(Canterbury, New Zealand) through three glaciation-interglaciation cycles. *Palaegeography, Palaeoclimatology, Palaeoecology* **152,** 101–127.
Soons, J. M. (1979). Late Quaternary environments in the central South Island of New Zealand. *New Zealand Geographer* **35,** 16–23.
Soons, J. M., and Burrows, C. J. (1978). Dates for Otiran deposits, including plant microfossils and macrofossils, from Rakaia Valley. *New Zealand Journal of Geology and Geophysics* **21,** 607–615.
Soons, J. M., Moar, N., Shulmeister, J., Wilson, H. D., and Carter, J. A. (2002). Quaternary vegetation and climate changes on Banks Peninsula, South Island, New Zealand. *Global and Planetary Change* **33,** 301–314.
Worthy, T. H. (1998). Quaternary fossil faunas of Otago, South Island, New Zealand. *Journal of the Royal Society of New Zealand* **28,** 412–521.

Late Pleistocene of Northern Asia

A Sher[1] and S Kuzmina[1,2], [1]Russian Academy of Sciences, Moscow, Russia, [2]University of London, Surrey, UK

© 2007 Elsevier B.V. All rights reserved.

Late Pleistocene Beetle Records from Northern Asia

Preservation, Abundance and Collecting Fossil Beetles in the Siberian Arctic

Insect fossils are common in various types of Quaternary deposits in Northern Asia. They are most abundant and well preserved in silt or sandy silt with plant detritus. Two main factors – the predominantly fine-grained composition of sediment matrix and ubiquitous permafrost – allow excellent preservation of the late Pleistocene insect fossils in this region (**Figs. 1** and **2**). Massive peat layers in the Arctic usually contain few insect remains, but thin-bedded peat intercalating with silt may contain rich insect faunas. The coarser sediment, such as sand with fine gravel deposited in rapidly running water, usually preserves only the most durable insect remains (**Fig. 3**).

The average abundance of insect fossils in the sediment is not very high (**Table 1**). This means that in order to obtain a statistically representative sample with a minimum number of 100 individuals, we must process 50 to 60 kg of moist sediment with an average content of fossils, and sometimes up to 200 kg of sediment with a poor content of fossils. Taking into account the difficulties and expense of working in remote arctic regions, we usually spend several weeks at one site and collect 20 to 30 samples there. The enormous cost of transportation forces us to reduce the weight of samples to be shipped, so we screen our samples in the field (**Figs. 4–6**).

The identification of insect fossils in Northern Asia is difficult because of insufficient knowledge of both taxonomy and distribution of modern species. That is why we always collect modern insects during our field season in these remote regions. This only marginally advances the cause of regional beetle taxonomy, however. Many groups are still poorly studied.

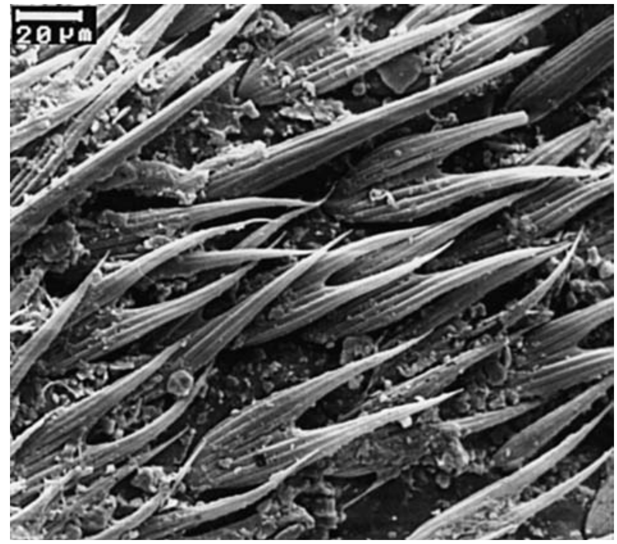

Figure 1 Fossil scales on the surface of the weevil, *Hypera ornata*, Bykovsky Peninsula, Late Pleistocene. The condition of fossil chitin in frozen silts is usually as good as in modern beetles. Even such delicate and fragile elements as scales, hairs, and antennae are sometimes preserved.

Figure 2 Fossil head, pronotum, and leg of a dung beetle *Aphodius* sp., from the Duvanny Yar site, Late Pleistocene. Excellent preservation is common for beetle remains recovered from buried ground squirrel nests, where some specimens preserve legs in their original position.

Figure 3 Fossil head capsules of weevils (above and right) and a predaceous diving beetle (below, left) from a sandy–gravel unit, Keremesit River.

Localities of Fossil Beetles in Northern Asia

The first studies of Pleistocene insects in Northern Asia took place in the 1960s (Grushevskiy and Medvedev, 1962). These studies were associated with famous discoveries of complete mammal carcasses in permafrost or rich accumulations of mammoth bones, the so called 'mammoth cemeteries' (Medvedev and Voronova, 1977). The regular sampling of Quaternary sediments for insect fossils in northeastern Siberia and their systematic research was started in the 1970s by Sergey Kiselyov (1981). Currently, Svetlana Kuzmina continues Kiselyov's work in that region, and Evgeny Zinovyev studies Quaternary insects in northwestern Siberia.

More than 30 years of regular paleoentomological research in Northern Asia has resulted in a large number of studied sites and analyzed assemblages, but their distribution over such a vast territory is uneven and discontinuous. For example, Zinovyev (1997) studied about 36 sites in northwestern Siberia, most of them of late Pleistocene age. However, further east, the huge region between the mouth of the Ob' River and almost to the Lena River Delta is virtually unstudied. From the Lena Delta to Chukotka (northeastern Siberia) the number of sites is much higher, but they are unevenly distributed (**Fig. 7**). More than 200 late Pleistocene beetle assemblages have been studied from 44 localities in this region (**Table 2**). The most important are discussed below.

Geological Background of the Late Pleistocene Beetle Record in Northern Asia

Northern Asia from west to east Even if we restrict our consideration of Northern Asia to the areas north of the Arctic Circle, it still remains a huge region comprising very different physiographic provinces with contrasting geological histories. While northwestern Siberia and the Taimyr Peninsula were strongly affected by the advances of the Barents-Kara Ice Sheet (Svendsen *et al.*, 2004), no ice sheets existed east of the Taimyr. Only some high mountain ridges received enough moisture to build valley glaciers. Marine sediments exposed above present sea level are also found mainly in the glacially-affected areas. Only at the easternmost part of Asia, close to the Bering Strait (Chukotka Peninsula), were both glaciations (mountain and piedmont types) and marine transgressions more significant in the Pleistocene. Thus, the huge territory of Northern Asia between the Taimyr and Chukotka (i.e., between about 112 and 175°E) has never experienced major glaciations. Instead, this area was a broad arena for permafrost and periglacial

Table 1 Concentration of insect fossils in the Late Pleistocene frozen silts. The Lena Delta, Late Weichselian, Mamontouy Khayata section

Sample No	*Weight of the screened wet sediment, kg*	*Number of insect fossils extracted*	*MNI (minimum number of individuals)*	*The number of fossils per kilo*	*The number of insect individuals per kilo*	*Weight of matrix to be screened to get 100 insect individuals, kg*
MKh99-18	9	52	30	6.1	3.5	28
MKh99-16	20	32	25	1.6	1.2	82
MKh99-14	20	10	9	0.5	0.4	227
MKh99-12	9	17	12	2.0	1.4	71
MKh99-22	17	160	88	9.4	5.2	19
MKh99-6	26	109	56	4.3	2.2	46
MKh99-5a	9	42	23	4.9	2.7	37
MKh99-5o	14	111	47	8.2	3.5	29
MKh99-5s	14	146	57	10.7	4.2	24
MKh99-3a	7	85	43	12.5	6.3	16
Average				6.0	3.1	62

NOTE. The volume of screened sediments in these samples is small, as they were screened by geologists. However, the weight of samples was measured, and this case can be used to estimate concentration of fossils.

Figure 4 We screen sediments in the field, using a large hand-made box with 0.5 mm mesh sieve, letting river, lake, or pond water in and out through the sieve only. The screening is aimed at removing most, but not all of the mineral component, so some amount of silt remains in the box, helping preserve the shape of many fossils smaller than 0.5 mm that might otherwise be lost. These specimens usually float on top of the silt and remain in the sample.

Figure 5 The screen residues are dried as much as the weather allows, at first openly, later in fabric bags.

Figure 6 Quite often, silt sticks to the fossils, or fills the insides of pronota, head capsules, or joined elytra. This limits the effectiveness of the laboratory flotation method. Instead, we separate dry residuals into the size fractions through regular soil sieves, then pick the insect and other fossils by hand, under binocular microscope for smaller fractions.

processes. At present, the environment of the vast lowlands bordering the East Siberian and Laptev Seas is strongly influenced by the Arctic Ocean, but in the late Pleistocene these flatlands had a much more continental climate, as they extended much further north during long periods when the shallow continental shelf was above sea level.

What is Yedoma? The most remarkable and widespread Pleistocene sedimentary unit on these flatlands is ice-rich silt and sandy silt with thick ice wedges (**Fig. 8**). It usually builds the main surface of the lowland (up to 60–100 m above the rivers) or its remaining hills when it is destroyed by thermokarst and erosion. Local people call these hills 'Yedoma', and geologists used that name for this kind of sediment (**Fig. 9**). The high content of ice in Yedoma sediments (up to 80%) (**Figs. 10** and **11**) explains another common name for this formation – Ice Complex. Some important features of Yedoma, or Ice Complex, are shown in **Figures 12–14**.

The same kind of ice-rich silt builds not only thick sequences of high Yedoma, but also lower terraces (**Fig. 15**). It is also found on the slopes of rock hills and fills the valleys of small creeks in the highlands. In other words, a similar kind of sediment can occur in many different depositional environments. That is

