraficheskim skhemam chetvertichnykh otlozhenii vostoka SSSR* (Resolutions of Interdepartmental Conference on Quaternary Stratigraphy of the Eastern USSR, Magadan, 1982: Explanatory Notes for the Regional Stratigraphic Schemes of the Quaternary Deposits of the Eastern USSR), Magadan: Min. Geol. SSSR, Severo-Vost. Kompl. Nauchno-Issled. Inst. Dal'nevost. Otd. Akad. Nauk SSSR, 1987.

Siegert, C., Schirrmeister, L., and Babiy, O., The sedimentological, mineralogical and geochemical composition of Late Pleistocene deposits from the Ice Complex on the Bykovsky Peninsula, Norhern Siberia, *Polarforschung,* 2002, vol. 70, pp. 3–11.

Silfverberg, H., Chrysomelidae in the Arctic, in *Novel Aspects of the Biology of Chrysomelidae,* Jolivet, P.H., Cox, M.L., and Petitpierre, E., Eds., Netherlands: Kluwer, 1994, pp. 503–510.

Slagoda, E.A., Genesis and microstructure of cryolithogenical deposits in the Bykovsii Peninsula and Muostakh Island, *Candidate's Dissertation in Geology and Mineralogy,* Yakutsk: Inst. Merzlotoved. Sib. Otd. Ross. Akad. Nauk, 1993.

Solov'ev, V.A. and Stanisheva, O.N., Environment of the Edoma Formation Time in the northeastern USSR, in *Osnovnye problemy paleogeografii pozdnego kainozoya Arktiki* (Main Problems of Paleogeography of the Late Cenozoic of the Arctic), Leningrad: Nedra, Leningr. Otd., 1983, pp. 203–217.

Spektor, V., Bulygina, E., Bunn, A., Chandra, S., Davydov, S., Frey, K., Holmes, R., Schade, J., Sobczak, W., and Falina, A., On genesis of the lower Kolyma Edoma based on new AMS 14C Dates from Duvanny Yar, *2010 State of the Arctic Meeting, March 2010,* Miami, 2010, pp. 16–19.

Strauss, J., Wetterich, S., and Schirrmeister, L., 2010. Permafrost properties of the Edoma key site at Duvanny Yar (Kolyma Lowland, Eastern Siberia), *IPY Oslo Science Conference 2010, June* hdl:10013/epic.35418.d001.

Svitoch, A.A., The latest deposits of the Main River valley and conditions of it creation, *Dokl. Akad. Nauk SSSR,* 1975, vol. 224, no. 6, pp. 1462–1466.

Svitoch, A.A., Conclusion on the Main River valley sites, in *Noveyshie otlozheniya i paleogeografiya pleistotsena Chukotki* (The Latest Deposits and Paleogeography of the Pleistocene in the Chukotka Peninsula), Kaplin, P.A., Ed., Moscow: Nauka, 1980, pp. 150–153.

Ter-Minasyan, M.E., *Zhuki-dolgonosiki podsemeistva Cleoninae fauny SSSR: Kornevye dolgonosiki (triba Cleonini)* (The Weevil Subfamily Cleoninae in the Fauna of the USSR: Root Weevil Tribe Cleonini), Leningrad: Nauka, 1988.

Tomirdiaro, S.V., *Vechnaya merzlota i osvoenie gornykh stran i nizmennostei na primere Magadanskogo regiona i Yakutskoi Avt. SSR* (Permafrost and Commercial Development of Mountain Regions and Lowlands, Using the Magadan Region and Yakut Auton. SSR), Magadan: Magad. Izd., 1972.

Tomirdiaro, S.V., Cryogenic evolution of the northeastern plains of Asia in the Late Pleistocene and Holocene, *Izv. Vsesoyuz. Geogr. Ob-va,* 1975, vol. 2, pp. 124–132.

Tomirdiaro, S.V., *Lessovo-ledovaya formatsiya Vostochnoi Sibiri v pozdnem pleistotsene i golotsene* (Loess–Ice Formation of Eastern Siberia in the Late Pleistocene and Holocene), Moscow: Nauka, 1980.

Tomirdiaro, S.V., Periglacial landscape and loess accumulation in the Late Pleistocene of Arctic and Subarctic, in *Late Quaternary Environments of the Soviet Union,* Velichko, A.A., Wright, H.E., Jr., and Barnosky, C.W., Eds., Minneapolis: Univ. Minnesota Press, 1984, pp. 141–146.

