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Invertebrates of the relict steppe ecosystems of Beringia, and the reconstruction of Pleistocene landscapes

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ABSTRACT

Studies of invertebrates from steppe patches in the tundra and taiga zones of Beringia provide additional evidence that these areas could be relict steppes. A number of insect species common to both modern relict steppes and fossil Beringian insect faunal assemblages have been found. These provide important information on the moisture and temperature preferences of some of the surviving members of Pleistocene steppe-tundra insect communities. The most significant species of West Beringian insects are weevils in the genus *Stephanocleonus* (Coleoptera, Curculionidae), indicators of thermophytic steppe, and the pill beetle *Morychus viridis* (Coleoptera, Byrrhidae), the indicator of hemicryophytic steppe. The East Beringian invertebrate population of relict steppe is substantially different. Fossil evidence suggests that biotic exchange between the two parts of Beringia was limited during the Pleistocene; populations of steppe insects did not move across the Bering Land Bridge (BLB), while tundra species had more flexibility. The tundra environment reconstructed for the Pleistocene BLB should have facilitated amphiberingian distributions for most tundra invertebrate species, but apparently only a few species achieved this.

1. Introduction

In the northern mountainous taiga and tundra regions of northeast Asia and northwest North America, small areas (from 1 ha to 1 km^2) of xerophytic vegetation remain. These areas are characterized by species of plants and insects that have their main range in the steppe zone. Since the first botanical description of these communities, researchers have considered them as "relict" (Sheludyakova, 1938). More recently, such azonal steppes, at least in northeast Asia, have been interpreted as refugia[1] for the steppe-tundra ecosystem of the Pleistocene and were described with detailed evidence as "relict steppes[2]" (Yurtsev, 1981). Our investigations (Berman, 1974; Berman et al., 2001a,b) show that the insect fauna of these azonal steppe sites also contains species from southern steppes; the same species have been found in fossil insect communities of West Beringia (Kiselev, 1981). These communities are a valuable source of information about the nature of ancient Beringia, rivaling the importance of the paleontological evidence. We have investigated these relict steppes, with the aim of (1) studying the invertebrate fauna of the relict steppes in northeast Asia and northwest North America to help reconstructions of Pleistocene landscapes, and (2) to recognize modern geographic trends in the distribution of relict species of the invertebrate fauna in these two regions, as a reflection of the distribution of steppe habitats in Beringia. Our study focused on beetles (Coleoptera) mostly in the families Curculionidae (weevils) and Carabidae (ground beetles).

2. Regional setting

Steppe associations, distributed on isolated areas inside taiga and tundra zones, have been discovered in the both West Beringia (Karavaev, 1958; Yurtsev, 1974a,b, 1981, 1982, 2001a,b; Korobkov, 1981; Polozova, 1983; Slinchenkova, 1984), and East Beringia (Douglas, 1974; Hoefs et al., 1975; Young, 1976; Ritchie, 1984; Yurtsev, 1984a,b; Edwards and Armbruster, 1989; Lausi and

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[1] The authors understand "refugia" as a location of an isolated population of the species what had widespread area in the past, following a classical term using (Haffer, 1969). Insect fauna of these steppes (see below) support this opinion.

[2] Here and below we use the term "relict" according to a definition: "species and associations, widespread in the past. "time intervals and survived only on restricted areas" (Makridin, Barskov, 1995, p.315)

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Nimis, 1991; Laxton et al., 1996; Vetter, 2000). These areas differ in a number of ways, including position in the landscape, microclimate, vegetation and fauna. Some authors (Karavaev, 1958; Yurtsev, 1981; Vetter, 2000; Berman et al., 2001a and others) consider these communities as "relict" on basis of their isolated position far from modern zonal steppes and the inclusion of some species that were far more widespread in the Pleistocene.