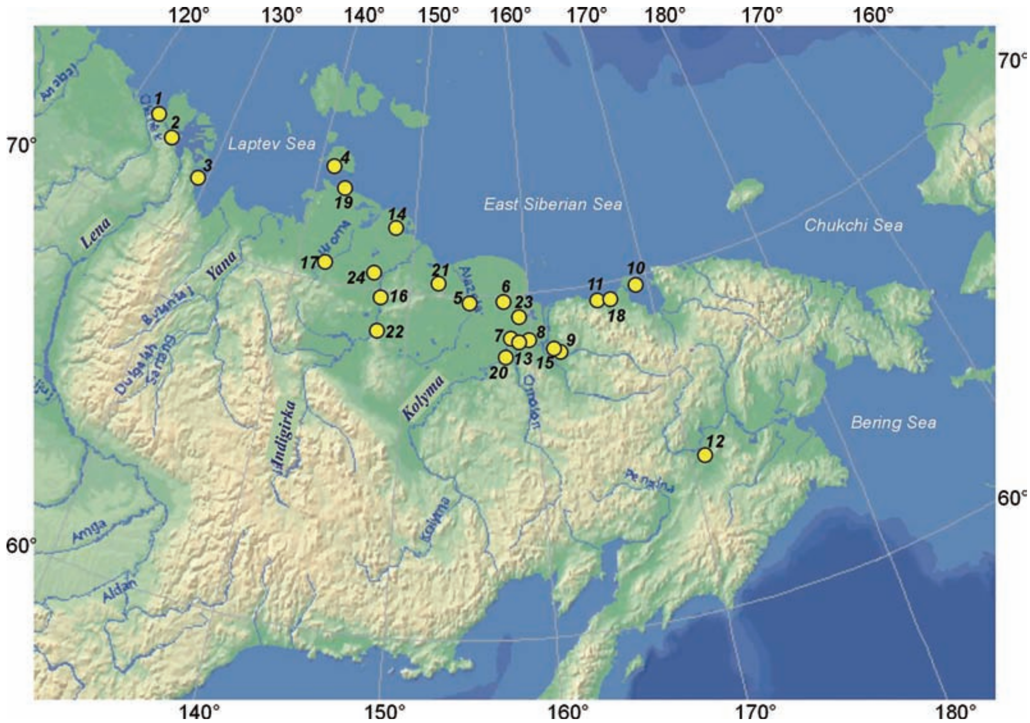

Figure 7 Map of Late Pleistocene fossil beetle localities in north-eastern Siberia.1 – 3 Lena Delta region: 1 – Olenyok Channel, Nagym, 2 – Byor-Khaya, 3 – Bykovsky Peninsula, 4 – Bolshoy Lyakhovsky Island, 5 – Alazeya, 6 – Chukochya, 7 – Alyoshkina Zaimka, 8 – Duvanny Yar, 9 – Stanchikovsky Yar, 10 – Ayon Island, 11 – Milkera, 12 – Main River, Ledovy Obryv (Ice Bluff), 13 – Omolon, 15 – Krasivoye, 16 – Shamanovo, 17 – Khroma River, 18 – Primorsky, 19 – Oyagosskiy Yar, 20 – Krestovka, 21 – Khomus-Yuryakh, 22 – Sypnoy Yar, 23 – Yakutskoe Lake, 24 – Achchagyy-Allaikha.

Table 2 The distribution of studied insect assemblages of the Late Pleistocene age in North–eastern Siberia

Region	*Number of studied sections*	*Number of insect samples with MNI >30*
Lena Delta	3	63
Indigirka Lowland	10	28
New Siberian Islands	4	11
Kolyma Lowland	16	50
Medvezhyi Islands	2	4
West Chukotka (Chaun)	3	16
Ayon Island	4	38
South Chukotka (Main R.)	2	7
TOTAL	44	217

Figure 8 One of the famous exposures of Late Pleistocene icy silts – Vorontsovskiy Yar on the Indigirka River. The top of this bluff, which is about 40 m high, lies about 90 m above the river level.

why earlier heated debates about the origin of Yedoma silts (fluvial, eolian, eluvial-colluvial, etc.) gradually gave way to the understanding that the ice-rich Yedoma silts are of polygenetic origin. They include sediments of different facies, which appear similar due to the homogeneity of the original material generated by cryogenic weathering during the Pleistocene and due to the activity of permafrost processes that universally affected sedimentation in various environments.

In closer proximity to mountain areas, active denudation yielded mostly coarser sediments, especially sands. These are the so-called Sand Yedoma sections known in various regions of northeastern Siberia. Usually, but not always, they include much smaller

Figure 9 The Duvannyy Yar site, in the lower course of the Kolyma River, is a cut bank exposure of the so-called Omolon-Anyuy Yedoma – the high eroded surface between the Omolon and Anyuy Rivers – large tributaries of the Kolyma.

Figure 10 Mamontovyy Khayata Cliff, Bykovsky Peninsula, eastern side of the Lena R. Delta. Extensive ice bodies such as this, which in earlier times were interpreted as buried glaciers, in fact represent polygonal systems of syngenetic (growing simultaneously with continued sedimentation) ice wedges.

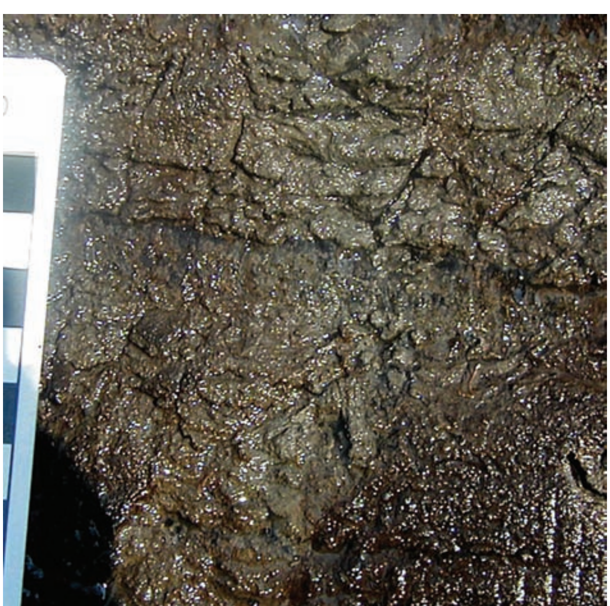

Figure 11 The ground pillars between the ice wedges also contain lots of ice, but as small layers and microscopic lenses segregated when the silt was freezing.

Figure 12 One of the typical features of Yedoma silts is the abundance of very thin plant roots, most likely belonging to grasses. They occur *in situ* and usually form complicated branching systems, permeating frozen silt.

Figure 13 Some frozen silt layers include woody roots of small shrubs.

ice wedges (**Figs. 16–17**). A similar situation can occur along large rivers, building sand terraces with scattered ice wedges.

Thus Yedoma is not a facies, but a type of sedimentation reflecting a specific climate and environment, and in this sense the synonym ‘Ice Complex’ seems more correct. Interestingly, similar sedimentation took place in northwestern Siberia, when the Barents-Kara ice sheet retreated north in the Late Weichselian (Svendsen *et al.,* 2004). The widest distribution of

Figure 14 The Yedoma silts are very rich in various kinds of fossils – plants, freshwater shells, and insects. The most famous remains are the large number of mammal bones and complete or partial frozen carcasses of Pleistocene mammals.

Figure 15 The same kind of ice-rich silt builds not only thick sequences of high Yedoma, but also terrace-like bodies of lower elevation (Low Yedoma, 15–25 m above the river), more clearly positioned in river valleys (Omolon River, Kolyma River basin).

Figure 16 Impressive sand sequences up to 60 m high are usually exposed where large rivers run in low mountain areas. The best known examples are Sypnoy Yar on the Indigirka River and in the city of Verkhoyansk area (Yana and Adycha River basins). A coarser sediment (sands) limited the scale of frost cracks, and the ice wedges in these fluvial sequences are much smaller than in classical Yedoma. They are restricted to the lenses of silty sand (floodplain and ox-bow deposits).

Figure 17 The Ice Bluff section, Main River, southern Chukotka. Sand sections such as this, with a higher contents of silt, allowed the continuous growth of ice wedges.

the Ice Complex sediments and their overall similarity make their stratigraphic characterization difficult.

Other types of sections Numerous sections of 'alasses' – thermokarst depressions formed by the thawing of the Ice Complex – are another widespread element of regional geology. The majority of them were formed at the Pleistocene–Holocene transition, and are composed of reworked Yedoma silt or sand with low ice content (**Fig. 18**) (*see* Ice Wedges and Ice Wedge Casts). They may include a lacustrine unit of former thermokarst lakes and are overlain by a more or less thick peat layer, usually of Early Holocene age. Earlier thermokarst events are recorded in buried alas units. They have a similar composition, but are overlain by an Ice Complex unit, and so mark periods of regional, or at least local, degradation of

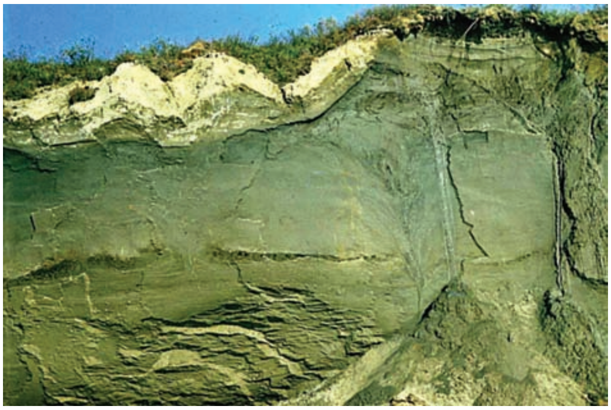

Figure 18 In the thermokarst (alas) sections the Ice Complex sediments have thawed through, i.e. reworked in place. As a result, the ice content is much lower here, as former ice wedges have been replaced by ice-wedge casts, or pseudomorphs.

permafrost in the past. In several sites where ancient alas sediments underlie the Weichselian Ice Complex, and overlie supposedly Middle Pleistocene units, they probably represent the Last Interglacial (Eemian). Only one such case has been documented by direct dating (IRSL, Krest-Yuryakh at Bolshoy Lyakhovsky Island, Andreev *et al.*, 2004). If a thermokarst lake reappeared several times in one place, then composite sections formed, consisting of a few superimposed alas complexes (**Fig. 19**).

The late Pleistocene stratigraphy in Northeastern Siberia The stratigraphic subdivision of Ice Complex (Yedoma) sequences is not easy because of the high homogeneity of the sediments. It is mostly based on radiocarbon dating, which allows us to reliably distinguish the late Weichselian units, but we encounter problems with the Middle Weichselian

Figure 19 One such reworked section, Molotkovsky Kamen' at the Malyy Anyuy River, had been selected as the regional type of Middle Weichselian Interstadial (Molotkov Horizon) with alternating warmings and coolings. Subsequent re-dating of the buried peat layers in this section, however, showed much earlier ^{14}C dates, so the age of the Molotkov Horizon should be revised (Sher et al., 2005).

(Sher and Plakht, 1988). Ice Complex sections are referred to the Early Weichselian if they have an infinite ^{14}C age and are overlain by the dated middle to late Weichselian sediments. Strictly speaking, such arguments are not fully conclusive. There are Ice Complex sections dated from the late Middle Pleistocene (Kaplina *et al.*, 1980), or even earlier. On the other hand, the Ice Complex units with 'finite' ^{14}C dates in the range 35 to 45 ka do not necessarily belong to the middle Weichselian, as there were many cases when such units turned out to be much older (Sher *et al.*, 2005).

Table 3 summarizes the geological position and the age of the late Pleistocene sites from which the insect assemblages have been studied.

Peculiar Features of Fossil Beetle assemblages in Northeastern Asia

General composition The species composition of the Pleistocene beetle fauna of northeastern Asia is strange, compared with the other arctic regions:

(1) It has higher diversity and abundance of plant-feeding insects, mostly weevils (Curculionidae) and leaf beetles (Chrysomelidae). Even among ground beetles (Carabidae), mostly a predatory family, one of the commonly found species is a plant-feeder *Curtonotus alpinus* in northeastern Siberia (although this has not been observed in its populations from northern Europe or arctic North America).

(2) Fossil assemblages usually include many species that currently live in tundra and forest tundra, but the diversity of some groups, such as litter inhabitants (rove beetles), carrion beetles, and fungus beetles, is notably lower than in modern tundra communities. Also, the diversity of water and riparian species in the fossil assemblages is less than today in the Arctic.

(3) Along with tundra species, most Pleistocene assemblages show significant numbers of steppe, meadow-steppe, and other xerophilic insects. Especially notable is the abundance of the pill beetle *Morychus viridis,* an inhabitant of cold steppe-like biotopes in northeastern Siberia today (see below). This species makes up as much as 90% of some late Pleistocene insect assemblages.