Tomirdiaro, S.V., Arslanov, Kh.A., Chernen'kii, B.I., Tertychnaya, T.V., and Prokhorova, T.N., New data on formation of loess–ice sequences in northern Yakutia and ecological conditions of the mammoth fauna in the Arctic during the Late Pleistocene. *Dokl. Akad. Nauk SSSR,* 1984, vol. 278, no. 6, pp. 1446–1449.

Tomirdiaro, S.V. and Chernen'ky, B.I., *Kriogenno-eolovye otlozheniya Vostochnoi Arktiki i Subarktiki* (Cryogenic Eolian Deposits of the Eastern Arctic and Subarctic), Moscow: Nauka, 1987.

Trufanov, G.V., Belousov, K.N., and Vakulenko, A.S., Materials to stratigraphy of the Cenozoic deposits of the Novosibirskie Islands, in *Kontinental'nye tretichnye tolshchi Severo-Vostoka Azii* (Continental Tertiary Strata of Northeastern Asia), Shilo, N.A. and Baranova, Yu.P., Eds., Novosibirsk: Nauka, 1979, pp. 30–40.

Tugarinov, A.Ya., On the origin of the Arctic fauna, *Priroda,* 1929, nos. 7–8, pp. 653–680.

Tumskoi, V.E., Features of cryolithogenesis in northern Yakutia (Middle Neopleistocene to Holocene). *Kriosf. Zemli,* 2012, vol. 16, no. 1, pp. 12–21.

Tumskoi, V.E. and Basilyan, A.E., Quaternary stratigraphy of the Dmitrii Laptev Strait coasts (northern Yakutia), in *Materialy VI Vserossiiskogo soveshchaniya "Fundamental'nye problemy kvartera: Itogi izucheniya i osnovnye napravleniya dal'neishikh issledovanii"* (Vl All-Russia Conference on the Fundamental Problems of the Quaternary: Results and Trends of Future Research), Kontorovich, A.E., Volkova, V.S., Khazina, I.V., and Khazin, L.B., Eds., Novosibirsk: Izd. Sib. Otd. Ross. Akad. Nauk, 2009, pp. 592–593.

Vangengeim, E.A., *Paleontologicheskoe obosnovanie stratigrafii antropogena Severnoi Azii (po mlekopitayushchim)* (Paleontological Foundation of Anthropogene Stratigraphy in Northern Asia Based on Mammals), Moscow: Nauka, 1977.

Vartanyan, S.L., Garutt, V.E., and Sher, A.V., Holocene dwarf mammoths from Wrangel Island in the Siberian Arctic, *Nature,* 1993, vol. 362, pp. 337–340.

Vasil'chuk, Yu.K., Vaikmae, R.A., Punning, J.-M. K., and Lebman, M.O., Oxygen isotope distribution, palynology and hydrochemistry wedge ice in organic–mineral complex of Duvanny Yar type section, Dokl. Akad. Nauk, Sec. Nauk Zemle, 1988, vol. 292, no. 5, pp. 69–72.

Vas'kovsky, A.P., Stratigraphic outline of Quaternary deposits in northeastern Asia, in *Geologiya Koryakskogo nagor'ya* (Geology of the Koryak Mountains), Egiazarov, B.Kh., Ed., Moscow: Gostoptekhizdat, 1963, pp. 24–53.

Velichko, A.A., Catto, N., Drenova, A.N., Klimanov, V.A., Kremenetski, K.V., and Nechaev, V.P., Climate changes in Eastern Europe and Siberia at the Late Glacial–Holocene transition, *Quat. Int.,* 2002, vol. 91, pp. 75–99.

Virina, E.I., 1997. Paleomagnetic stratigraphy of the Pliocene/Pleistocene sediments of the Kolyma Lowland and some problems of correlation with sites in Alaska and the Yukon, in *Terrestrial paleoenvironmental studies in Beringia,* Edwards, M.E., Sher, A.V., and Guthrie, R.D., Eds., Fairbanks: Univ. Alaska Mus., pp., 19–24.