(4) Xylophages and other dendrophilic species are very rare in the late Pleistocene insect assemblages in this region, so no true forest environment can be reconstructed here for any part of the late Pleistocene.

The above features characterize many late Pleistocene insect assemblages in northeastern Asia, which combine species presently inhabiting a variety of different regions and ecosystems. For example,

Table 3 Geological position and the age of the Late Pleistocene sites in Northeastern Siberia, from which the insect assemblages have been studied

The section type	*Sediment*	*Geocryology*	*Sections* & *Map No, Fig*	*Age range*	*Reference*
High Yedoma section (40–60 m and more above the river or sea level)	Mostly silt with sandy silt	One penetrating system of large ice wedges	Mamontovyy Khayata (**Fig. 7**, No 3, **Fig. 10**)	EW (?) - MW-LW (>50–12 ka)	Sher *et al.*, 2005
			Duvannyy Yar (**Fig. 7**, No 8, **Fig. 9**)	Mostly EW (?) - MW?. Probably LW at the top (>50–18 ka)	Sher and Plakht, 1988
		Multiple (2–3) overlying systems of ice wedges	Khomus-Yuryakh, Loc. 83 (**Fig. 7**, No 21)	Late middle Pleistocene	Sher, unpublished
High Sand section (>30, up to 60 m and more above the river or sea level)	Sand, silty sand	Relatively small ice wedges are restricted to more silty lenses.	Sypnoy Yar (**Fig. 7**, No 22, **Fig. 16**)	LP undivided (>45,000 yr BP in the lower third of the section)	Kaplina, 1981
			Utatgyr Suite, Ayon Island (**Fig. 7**, No 10)	LP undivided	Svitoch, 1980; Kiselyov, 1994
		One penetrating system of large ice wedges	Ledovyy Obryv (Ice Bluff) (**Fig. 7**, No 12, **Fig. 17**)	MW-LW (42–15,000)	Anderson and Lozhkin, 2002; Sher, unpublished
Topping Yedoma - Ice Complex up to 20–25 m thick on the top of composite sections	Mostly silt with sandy silt	One penetrating system of large ice wedges	Buor-Khaya (**Fig. 7**. No 2)	EW-LW (>50–17 ka)	Schirrmeister *et al.*, 2003
			Nagym (**Fig. 7**, No 1)	MW ? (44–45 ka)	Schirrmeister *et al.*, 2003
			Zimovye R. Mouth, Bol. Lyakhovsky Island (**Fig. 7**, No 4)	EW-MW (100–28 ka)	Schirrmeister *et al.*, 2004
			Yakutskoe Lake (**Fig. 7**, No 23)	LW ?	Kiselyov, 1994
			Khroma, Alazeya, Chukochya, Krestovka (**Fig. 7**, No 17, 5, 6, 20)	EW-MW? (Alazea, the date of 38 ka in the lower part of the unit)	Kaplina *et al.*, 1981
			Achchagyy-Allaikha (**Fig. 7**, No 24)	Late middle Pleistocene	Kaplina *et al.*, 1980
			Oyagosskiy Yar (**Fig. 7**, No 19)	Late middle Pleistocene - LW	Nikol'skiy and Basilyan, 2003
Low Yedoma terraces (20–30 m high above the river level)	Mostly silt with sandy silt	One penetrating system of large ice wedges	Omolon I (**Fig. 7**, No 13, **Fig. 15**)	LW (24–15 ka)	Sher, unpublished
			Krasivoye Bluff (**Fig. 7**, No 15)	LW (18,700 yr BP)	Kiselyov, 1994
			Shamanovo (**Fig. 7**, No 16)	MW-LW (33 ka and younger)	Kaplina *et al.*, 1980

(*Continued*)

Table 3 (*Continued*)

The section type	*Sediment*	*Geocryology*	*Sections & Map No, Fig*	*Age range*	*Reference*
Low Sand terraces (20–25 m high above the river level)	Sand, silty sand	Relatively small ice wedges are restricted to more silty lenses.	Alyoshkina Zaimka (**Fig. 7**, No 7)	LW (17.2–13.2 ka)	Sher *et al.*, 1979; Alfimov *et al.*, 2003
Multilayer alasses	Silt, peat	Ice-wedge pseudomorphs	Primorskiy, coast near Rauchua R. mouth (**Fig. 7**, No 18)	>28,000 yr BP in the lower part of the sequence, 24,800 yr BP in the middle part, 10.4 ka at the top	Kiselyov, 1994
Buried alass complexes	Silt, peat	Ice-wedge pseudomorphs	Khroma, Kyl-Bastakh Layers (**Fig. 7**, No 17)	LI ? (overiles mid-Pleistocene Khroma Suite, overlain by Ice Complex)	Kaplina *et al.*, 1983
			Alazeya, Kuobakh Unit (**Fig. 7**, No 5)	LI ? (overiles mid-Pleistocene (?) Maastakh Suite, overlain by Ice Complex)	Kaplina *et al.*, 1981
			Zimovye R. Mouth, Bol. Lyakhovsky Island (**Fig. 7**, No 4)	LI ? (overiles mid-Pleistocene (?) Kuchchuguy Suite, overlain by Ice Complex)	Andreev *et al.*, 2004
Low terraces		16 m terrace	Mil'kera (**Fig. 7**, No 11)	MW (32,800) ?	Kiselyov, 1994

NOTES

Abbreviations: LI – Last Interglacial, LP – Late Pleistocene, EW – Early Weichselian, MW – Middle Weichselian. LW – Late Weichselian

Sources:

Alfimov, A.V., Berman, D.I., Sher, A.V., 2003. Tundra-steppe insect assemblages and reconstruction of Late Pleistocene climate in the lower reaches of the Kolyma River. Zoologicheskiy Zhurnal, 82, 2, 281–300 (In Rissian).

Anderson, P.M., Kotov, A.N., Lozhkin, A.V., and Trumpe, M.A. 2002. Palynological and radiocarbon data from Late Quaternary deposits of Chukotka. In: Anderson, P.M., Lozhkin, A.V., Eds., Late Quaternary Vegetation and Climate of Siberia and Russian Far East (Palynological and Radiocarbon Database. Magadan: NESC FEB RAS, 35–79.

Kaplina, T.N. 1981 History of frozen sequences of northern Yakutia in the late Cenozoic. In: Dubikov G.I., Baulin V.V., Eds., Istoriya razvitiya mnogoletnemerzlykh porod Evrazii., M., Nauka, 1981, 153–181 (In Russian)

Kaplina, T.N., Lakhtina, O.V., Rybakova, N.O. 1981 Cenozoic deposits in the middle course of the Alazeya R. (Kolyma Lowland). Izvestiya Academii Nauk SSSR. Ser. Geologicheskaya, 8, pp. 51–63 (In Russian)

Kaplina, T.N., Ovander, M.G., Lozhkin, A.V., Zhigulyovtseva, S.N., Rybakova, N.O., Nikitin, V.P., Kiselyov, S.V., Bakhtin, A.V., Pirumova, L.G., Virina, E.I. 1983 Quaternary deposits in the middle current of the Khroma River (Yana-Indigirka Lowland). In: Shilo N.A., Ed., Stratigrafiya i paleogeografiya pozdnego kaynozoya Vostoka SSSR., Magadan, SV KNII DVNTs AN SSSR, 1983, 80–95 (In Russian)

Nikolsky, P.A. and Basilyan, A.E. 2003 Svyatoy Nos Cape – the key section of the Pleistocene in the North of Yana-Indigirka Lowland. In: The natural history of the Russian East Arctic in the Pleistocene and Holocene. GEOS Publishers, Moscow, 5–13. (In Russian)

Schirrmeister, L., Andreev, A., Grosse, G., Meyer, H. 2004 Saalian to Holocene Paleoenvironmental History Documented in Permafrost Sequences of Arctic Siberia (New Siberian Archipelago, Bolshoy Lyakhovsky Island) AGU Fall Meeting, 13–17 December 2004 San Francisco, California C13B-0286

Schirrmeister, L., Kunitsky, V. V., Grosse, G., Schwamborn, G., Andreev, A. A., Meyer, H., Kuznetsova, T., Bobrov, A., Oezen, D. 2003. Late Quaternary history of the accumulation plain north of the Chekanovsky Ridge (Lena Delta, Russia) – a multidisciplinary approach, Polar Geography, 27 (4), 277–319.

Svitoch, A.A. 1980. The description of the lates deposits [of the Ayon Island]. In Kaplin, P.A. (ed.). The latest deposits and paleogeography of the Pleistocene in Chukotka. Moscow, Nauka, 180–202. (In Russian).

such arctic species as the ground beetle *Pterostichus costatus*, the leaf beetles *Chrysolina tolli* and *Ch. subsulcata*, and the willow weevil *Isochnus arcticus*, are often found in one fossil assemblage with such steppe leaf beetles as *Chrysolina perforata,* and the weevils *Stephanocleonus eruditus, S. fossulatus,* and *S. incertus,* which now live in southern Siberian and Mongolian steppe. On the other hand, these assemblages sometimes include a few species of insects whose current distribution is restricted mostly to the taiga zone, such as the boreal ant species *Camponotus herculeanus* and *Formica gagatoides*, the weevils *Hylobius piceus* and *Pissodes irroratus*, and others.

Table 4 lists the most common species of late Pleistocene beetles found in more than 40% of all late Pleistocene (LP) assemblages and, additionally, a few less abundant, but rather indicative species. **Figure 20** shows the fossils of some beetle species found in the LP sediments in Northeastern Siberia.

Non-analog assemblages. What is tundra-steppe? The fossil insect assemblages of the kind discussed above have no modern analog. They resemble non-analog Pleistocene mammal communities, in which, for example, saiga antelope, a modern inhabitant of dry steppe and semi-desert, existed together with arctic fox and musk ox. It has been shown that such assemblages are not a random mixture of fossils, but a natural combination of species related to a peculiar type of Pleistocene environment (Vangengeim, 1977; Sher, 1988, 1990). In Russia, this environment and associated plant and animal communities are traditionally called 'tundra-steppe' after Tugarinov (1929). In Europe, tundra-steppe communities were related mostly to the periglacial zone south of the ice sheets, but in Siberia, under a more continental climate, they were distributed much more widely and existed more permanently (Vangengeim and Ravsky, 1965). Kiselyov (1981) has shown that insect assemblages of the tundra-steppe type were very common in northeastern Siberia during the Pleistocene. Moreover, he demonstrated that such insect communities developed in Siberia as early as the late Pliocene. Steppe elements were especially abundant in tundra faunas during relatively cold (glacial) periods, but they survived even during warmer (interglacial) times (Kiselyov, 1981, 1994). The significant destruction of tundra-steppe communities occurred only at the Pleistocene-Holocene boundary, when the dry Pleistocene grassland mostly disappeared, giving way to wet tundra and bogs. This brought about the extinction of the most remarkable large mammalian herbivores, such as mammoth and woolly rhino, and the dramatic shrinkage of ranges of others, including horses, bison, and saiga antelope. However, the plant communities of the tundra-steppe type persisted in relatively small relic habitats (Yurtsev, 1981). The ranges of steppe insects also shrank, but many of them survived in relic steppe habitats. Such habitats are widespread in the inner mountains of northeastern Siberia that have an extremely continental climate. Many thermophilic steppe species found refugia there on south-facing slopes (Berman, et al., 2001). Less thermophilic steppe beetles were able to survive in the warmest localities in the Arctic, these habitats being especially abundant on Wrangel Island (Berman, 1986; Khruleva, 2004). The persistence of these beetle species – relics of the Pleistocene tundra-steppe – is one of the most remarkable features of the present insect fauna of northeastern Siberia.

Comparison of Insect Assemblages of Different Ages using Ecological Grouping

The high frequency of occurrence of a restricted number of species in fossil assemblages (**Table 4**), and the permanent presence of insects associated with tundra, steppe and other xerophilic habitats makes the species composition of various assemblages from the Pleistocene of northeastern Siberia rather monotonous. They differ from each other mostly in the relative abundance of fossils of certain taxa. That is why Kiselyov (Sher *et al.,* 1979; Kiselyov, 1981) used a quantitative approach to trace faunal and environmental changes through time. He classified all species into a number of ecological groups according to their preferred modern habitat, then he counted the total number of individuals belonging to all species in each group. It was much easier to compare assemblages from different horizons or even sites by the percentage of ecological groups. We use the same method with minor variations (**Table 5**).

For large sections with many insect samples, we use percentage diagrams for better presentation. Recently, we suggested the establishment of Insect Faunal Zones in such sections, based on the ecological structure of assemblages. This zonation scheme is similar in some ways to pollen zones (Sher *et al.*, 2005). In **Figure 21** you can see how the composition of insect assemblages changed in the Lena Delta during the last 50 ka (this sequence will be considered in more detail below).

The Late Pleistocene Beetle Faunas of Certain Periods and Areas

Below we describe the most important Late Pleistocene beetle assemblages, starting with the

Table 4 Characteristics of the most common and some indicative beetle species in the Late Pleistocene assemblages in Northeastern Siberia

Family and species	*% of all LP assemblages, where the species is found*	*Description*	*Taxonomic notes*
Ground beetles, Carabidae			
Pterostichus (Cryobius) spp.	78	Most *Cryobius* are common in modern tundra and northern taiga and prefer boggy and wet habitats. *P. (C.) nigripalpis* Popp. is abundant today on Wrangel Island on dry patches with xeropilic vegetation (O. Khruleva, personal comm.).	Of numerous species in this subgenus we can identify fossils of *P. (C.) ventricosus* Esch., *P. (C.) pinguedineus* Esch., *P. (C.) brevicornis* (Kirby) and probably *P. (C.) nigripalpis* Popp.
Curtonotus alpinus (Payk)	92	Very widespread species from taiga to arctic tundra; prefers relatively dry and warm patches; feed on grasses. Hardly distinguishable fossils of a close species, *C. bokori*, can be present in some assemblages, but *C. alpinus* is much more common.	In Europe and America this species is usually called *Amara alpina* Payk. In Russia, the subgenus *Curtonotus*, to which this species belongs, was raised to the generic level (Kryzhanovsky 1965, Kryzhanovsky *et al*, 1995).
Poecilus (Derus) nearcticus Lth.	49	Modern specimens of *P. nearcticus* were collected on dry sandy slopes at a few sites in the Siberian Arctic and Alaska. In the Pleistocene, it was much more common, though not very abundant. It is a typical relict of the tundra-steppe beetle complex.	
Pterostichus (Tundraphilus) sublaevis Sahlb.	35	This beetle lives now in tundra and prefers dry and warm habitats, but it is relatively rare. It was more widespread and abundant during the Pleistocene.	
Small carrion and round fungus beetles, Leiodidae			
Cholevinus sibiricus (Jean.)	47	This is a rare species in modern tundra, preferring wet habitats. It is probably necro-, copro-, or/and detritophagous. *Ch. sibiricus* was more important in the Pleistocene tundra-steppe communities (Perkovsky, Kuzmina, 2001). Despite rather large populations of grazing mammals in tundra-steppe ecosystem, the revealed diversity of necro- and coprophagous beetles is very low. *Ch. sibiricus* might use this kind of food resources.	Prior to 1999, this species was called *Cryocatops poppiusi* Jean., family Catopidae (Perkovsky, 1999)
Rove beetles, Staphylinidae			
Tachinus arcticus Motsch. and *T. brevipennis* Sahlb.	45	Both species live in wet tundra habitats, but *T. arcticus* is more abundant in the north, while *T. brevipennis* – in the south of the zone, and is probably more thermophilic.	Earlier these fossils were referred to *T. apterus* Maekl (Kiselyov, 1981). Later, the identification was changed to *T. arcticus*. Now we suspect that it can be a mixture of fossils of two different species.

(*Continued*)

Table 4 (*Continued*)

Family and species	*% of all LP assemblages, where the species is found*	*Description*	*Taxonomic notes*
Dung beetles, Scarabaeidae			
Aphodius sp.	44	This dung beetle occurs in many Pleistocene sites and is clearly associated with tundra-steppe assemblages. Its well-preserved fossils have been found in buried ground squirrel nests.	Probably an extinct species
Pill beetles, Byrrhidae			
Morychus viridis Kuzm. et Kor.	86	This beetle is a real symbol of the Pleistocene biota in Northeastern Siberia. Found in the majority of fossil assemblages, often in very high numbers, it is clearly associated with thermophilic steppe. At present, it lives in cold steppe-like habitats in the Kolyma Highlands, Chukotka, and Wrangel Island, called 'hemicryophytic steppe' after Yurtsev (1981). Modern habitats of *M. viridis* have extremely contrasting microclimatic conditions – very hot and dry in summer, and snowless and very cold in winter (Berman *et al*., 2001).	Before this species was described (Kuzmina and Korotyaev, 1987), its fossils were referred to *Chrysobyrrhulus rutilans* Motsh. (Medvedev, Voronova, 1977; Kiselyov 1981).
Leaf beetles, Chrysomelidae			
Chrysolina tolli Jac.	25	This is one of the most cold-resistant species of beetles in the world. *Ch. tolli* was found in polar desert on Novaya Zemlya, Severnaya Zemlya and Novosibirsk Islands. In the tundra zone, it occupies different habitats, and feeds on Crucifera. *Ch. tolli* is found in many Pleistocene assemblages, though in low numbers, and is most common in northern sites.	The fossils were referred to *Ch cavigera* Sahlb. until the recent revision by Bienkowski (1999), who showed that the modern arctic populations belong to *Ch. tolli*, while *Ch cavigera* is restricted to the Kamchatka Peninsula and the Okhotsk Sea coast
Weevils, Curculionidae			
Sitona borealis Kor.	46	This weevil feeds on legumes. Currently it lives mostly in meadow-steppe habitats in the taiga zone, but it also occurs on dry warm patches in tundra. It was more common in the Pleistocene than it is now.	Formerly named as *S. ovipennis* Hochh. (Kiselyov, 1981), then *S. ovipennis borealis* Kor., this weevil is now considered as a separate species *S. borealis* Kor. (Korotyaev, 1996).
Stephanocleonus eruditus Faust	45	The main modern range of this weevil is Southern Siberia and Mongolia (mountain steppe). It is the most common steppe element in the Pleistocene assemblages. Having been very widely distributed in the Pleistocene, it survived in scattered relic steppe communities in the Kolyma-Indigirka Highlands (Berman *et al*., 2001). This species is a good indicator of relatively high summer temperature (Berman and Alfimov, 1993).	

(*Continued*)

Table 4 (*Continued*)

Family and species	*% of all LP assemblages, where the species is found*	*Description*	*Taxonomic notes*
Lepyrus nordenskioeldi Faust	46	This weevil lives on willow, rarely on birch, and is common in tundra, taiga and relic steppe modern environments, but prefers drier habitats with sandy soil. Thus, being very often a single representative of shrub insect group in the Pleistocene assemblages, *L. nordenskjoeldi* can be considered as an indicator of relatively dry environment, although we count this species among the forest-tundra species.	
Hypera ornata (Cap.)	48	The distribution and ecology of this weevil *are* similar to those of *Sitona borealis* (see above).	Former name *Phytonomus ornatus* Cap.
Isochnus arcticus (Kor.)	44	This species lives on willows, but its distribution is restricted to the typical tundra subzone. It is most abundant on Wrangel Island, but was also found on the Taimyr Peninsula, in western Chukotka and northern Alaska. It can be found in the Pleistocene assemblages of different age in small numbers, but became the dominant species during the Last Glacial Maximum at some (mostly northern) sites.	Former name *Rhynchaeus arcticus* Kor.

Sources

Alfimov, A.V., Berman, D.I., Sher, A.V., 2003. Tundra-steppe insect assemblages and reconstruction of Late Pleistocene climate in the lower reaches of the Kolyma River. Zoologicheskiy Zhurnal, 82, 2, 281–300 (In Rissian).

Berman, D.I., Alfimov, A.V., 1993. Microclimatic conditions of existence of steppe ecosystems in the Subarctic of north-east Asia. Bulletin of Moscow Society of Naturalists, Biology Section 98 (3) (In Rissian).

Bienkowski, A.O. 1999. A review of the species of the subgenus Chrysolina (Pleurosticha) Motschulsky (Insecta: Coleoptera, Chrysomelidae). Ent. Abhandl., 58, 10, p. 165–179.

Korotyaev, B.A. 1996. 165. Sitona Germ. In: Egorov, A.B., Zherichin, V.V., and Korotyaev, B.A. Sem. Curculionidae - Dolgonosiki. Key to the insects of the Russian Far East, Vol. 3, Coleoptera, Pt. 3, Supplement. Vladivostok, Dal'nauka: 499–503. (In Russian).

Kryzhanovsky, O.L., 1965. Fam. Carabidae – ground beetles. Guide book to the identification of the insects of European part of USSR. V.2. Moscow-Leningrad, Nauka, p. 29–77. (In Russian).

Kryzhanovsky, O.L., Belousov, I.A., Kabak, I.I., Kataev, B.M., Makarov, K.V., Shilenkov, V.G. 1995. A checklist of the ground-beetles of Russia and adjacent lands (Insecta, Coleoptera, Carabidae). Sofia - Moscow: Pensoft Publishers. 272 p.

Kuzmina, S.A., Korotyaev, B.A. (1987). New species of the pill beetle genus Morychus Er. (Coleoptera, Byrrhidae) from the North-East of the USSR. Entomol. Review, v. 66,N 2, p. 342–344 (in Russian).

Perkovsky, E.E. 1999. Species of Cholevinus (Coleoptera, Leiodidae, Cholevini) from North of Eastern Siberia and Chukotka. Vestnik zoologii, 33, 3, p. 66 (in Russian).

Perkovsky, E.E., Kuzmina, S.A. (2001). Beetles of the genus Cholevinus (Coleoptera, Leiodidae, Cholevinae) from the Nord-West of Asia from the Pleistocene to today. Vestnik Zoologii, pp. 31–38. (in Russian).

youngest, because they are the most reliably dated (**Table 3**).