Vol'nov, D.A., History of geological development of the region of the Novosibirskie Islands, in *Geologiya i poleznye iskopaemye Novosibirskikh ostrovov i ostrova Vrangelya* (Geology and Mineral Resources of the Novosibirskie Islands and Wrangel Island), Vol'nov, D.A., Ed., Leningrad: Nauchno-Issled. Inst. Geol. Arkt., 1975, pp. 61–71.

Vtyurin, B.I., Geocryological essay of the Markovo Depression, in *Geokriologicheskie usloviya Zapadnoi Sibiri, Yakutii i Chukotki* (Geocryological Conditions of West Siberia, Yakutia, and the Chukotka Peninsula), Vel'min, N.I. and Vtyurin, B.I., Eds., Moscow: Nauka, 1964, pp. 115–133.

Whitehouse, N.J., The Holocene British and Irish ancient woodland fossil beetle fauna: Implications for woodland history, biodiversity and faunal colonisation. *Quat. Sci. Rev.*, 2006, vol. 25, nos. 15–16, pp. 1755–1789.

Wetterich, S., Kuzmina, S., Andreev, A.A., Kienast, F., Meyer, H., Schirrmeister, L., Kuznetsova, T., and Sierralta, M., Paleoenvironmental dynamics inferred from

Late Quaternary permafrost deposits on Kurungnakh Island, Lena delta, Northeast Siberia, Russia *Quat. Sci. Rev.*, 2008, vol. 27, nos. 15–16, pp. 1523–1540.

Wetterich, S., Rudaya, N., Tumskoi, V., Andreev, A.A., Opel, T., Schirrmeister, L., and Meyer, H., Last glacial maximum records in permafrost of the East Siberian Arctic, *Quat. Sci. Rev.,* 2011, vol. 30, pp. 3139–3151.

Yurtsev, B.A., Steppe communities of Chukotka tundra and the Pleistocene "tundra–steppe", *Bot. Zh.,* 1974, vol. 59, no. 4, pp. 484–501.

Yurtsev, B.A., Beringia and its biota in the Late Cenozoic: Synthesis, in *Beringiya v kainozoe* (Beringia in the Cenozoic), Korotky, A.M., Ed., Vladivostok, 1976, pp. 202–212.

Yurtsev, B.A., *Reliktovye kompleksy stepnoi rastitel'nosti Severnoi Azii (Problemy rekonstruktsii kriokseroticheskikh landshaftov Beringii)* (Relict Steppe Vegetation Assemblages of Northern Asia: Problems of Reconstruction of the Cryoxerotic Landscapes of Beringia), Novosibirsk: Nauka, 1981.

Yurtsev, B.A., The Pleistocene "tundra–steppe" and the productivity paradox: The landscape approach, *Quat. Sci. Rev.*, 2001, vol. 20, pp. 165–174.

Zanina, O.G., Gubin, S.V., Kuzmina, S.A, Maximovich, S.V., and Lopatina, D.A., Paleoenvironmental and paleoclimatic records from the Late Pleistocene paleosols and sediments of Duvanny Yar section, *Quat. Sci. Rev.*, 2011, vol. 30, nos. 17–18, pp. 2107–2123.

Zazula, G.D., Froese, D.G., Elias, S.A., Kuzmina, S., and Mathewes, R.W., Arctic ground squirrels of the mammoth–steppe: Paleoecology of Late Pleistocene middens (~24000–29450 ^{14}C yr BP), Yukon Territory, Canada, *Quat. Sci. Rev.*, 2007, vol. 26, pp. 979–1003.

Zazula, G.D., Froese, D.G., Elias, S.A., Kuzmina, S., and Matthewes, R.W., Early Wisconsinan (MIS 4) Arctic ground squirrel middens and a squirrel-eye-view of the mammoth–steppe, *Quat. Sci. Rev.*, 2011, vol. 30, nos. 17–18, pp. 2220–2237.

Zimov, S.A., Pleistocene park: Return of the mammoth's ecosystem, *Science,* 2005, vol. 308, pp. 796–798.

Zimov, S.A., Chuprynin, V.I., Oreshko, A.P., Chapin III, F.S., Reynolds, J.F., and Chapin, M.C., Steppe–tundra transition—a herbivore-driven biome shift at the end of the Pleistocene, *Am. Natur.,* 1995, vol. 146, pp. 765–794.

Translated by G. Rautian