Late Weichselian insect assemblages The fossil insect assemblages dated from about 24 to 12 ka were first studied in the Kolyma Lowland, which later proved to be almost the centre of continentality and formation of steppe habitats in the whole of Northern Asia during the Pleistocene. The most interesting of these sites is Alyoshkina Zaimka on the lower course of the Kolyma River (**Fig. 7**, No. 7, **Table 3**). This site yielded four rich insect faunas within the range of 17 to 13 ka (all dates in this article are uncalibrated radiocarbon ages), almost completely (up to 80–95%) dominated by thermophilic xerophiles, including true steppe species (10–20% of the whole assemblage), with a very

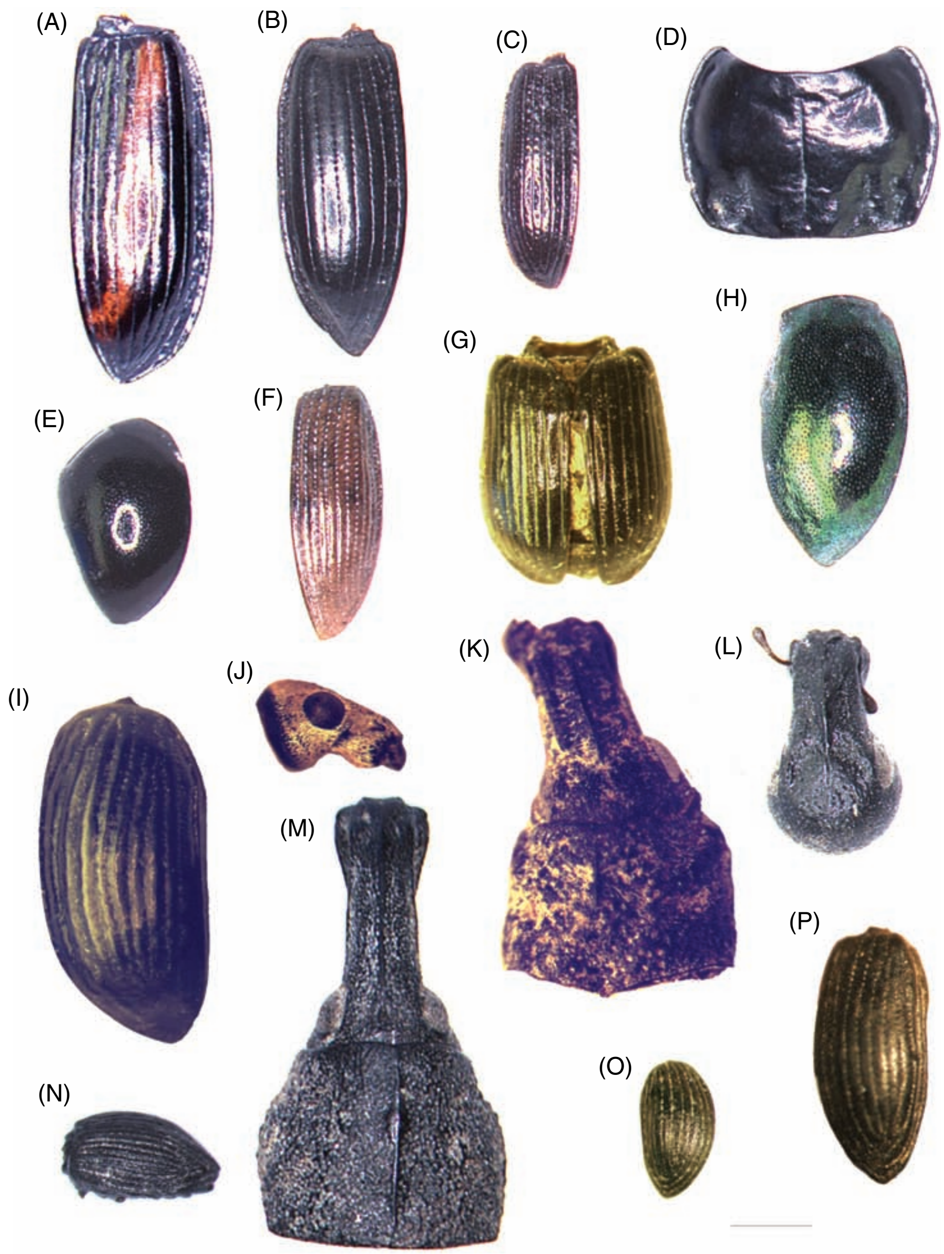

Figure 20 Late Pleistocene fossil beetles from Western Beringia: A – *Harpalus vittatus kiselevi* Kat. et Shil., right elytron; B – *Amara glacialis* Mnnh. – left elytron; C – *Dicheirotrichus mannerheimi* Sahlb., left elytron; D – *Pterostichus agonus* Horn., pronotum; E – *Cyrtoplastus irregularis* Rtt., right elytron; F – *Helophorus splendidus* Sahlb.right elytron; G – *Aphodius sp.*, body without head and pronotum; H – *Morychus viridis* Kuzm. et Kor., left elytron; I – *Chrysolina tolli* Jac., left elytron; J – *Sitona borealis* Kor., head; K – *Coniocleonus cinerascens* Hochh., head and pronotum; L – *Stephanocleonus eruditus* Faust, head; M – *Lepyrus nordenskioeldi* Faust, head and pronotum; N – *Isochnus arcticus* Kor., body without head and pronotum; O – *Mesotrichapion wrangelianum* Kor., left elytron; P – *Hypera diversipunctata* Schrank., right elytron. A–F, H–L, N – Lena Delta region; M, O, P – Chukotka. Light microscope photographs, scale bar equals 1 mm.

low percentage of tundra beetles (Kiselyov, 1981). The assemblages show high diversity and abundance of steppe and meadow steppe species (**Table 6**). Either meadow steppe beetles, or a pill beetle *Morychus viridis* dominate all samples. These faunas represent the most 'steppic' dominated type of non-analog tundra-steppe assemblages.

Scattered similar assemblages of the same age are known elsewhere, but mostly within the Kolyma Lowland. For example, they are found in the Omolon-I section on the Kolyma River (**Fig. 7**, No 13, **Fig. 15**, **Table 3**), Assemblages with more than 40% of meadow-steppe and steppe species are present here in the interval between 7.0 and 12 m depth

Table 5 Ecological groups of insects, used for quantitative comparison of fossil assemblages

Ecological group and symbol	*Group description*	*Main species*
Steppe (**st**)	The members of this group live today in the steppe zone, some in the mountain belt of southern Siberia and Mongolia. Some of them survive under special microclimatic conditions in the relic steppe patches in NE Asia. However, the presence of any of these species can be considered evidence of unusually high summer temperatures (Berman *et al*., 2001).	Ground beetles *Harpalus pusillus* Motsch., *Cymindis arctica* Kryzh. et Em., leaf beetles *Chrysolina perforata* Gebl., *Ch. brunnicornis bermani* Medv., *Galeruca interrupta circumdata* Duft. weevils *Stephanocleonus eruditus* Faust, *S. fossulatus* F-W. *S. incertus* T-M.
Meadow-steppe (**ms**)	This group consists of species common in dry (steppe-like) meadows in various ecosystems. They are more cold-tolerant than the previous group. They survive today even in the tundra zone, on the warmest localities.	Ground beetles *Harpalus vittatus kiselevi* Kat. et Shil, soft-winged beetle *Troglocollops arcticus* L. Medv., the leaf beetle *Chrysolina arctica* Medv., weevils *Phyllobius kolymensis* Kor. et Egorov, *Coniocleonus cinerascens* Hochh., *C. ferrugineus* Fahr., *C. astragali* T.-M.et Kor.
Insects of hemicryophytic steppe (**ss**)	Hemicryophytic steppe (Yurtsev, 1981) is a cold steppe-like environment, dominated by a few species of xerophilic sedges and mosses. It has extremely contrasting microclimatic conditions – very hot and dry in summer, and snowless and very cold in winter. It occurs on very dry, snowless hill tops in the taiga or, rarely in tundra zone; (Berman *et al*., 2001). This environment is currently found in the Kolyma Highlands, Chukotka, and Wrangel Island. It is believed to have many features in common with some kinds of Pleistocene tundra-steppe.	Pill beetle *Morychus viridis* Kuzm. et Kor. is the only represenatative of this group
Xerophilic insects of various habitats (**ks**)	Insects of xerophilic habitats of tundra, taiga and steppe.	Ground beetle *Notiophilus aquaticus* L., dung beetle *Aphodius* sp
Insects of dry tundra habitats (**dt**),	The insects of this group usually occupy the warmest sites in the tundra zone, most commonly well-drained sites with diverse grasses and herbs. Most of them do not reach the Arctic tundra today, but they quite often occupy parts of the taiga zone, in suitable biotopes. Some species can also be found today on relict steppe patches.	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., leaf beetle *Chrysolina marginata borealis* Medv., weevils *Mesotrichapion wrangelianum* Kor., *Hemitrichapion tschernovi* T.-M., *Sitona borealis* Kor., *Hypera ornata* Cap., *H. diversipunctata* Schrank., *Vitavitus thulius* Kiss.
Insects of typical and arctic tundra (**tt**)	Most cold-resistant species from different habitats in the Arctic	Leaf beetles *Chrysolina tolli* Jac., *Ch. subsulcata* Mnnh., *Ch. bungei* Jac., weevil *Isochnus arcticus* Kor.
Insects of mesic tundra habitats (**mt**)	The insects of this group are now found in different, mostly wet and relatively cold habitats in tundra; some occur on boggy patches in forest-tundra.	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.), rove beetles *Olophrum consimile* Gyll., *Tachinus arcticus* Motsch., *T. brevipennis* Sahlb., leaf beetle *Chrysolina septentrionalis* Men.
Shrub (**sh**)	These beetles feed on shrubs, mostly willows, except dwarf shrubs of typical and Arctic tundra	Leaf beetles *Chrysomela blaisdelli* Van Dyke, *Phratora polaris* Schn., *Ph. vulgatissima* L., weevils *Lepyrus nordenskioeldi* Faust, *L. gemellus* Kirby, *Dorytomus rufulus amplipennis* Tourn., *Isochnus flagellum* Erics.

(*Continued*)

Table 5 (*Continued*)

Ecological group and symbol	*Group description*	*Main species*
Meadows (**me**),	Mostly in the forest zone, although some species can occur on tundra meadows	Pill beetles *Byrrhus fasciatus* Forst., *Cytilus sericeus* Forst., click beetle *Hypnoidus hyperboreus* Gyll., leaf beetles *Bromius obscurus* L., *Phaedon concinnus* Steph., *Ph. armoraciae* L., weevils *Phyllobius virideaeris* Laich., *Sitona lineellus* Bonsd.
Taiga (**ta**),	Tree-associated insects and insects whose range is restricted to the taiga zone.	Ground beetle *Pterostichus (Petrophilus) magus* Man., click beetle *Denticollis varians* Germ., weevils *Hylobius piceus* DeG., *Pissodes insignatus* Boh., *P. irroratus* Reitt., bark beetles *Ips cembrae* Heer, *Polygraphus* sp., ants *Leptothorax acervorum* Fabr., *Formica gagatoides* Ruzs., *Camponotus herculeanus* L.
Riparian (**ri**),	These insects live near water in several zones, but most of them are restricted to the taiga zone.	Ground beetles *Pelophila borealis* Payk., *Nebria frigida* Sahlb., *Elaphrus lapponicus* Gyll., *E. riparius* L., *Dyschiriodes nigricornis* Motsch., *Bembidion umiatense* Lindrt., *Agonum quinquepunctatum* Motsch., rove beetles *Stenus sp.*, lady-bird *Hippodamia arctica* Schneid., leaf beetles *Donacia sp., Hydrothassa hannoverana* F., weevils *Phytobius leucogaster* Marsh., *Tournotaris bimaculatus* F., bugs of Saldidae family.
Aquatic (**aq**),	These insects live in various tundra and taiga water bodies, mostly small ponds.	Predaceous diving beetles *Hydroporus acutangulus* Thoms., *Agabus moestus* (Curt.), *Colymbetes dolabratus* (Payk.), whirligig beetle *Gyrinus opacus* Salb. water scavenger beetles *Helophorus splendidus* Sahlb., *Hydrobius fuscipes* F., water bug *Sigara* sp.
Others (**oth**).	Insects of intrazonal habitats (such as plant litter, or fungi) and fossils unresolved to a species (of genera with ecologically various members)	Small carrion beetle *Crytoplastus irregularis* R++., carrion beetle *Thanatophilus dispar* Hbst., rove beetles *Eucnecosum* sp., *Lathrobium* sp., *Quedius* sp., lady-bird *Coccinella* sp., minute brown savenger beetle *Corticaria* sp.

(ca. 23–18 ka) (Kiselyov *et al.*, 1987). Tundra-steppe assemblages with extremely high numbers of *M. viridis* (**Table 7**), but less diverse and abundant steppe species occur below and above this interval.

The *M. viridis*-dominated late Weichselian assemblages were distributed much more widely than just in the Kolyma Lowland. They are also known from the Yedoma sections in the Indigirka and Khroma valleys (**Table 3**), and much further north, in sites from the Lena Delta. In the Mamontovy Khayata (MKh) section (**Fig. 7**, No 3) they form a series of samples associated with the termination of the late Weichselian (IFZ 4) and dated about 14 to 12 ^{14}C ka (**Fig. 21**). *M. viridis* exclusively dominates four samples (50–60%). In the Lena Delta, these samples represent the highest content of *Morychus*, steppe and other xerophilic species during the whole Weichselian, so this stage has been recognized as the Late Glacial Event (LGE), a brief interval of higher summer temperatures and drier environments in this Arctic region (Sher *et al.*, 2005).

The LGM insect assemblages in the Lena Delta are strikingly different from those in the Kolyma Lowland. In the MKh section they are recognized as IFZ 3 (**Fig. 21**). Of nine samples within the range of 24 to 14 ka, six are strongly dominated by Arctic tundra insects (40–67%), mainly *Isochnus arcticus*. Xerophilic insects constitute only 1.5 to 3%, with a maximum of 5% of the fauna – the lowest values in the whole Weichselian. Even the ubiquitous *M. viridis* was encountered in only 4 of 9 samples (below 2%). True steppe insects were totally absent between ca. 23 and 20 ka and comprised just 1 to 3% of the faunas in the other samples. These peculiar assemblages (Arctic type of tundra-steppe) are interpreted as evidence of a very cold climate with dry summers (Sher *et al.*, 2005). This reconstruction is corroborated by the plant macrofossil assemblages from the same sites (Kienast *et al.*, 2005).

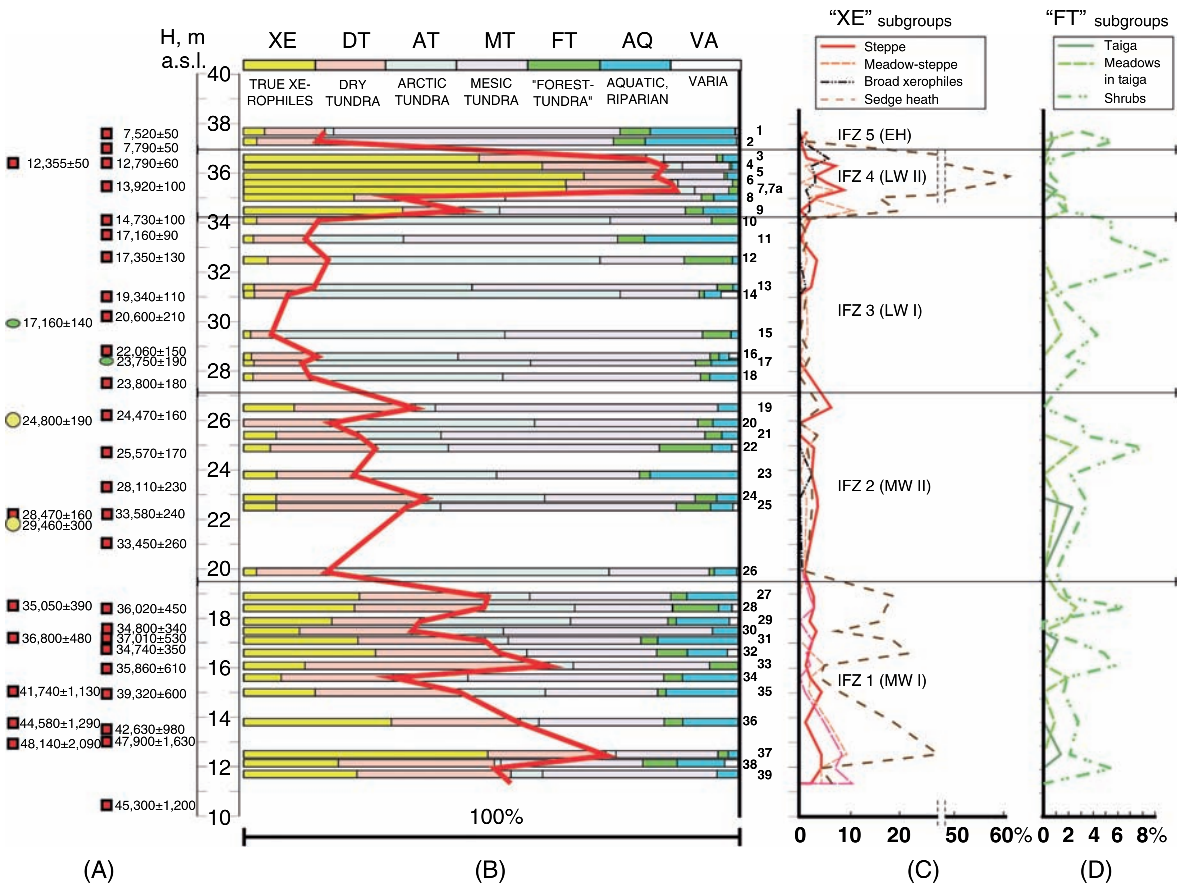

Figure 21 The sequence of fossil beetle assemblages in the Mamontovy Khayata key section, Bykovsky Peninsula, Lena Delta, ranging in age from greater than 50 ka to 8 ka (from Sher et al., 2005).

A similar assemblage is known from the Buor-Khaya exposure on the Central Lena Delta (from the upper part of the Ice Complex), where it is dated about 17 ka (Kuzmina, 2001). Outside the Lena Delta, the Arctic-type tundra-steppe fauna was found in a single, poor sample from the late Weichselian Ice Complex in the northern Yana-Indigirka Lowland (Volchya River, 71.7° N).

Thus, during the LGM, tundra-steppe insect faunas of the Arctic type existed only in the northernmost parts of the continent. Further south, they included increasingly thermoxerophilic and steppe elements. For example, at the Krasivoye site on the Malyy Anyuy River (68.3° N) (**Fig.** 7, No 15, **Table** 3), the Ice Complex assemblage dated about 19 ka was dominated by dry tundra (29%) and xerophilic beetles (53%), with sedge steppe, meadow steppe and true steppe components each comprising over 15%. Assemblages with an even more pronounced xerophilic component are common in sections (or their members) that are tentatively referred to the late Weichselian, all over northeastern Siberia. Many exposures in the Kolyma Lowland have yielded faunas with 65 to 90% xerophiles (alternatively dominated by sedge steppe or meadow steppe beetles) in the upper part of the Ice Complex (Duvanny Yar, Lakes Yakutskoye and others (**Fig.** 7, No 8, **Fig.** 9, **Table** 3). In the Indigirka Lowland, the late Weichselian (LW) sites on the Khroma, Indigirka (Suturuokha), and Keremesit Rivers are also dominated by xerophiles (60–80%), with *Morychus viridis* dominating the whole spectrum (30–60%). Similar kinds of insect assemblages (with xerophiles forming 50 to 95% of the whole spectrum) have been described from the upper part of the Ice Complex of Ayon Island (Utatgyr Suite, Northwestern Chukotka, ca. 69.5° N (**Fig.** 7, No 10, **Table** 3), but here they have an even stronger contribution of meadow-steppe or/and true steppe species (30–90%). In contrast to this, at the eastern edge of Asia, closer to the Pacific, the steppe component in the LGM faunas is much less pronounced, or absent altogether. In southern Chukotka, for example (the Ice Bluff section on the Main River, **Fig.** 7, No 12, **Table** 3), throughout the

Table 6 Occurrence of xerophilic beetles in the Alyoshkina Zaimka Late Weichselian sequence of samples

Family	*TAXON*	*Eco Code*	*% in the sample*	
			MIN	*MAX*
Carabidae	Curtonotus fodinae Mnnh.	st	0.1	1.7
Carabidae	*Harpalus amputatus amputatoides* Mlynar	ms	0.4	1.4
Carabidae	Harpalus vittatus kiselevi Kat. et Shil.	ms	0.4	3.9
Carabidae	Harpalus pusillus Motsch.	st	0.73	0.73
Carabidae	Cymindis arctica Kryzh. et Em.	st	0.7	3.9
Silphidae	Aclypea cf. jacutica (Rjab.)	ms	0.24	0.24
Scarabaeidae	Aphodius sp. nov. ?	ks	0.98	8.92
Byrrhidae	Morychus viridis Kuzm. et Kor.	ss	7.51	64.0
Melyridae	Troglocollops cf. arcticus L.Medv.	ms	0.7	5.9
Chrysomelidae	Chrysolina aurichalcea Mnnh.	ms	2.44	2.44
Chrysomelidae	Chrysolina perforata Gebl.	st	0.65	0.85
Chrysomelidae	Chrysolina aeruginosa Fald.	st	0.48	0.65
Chrysomelidae	Chrysolina brunnicornis bermani Medv.	st	1.45	4.89
Chrysomelidae	Chrysolina rufilabris Fald.	st	0.47	3.91
Chrysomelidae	Colaphellus alpinus Gebl.	ms	0.24	0.24
Chrysomelidae	Galeruca daurica Jeann.	st	0.49	0.49
Apionidae	*Loborhynchapion* cf. *amethystinum* Miller	ms	0.5	29.6
Curculionidae	*Phyllobius* cf. *kolymensis* Kor. et. Egorov	ms	5.1	29.1
Curculionidae	Phyllobius (Angarophyllobius) sp.	ms	0.72	0.72
Curculionidae	Coniocleonus cinerascens Hochh.	ms	0.97	0.97
Curculionidae	Coniocleonus ferrugineus Fahr.	ms	0.12	0.98
Curculionidae	Coniocleonus astragali T.-M. et Kor.	ms	0.22	0.22
Curculionidae	Stephanocleonus eruditus Faust	st	0.43	4.16
Curculionidae	Stephanocleonus fossulatus F.-W.	st	0.65	1.22
Curculionidae	Stephanocleonus foveifrons Chevr.	st	2.42	13.9
Curculionidae	Stephanocleonus cf. anceps Chevr.	st	0.22	0.22

Table 7 Change of percentage of xerophilic insects along the late Weichselian section Omolon-I

Estimated age, years BP	*Steppe species (st)*	*Morychus viridis (ss)*	*Meadow-steppe species (ms)*
15,000	6.44	77.65	8.14
17,000	5.49	83.65	3.64
19,000	16.13	41.40	26.88
21,000	1.73	49.14	41.29
23,000	4.29	39.64	41.79
24,000	11.45	76.72	5.34

interval from 25 to 15 ka, all groups of xerophilic insects rarely reach 30% (usually below 10%) and are mostly represented by *Morychus viridis*. On the other hand, arctic beetles are abundant in assemblages dated around 21 ka (up to 40%). This is probably indicative of a milder (Pacific) version of the cold-adapted (Arctic type) LGM faunas.

Middle Weichselian insect assemblages The middle Weichselian interval (from about 50 to 25 ka) was traditionally considered as a 'warmer climate interstadial' interval in Northern Asia (called 'Karginsky'), including several cycles of cooling (Kind, 1974). In many natural sections, where organic-rich deposits (usually peat) occurred under the Ice Complex, or inside it, or separating two 'Ice Complexes' (two members with their own system of polygonal ice wedges), these peats have been ^{14}C dated to 35 to 40 ka. The pollen spectra of these layers usually show a high percentage of arboreal (mostly shrub) pollen, in contrast to the completely grass-herb dominated spectra of the Ice Complex itself. In recent years, however, several important new discoveries have been made about this interval. First, repeated ^{14}C dating showed that most of the samples that yielded ^{14}C ages near 35 ka and older, were indeed much older and could actually represent ages beyond the ^{14}C age range (Sher and Plakht, 1988). Second, it was shown that the 'Karginsky' sections in the type area (Lower Yenissey) had been misinterpreted, and their dating was erroneous. In fact, they turned out to be much older, probably as old as the last interglacial (Astakhov, 2001). Third, new radiocarbon ages from the regional type sections of the 'Karginsky Interstadial' in northeastern Siberia also yielded much older dates (Sulerzhitsky, 1998). Finally, the multidisciplinary study of a continuous section through most of the late Weichselian in the Lena Delta, well-dated by ^{14}C, revealed a completely different regional history of this period (Andreev *et al*., 2002; Schirrmeister *et al*., 2002). The study of the detailed record of fossil insect assemblages through this sequence allowed us (Sher *et al*., 2005) to suggest a very different reconstruction of middle Weichselian environments.

It has been shown that tundra-type insect assemblages persisted in the Lena Delta throughout the middle Weichselian interval, with a variable, but almost consistent presence of xerophilic species. Although today the northern limit of taiga (sparse larch forest) is not far south of the site, no fossil assemblages of the forest or even forest-tundra type have ever been found here. The contribution of xerophilic species was more noticeable in the first half of the middle Weichselian interval, especially in the assemblages ^{14}C dated about 45 to 48 ka, when they reached 30 to 50%. We cannot exclude the possibility, however, that these assemblages are actually early Weichselian in age. Taken together with the dry tundra species contribution, the percentage of relatively thermophilic forms gradually decreased from 48 to 34 ka (Insect Faunal Zone 1, **Fig. 21**). At the same time, the contribution of arctic species increased, and by 34 ka it almost reached LGM levels (more than 50%). The second half of the middle Weichselian (34–24 ka, IFZ 2 on **Fig. 21**) is marked by the lowest levels of xerophilic species (usually below 7%) and the predominance of mesic tundra insects, sometimes with a high contribution of arctic species. This sequence, the most complete in Northern Asia, is interpreted as a gradual decrease in summer temperatures towards the LGM, probably accompanied by some increased moisture. However, these moisture levels did not reach the levels observed in modern tundra environments. This indicates that during the middle Weichselian the climate was more continental than today in this coastal area. This conclusion is in agreement with various observations that sea level in the Eastern Arctic remained low at that time.

Several sites in more southern areas of northeastern Siberia yielded representative insect assemblages obtained from the Ice Complex and associated with late middle Weichselian ^{14}C dates. For example, in the Shamanovo Yedoma section on the Indigirka River (**Fig. 7**, No 16, **Table 3**) a rich insect sample came from the unit dated by *in situ* grass roots at 29,300 to 32,900 yr BP (Kaplina et al., 1980). The assemblage is dominated by *M. viridis* and other xerophilic insects (66%) and dry habitat species prevail in the tundra group (Kiselyov, 1994). On the Khroma River (**Fig. 7**, No 17, **Table 3**), the assemblage dated 28,800 yr BP (Kaplina et al., 1983) has the same percentage of xerophilic species, but *M. viridis* is much more abundant, while the contribution of steppe species is low.

Interesting assemblages, presumably associated with the middle Weichselian, were found in the Primorsky alas section in western Chukotka (**Fig. 7**, No 18, **Table 3**). The sampled unit contains tree birch wood, and is dated more than 27,870 yr BP (Kiselyov, 1994). The assemblages (**Table 7**) include unusually high percentages of forest-tundra species (7%), comprising such forest inhabitants as the rove beetles *Acidota* sp., *Arpedium* sp., *Xantholinus* sp., *Anthobium* sp., and *Bolitobius* sp., as well as the birch-associated weevil *Betulapion simile*. On the other hand, these assemblages contain high percentages of *M. viridis* and a few true steppe beetles. A peat layer from about 12 m higher in the section is dated at $24,800 \pm 400$ yr BP. Two insect assemblages from this unit are similar to the lower ones, but show even higher percentages of forest-tundra beetles (up to 12%) represented by the same species. The steppe, meadow-steppe beetles and *M. viridis* are still present, although in lower numbers.

However, in southern Chukotka, insect assemblages from the same age interval (34–24 ka) (Ice Bluff locality, **Fig. 7**, No 12, **Fig. 17**, **Table 3**) do not contain any forest beetles (Kiselyov, 1994). The percentage of xerophilic species is high (38%), mostly at the expense of dung beetles (*Aphodius* sp. nov. ?) and *M. viridis*. True steppe and meadow-steppe species are represented only by single specimens.

Early Weichselian insect assemblages Taking into account the dating problems, it is difficult to confidently assign any fossil insect assemblage to the early Weichselian interval. On the other hand, the lower parts of many thick Ice Complex sections may belong to this time interval. For example, in the key section of the Ice Complex of Duvannyy Yar (**Fig. 7**, No 8, **Fig. 9**, **Table 3**) a large number of infinite ^{14}C dates (>45 ka) in the lower part of the section (mixed with dates in the range of 33 to 45 ka) may suggest an early Weichselian age (Sher, 1991). The same is possible for the Oyagosskiy Yar assemblage (**Fig. 7**, No 19, **Table 3**) and the sections on the southern coast of Bol. Lyakhovsky Island. (**Fig. 7**, No 4, **Table 3**) In the Kolyma Lowland, the insect assemblages from the lower parts of Ice Complex sections are dominated by *M. viridis* with a small admixture of other xerophiles (usually below 10%) (Duvannyy Yar, Sher *et al*., 1979). However, the northern localities, such as Oyagos, Lyakhovsky, or Nagym in the Lena Delta (**Fig. 7**, No 1, **Table 3**), are mostly dominated by tundra species, sometimes with a high percentage of Arctic tundra species or mesic tundra inhabitants. The total percentage of all xerophiles is usually below

15%, and the main role in this group is played by *M. viridis*, while true steppe species are either extremely rare or completely absent (Kuzmina, 2001).

Thus, we may conclude that the same regularities in spatial distribution of insect assemblages in the late Weichselian existed during early Weichselian time.

'Last Interglacial' insect assemblages The problems of recognition of Last Interglacial sediments were discussed above (cf. also Sher, 1991). Tentatively, we refer some parts of particular complex sections to this interval. These sediments overlie sediments of presumed middle Pleistocene age and they underlie the late Pleistocene Ice Complex. Also, they contain abundant organic remains. Such localities usually represent buried alas complexes (**Table 3**). The characteristics of insect assemblages forming three of them are shown in **Table 8**.

Table 8 The insect assemblages of presumably 'Last Interglacial' age in Northeastern Siberia

Unit	*Location*	*Sediment description*	*Insect assemblages*
Kyl-Bastakh Layers	Khroma River (**Fig. 7**, No. 17).	Organic-rich filling of ice-wedge pseudomorphs (the casts of former ice wedges), intruding the top of the Khroma Suite, presumably referred to the late middle Pleistocene, and overlain by the Yedoma Suite (Ice Complex).	Three fossil assemblages are dominated by tundra species (>30%), both mesic and xeric, and the percentage of forest-tundra species is probably the highest elsewhere in the regional record (about 10%). Among the latter, such forest zone species as *Phyllobius virideaeris* Laich. (a meadow weevil) and *Carabus maeander* Fisch. (a taiga ground beetle), shrub leaf beetles *Chrysomela lapponica* L. and *Phratora polaris* Schn. are recorded. At the same time, the thermophilic xerophiles comprise 15–20% of the whole fauna, and among them are not only the 'sedge-steppe' species *Morychus viridis* Kuzm. et Kor. and the dung beetles *Aphodius* sp. nov., but true steppe insects, such as the ground beetles *Harpalus pusillus* Motsch. and *Cymindis arctica* Kryzh. et Em., a leaf beetle *Chrysolina perforata* Gebl. and a weevil *Stephanocleonus foveifrons* Chevr. Remarkably, the assemblages include a few specimens of Arctic tundra leaf beetle *Chrysolina subsulcata* Mnnh. and an arctic weevil *Isochnus arcticus* Kor. They also contain a large numbert of hydrophilic beetles, which is commonly found in peat deposits.
Kuobakh Unit	Alazeya River (**Fig. 7**, No. 5)	A peat layer and organic-rich ice-wedge pseudomorphs are observed between the late middle Pleistocene Maastakh Suite and the Yedoma Ice Complex	Similarly to the Kyl-Bastakh, the assemblages combine a high percentage of hydrophilic and tundra species with a large number (up to 33%) of forest-tundra insects. The latter include mostly the ant *Formica (Serviformica) gagatoides* Ruzs. and various meadow species from the forest zone, such as a click beetle *Hypnoidus hyperboreus* Gyll., an ant-like beetle *Anthicus ater* Pz., a leaf beetle *Phaedon concinnus* Steph., and a weevil *Phyllobius virideaeris* Laich. Xerophiles comprise up to 8–10% of the faunal assemlages, but do not include steppe species
Krest-Yuryakh Unit	Bolshoy Lyakhovsky Island (**Fig. 7**, No. 4)	Two layers of organic-rich ice-wedge pseudomorphs	The unit is in the same stratigraphic position, but the locality is much further north, so it is dominated by mesic tundra species (35–45%) and dry tundra insects (20–30%). However, the Krest-Yuryakh assemblages include both forest-tundra species (2–5%) and up to 10–20% of thermophilic xerophiles, including a few occurrences of steppe species, such as the ground beetle *Cymindis arctica* Kryzh. et Em., and the weevils *Stephanocleonus eruditus* Faust and *S. fossulatus* F.-W.

The most remarkable character of all these assemblages is the extreme heterogeneity of their ecological composition, combining representatives from practically all ecological groups. Many species comprising those assemblages do not occur together today. At present their ranges are often separated by many hundreds of kilometers. This is especially evident for the northernmost assemblages (Bolshoy Lyakhovsky Island), where about 80% of identified insect species currently live much further south. This indicates the non-analog character of the assemblage, which certainly existed in a warmer climate than today, with higher summer and probably somewhat higher winter temperatures. According to the paleobotanical data (Andreev *et al.*, 2004), summer temperatures could have been 4 to 5° C higher than present. In general, the climate was more continental than today on Lyakhovsky Island, but less so than during the Weichselian interval. Compared with the modern environment of the island, the humidity was certainly lower in summer, but probably somewhat higher in winter. A thicker snow cover would have allowed the growth of tall shrubs at this high latitude.

Summary

This review demonstrates the large scope of the Pleistocene beetle research in Northeastern Siberia during the recent years. However, many gaps remain in our knowledge and some significant problems are still unsolved. Evidently, the characterized beetle faunas are peculiar, but we have a poor idea of how far south and west they were distributed. Very few fossil assemblages are known south of the Arctic Circle in this region, and none to the west of the Lena Delta. We also have serious problems with the dating of fossil assemblages older than 30 ka. We believe that future research should be concentrated on continuous sedimentary sequences, such as the Bykovsky section, and this research must be a part of broad multidisciplinary projects. Recent experience shows that successful projects of such kinds must be based on international collaboration.

Glossary

Dendrophilic – species that live and feed on trees.
Thermophilic – species that live in relatively warm climates.
Xerophilic – species that prefer dry and relatively warm habitats, often on open ground, with or without sparse shrubs and trees.
Xylophages – species that feed on wood.

See also: **Beetle Records**: Overview. **Periglacial Landforms**: Ice Wedges and Ice Wedge Casts.

References

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

Andreev, A. A., Schirrmeister, L., Siegert, C.h, Bobrov, A. A., Demske, D., Seiffert, D., and Hubberten, H.-W. (2002). Paleoenvironmental changes in Northeastern Siberia during the Late Quaternary – evidences frompollen records of the Bykovsky Peninsula. *Polarforschung* **70**, 13–25.

Astakhov, V. (2001). The stratigraphic framework for the Upper Pleistocene of the glaciated Russian Arctic: changing paradigms. *Global and Planetary Change* **31**(1–4), 283–295.

Berman, D. I. (1986). Invertebrate fauna and population in tundrasteppe communities of Wrangel Island. In pp. 146–160 (in Russian).

Berman, D. I., Alfimov, A. V., Mazhitova, G. G., Grishkan, I. B., and Yurtsev, B. A. (2001). *Cold steppe in north-eastern Asia. – Vladivostok, Dal'nauka,* p. 183. (in Russian).

Eremin, P. K. (1990). For systematic of the ground beetles of *Cryobius* Chd. subgenus (Coleoptera, Carabidae, *Pterostichus*) from USSR fauna. In *Fauna and ecology of ground beetles. Kishinev*, pp. 18–19. (In Russian).

Grushevskiy I. I, and Medvedev, L. N. (1962). Preliminary data on the application of coleopterological analysis to the study of Quaternary deposits of Northern Yakutiya. In *Collected articles on paleontology and biostratigraphy of Scientific Research Institute of Arctic Geology* (Shvedev, Ed.), (In Russian), pp. 38–72. Scientific Research Institute of Arctic Geology, Leningrad.

Kaplina, T. N., Sher, A. V., Giterman, R. E., Zazhigin, V. S., Kiselyov, S. V., Lozhkin, A. V., and Nikitin, V. P. (1980). Key section of Pleistocene deposits on the Allaikha river (lower reaches of the Indigirka). Bulletin of the Commission on Quaternary Period Research. *USSR Academy of Sciences* **50**, 73–95, (In Russian).

Kaplina, T. N., Shilova, G., and Pirumova, L. G. (1980). Shamanovo key section of Late Pleistocene and Holocene deposits on the Indigirka. *Izvestiya Academii Nauk SSSR. Ser. Geologicheskaya* **9**, 74–171, (In Russian).

Khruleva, O. A. (2004). Tundra-steppe leaf beetle *Chrysolina brunnicornis vrangeliani* (Coleoptera, Chrysomelidae): distribution, life history and habitats. In *New developments in the biology of Chrysomelidae* (P. PJolivet, J. A. JSantiago-Blay and M. Schmitt, Eds.), pp. 541–550. SPB Academic Publishing bv, The Hague.

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

Kind, N. V. (1974). *Late Quaternary Geochronology According to Isotope Data (Geokhronologia Pozdniego Antropogena Po Izotopnym Dannym)* Moscow: Nauka. p. 255. (in Russian).

Kiselyov, S. V. (1981). *Late Cenozoic Coleoptera of North-East Siberia*. Nauka, Moscow. (In Russian).

Kiselyov SV (1994) Northern Eurasia environment in the Pleistocene and Holocene (according to Coleoptera researches). Thesis in Geology, p. 32 Moscow: MSU, (in Russian).

Kiselyov, S. V., Kolesnikov, S., and Rybakova, N. O. (1987). Climate of the vegetation period during the 'Ice Complex' deposits forming from the Omolon River Site). *Byulleten Moskovskogo obshchestva ispytatelei prirody* **62**, 113–119, (In Russian).

Kuzmina, S. A., and Korotyaev, B. A. (1987). A new species of a pill beetle Morychus Er. Coleoptera, Byrrhidae) from Northern-East of USSR. *Entomol. obozrenie* 66 **2**, 342–344, (in Russian).

Kuzmina, S. A. (2001) Quaternary Insects of the Coastal Lowlands of Yakutia. PhD (Candidate) Thesis in Biology. Paleontological Institute. Moscow: RAS. (In Russian).

Medvedev, L. N., and Voronova, N. N. (1977). Coleopterological analysis of geological sections of mammoth cemeteries in northern Yakutia. In *The mammoth fauna of the Russian Plain and Eastern Siberia* (O. Scarlato, Ed.), (In Russian), pp. 72–76. Nauka, Leningrad.

Schirrmeister, L., Siegert, C., Kuznetsova, T., Kuzmina, S., Andreev, A. A., Kienast, F., Meyer, H., and Bobrov, A. (2002). Paleoenvironmental and paleoclimatic records from permafrost deposits in the Arctic region of northern Siberia. *Quaternary International* **89**, 97–118.

Sher, A. V. (1988). Problems of ecology of Pleistocene mammals. In *Aktual'nye problemy morfologii i ekologii vysshikh pozvonochnykh*, pp. 432–464, Chast' II, Moskva: Izdatelstvo AN SSSR. (In Russian).

Sher, A. V. (1990). Actualism and disconformism in the studies of Pleistocene mammals ecology. *Journal of General Biology* **51**(2), 163–177.

Sher, A. V. (1991). Problems of the last interglacial in Arctic Siberia. *Quaternary International* **10–12**, 215–222.

Sher, A. V., Kaplina, T. N., Giterman, R. E., Lozhkin, A., Arkhangelov, A. A., Kiselyov, S. V., Kouznetsov, Yu. V., Virina, E. I., and Zazhigin, V. S., (1979) Late Cenozoic of the Kolyma Lowland: XIV Pacific Science Congress, Tour Guide XI, Khabarovsk August 1979, pp. 1–116. Academy of Sciences of the USSR: Moscow.

Sher, A. V., Kuzmina, S. A., Kuznetsova, T. V., and Sulerzhitsky, L. D. (2005). New insights into the Weichselian environment and climate of the Eastern-Siberian Artic, derived from fossil insects, plants, and mammals. *Quaternary Science Reviews* **24**533–569.

Sher, A. V., and Plakht, I. R. (1988). Radiocarbon dating and problems of the Pleistocene stratigraphy in lowlands of the Northeast USSR. Izvestiya AN SSSR, ser. Geol. 8, 17–31 (in Russian); In English. *International Geology Review* **30**(8), 853–867.

Sulerzhitsky, L. D. (1998). On the microbial contamination organic matter from permafrost observed during radiocarbon dating. *Kriosfera Zemli* (*Earth Cryosphere*) **2**(2), 76–80, (in Russian).

Svendsen, J. I., Alexanderson, H., Astakhov, V. I., Demidov, I., Dowdeswell, J. A., Funder, S., Gataullin, V., Henriksen, M., Hjort, C., Houmark-Nielsen, M., Hubberten, H. W., Ingólfsson, O., Jakobsson, M., Kjær, K. H., Larsen, E., Lokrantz, H., Lunkka, J. P., Lyså, A., Mangerud, J., Matioushkov, A., Murray, A., Möller, P., Niessen, F., Nikolskaya, O., Polyak, L., Saarnisto, M., Siegert, C., Siegert, M. J., Spielhagen, R. F., and Stein, R. (2004). Late Quaternary ice-sheet history of Northern Eurasia. *Quaternary Science Reviews* **23**, 1229–1271.

Tugarinov, A.Ya (1929). On the origin of arctic fauna. *Priroda* **7–8**, 653–680, (in Russian).

Vangengeim, E. A. (1977). *Paleontological foundation of Anthropogene stratigraphy in Northern Asia (by mammals)*, pp 1–172, Moscow: Nauka. (In Russian).

Vangengeim, E. A., and Ravsky, E. I. (1965). On the intra-continental type of natural zonality in Eurasia during the Quaternary Period (Anthropogene). In *The problems of Cenozoic stratigraphy* (V. V. Menner, Ed.), (In Russian), pp. 128–141. Nedra Publishers, Moscow.

Yurtsev, B. A. (1981). *Relict steppe vegetation complexes of Northern Asia (Problems of reconstruction of the cryoxerotic landscapes of Beringia)*. Nauka, Novosibirsk. (in Russian).

Zinoviev, E. V. (1997). Quaternary insects of West Siberian Plain. In *Successes of entomology on Ural*, pp. 153–157, Ekaterinburg. (In Russian).

Postglacial Europe

P Ponel, Mediterranean Institute for Ecology and Paleoecology, France

© 2007 Elsevier B.V. All rights reserved.

Insect analyses carried out from Holocene sequences are relatively rare in Britain and northern Europe, in contrast to late Pleistocene and Late Glacial sequences, which have been thoroughly investigated during the past 50 years. Therefore, the early to mid-Holocene history of the coleopteran fauna in western Europe relies for the most part on the analysis of scattered assemblages obtained from natural or seminatural deposits. Late Holocene studies, especially from the historical period, are much more abundant, but the vast majority of data concerning this period derive from analyses carried out in archeological sites from anthropogenic contexts and are dominated by synanthropic insects. These studies provide a wealth of data, mainly concerning the living conditions of man. However, they offer relatively restricted information on past environments. A further complication hampering the paleoenvironmental interpretation of postglacial beetle records is the growing influence of man on natural ecosystems from the mid-Holocene onwards through forest clearance, development of agriculture, pastoralism, and fragmentation of habitats. These landscape modifications make it difficult to disentangle the respective role of climate and human impact on coleopteran faunas.

Considering the wide range of subjects treated by Quaternary entomologists and archeoentomologists from postglacial beetle records, this article is necessarily focused on a selection of issues, such as changes in coleopteran faunal assemblages at the onset of the Holocene and their paleoclimate and paleoenvironmental implications, the impact of human activities on landscapes and Coleoptera (especially the effect of forest clearance on saproxylophagous species), and