The most common azonal steppes in the studied region usually occur on steep south-facing slopes of the valleys in the upper reaches of large rivers, such as the Yana, Indigirka and Kolyma, Yukon, Tanana, and their tributaries (Pivovarova et al., 1975; Young, 1976; Yurtsev, 1981, 2001a,b; Murray, 1987; Edwards and Armbruster, 1989; Laxton et al., 1996; Vetter, 2000). In Asia, a specific kind of steppe vegetation has been recorded (Yurtsev, 1982; Berman et al., 2001a) on less warm localities. Based on plant community composition and position in relief, Yurtsev (1981, 1982) has divided these steppe communities into two main types. The first is thermophytic steppe. This steppe is characterized by grasses and other herbaceous vegetation and is situated on well drained soils with good summer warmth (the sum of positive temperatures[3] of the upper cm of the soil is not lower than 2000°). These steppes occur mostly on south-facing slopes, but in one place – the valley of the Indigirka River near the village of Tybelyakh (65.4°N) (Yurtsev, 1981), the steppe vegetation also occupies river terraces. The Indigirka steppes are the most developed in the region. This place is dry in summer (the driest in the region) and almost snowless in the winter (Yurtsev, 1981), thus providing unique conditions for steppe vegetation. The steppe patches here are quite large – up to 4 km across the river valley and up to 30 km along it.

In Asia (Yurtsev, 1981) thermophilous steppe vegetation prefers steep slopes of the high river terraces and mountains, the size of such areas is up to few dozen m in vertical relief and up to a few hundred m in horizontal extent. Forest-covered deep ravines often break up these areas. The vegetation is dominated by turf forming grasses (*Festuca kolymensis*, *F. lenensis*, *Poa botryoides*, *Helictotrichon krylovii*, *Agropyron jacutorum* (=*Elytrigia jacutorum*), sometimes *A. karawaewii*) and sagebrushes *Artemisia kruhsiana*, *A. gmelinii*, *A. lagopus*, *A. borealis* with a secondary, but sometimes significant cover of sedges (*Carex duriuscula* or *C. pediformis)*. The invertebrate fauna has its own characteristic features (see below). The small size of steppe areas and their discontinuous cover may explain why large steppe-adapted animals do not live there. Among the vertebrates are some species that live at the edges of the steppe areas: the ground squirrel *Spermophilus parryi* on the edges of steppe slopes where the vegetation is meadow-steppe and the chipmunk *Tamias sibiricus* that lives close to the surrounding forest. Mouse-like rodents are usually absent there due to the extreme aridity.

Hemicryophytic[4] steppes (Yurtsev, 1982; Berman et al., 2001a) are found only in Asia. Hemicryophytic steppe vegetation is dominated by small sedges (*Carex argunensis*, *C. rupestris*, *C. obtusata*, etc.). Hemicryophytic steppes are also important to our understanding of Pleistocene environments (Berman et al., 2001a). Various types of sedge associations are usually found on dry sites that are snowless in winter, and may be located in a wide altitudinal range – from the bottom of valleys to the watersheds. They are rare, but may occur throughout northeast Asia.

The extant flora and invertebrate fauna in these communities is less diverse than on thermophytic steppes, but here the pill beetle *Morychus viridis* (Coleoptera, Byrrhidae) is found in enormous quantities. This fact became the main reason for our intense study of this community. The investigation of the modern habitat of *M. viridis* provides a key for understanding Pleistocene environments of West Beringia where this beetle was dominant in most fossil assemblages among more than 200 insect species identified (Kiselev, 1981; Kiselev and Nazarov, 2009; Sher et al., 2006).

East Beringian steppes are well described (Young, 1976; Yurtsev, 1984a,b; Murray, 1987; Edwards and Armbruster, 1989; Laxton et al., 1996; Vetter, 2000). The most common plant association in steppe communities along the Yukon River is *Artemisia frigida* and *Carex filifolia* (Vetter, 2000). There are many differences between East and West Beringian steppes, but in our opinion, due to their position on the landscape and the dominant plant communities, East Beringian steppes should be considered thermophilic steppe. According to the opinion of Yurtsev (pers. comm.) and our observations, hemicryophytic steppes are not found today in Alaska and the Yukon. Only small areas (a few square meters each) are completely dominated by the xerophilous sedge *C. filifolia*.

Besides thermophytic and hemicryophytic relict steppe areas, we investigated many other xerophilous open grasslands, extending south into the northern taiga region. These regions include fire-created meadows where the absence of shade and the presence of dry soils create environmental conditions very close to steppe ones, various debris slides on south-facing slopes, relatively dry meadows with steppe species (steppe-like meadows) and patches of tundra. Both arctic and alpine tundra regions contain steppe-like areas with xerophilous tundra plants (for example some species of *Dryas*). This aspect of the flora leads us to describe such communities as tundra-steppe (Yurtsev, 2001a,b).

The term tundra-steppe can cause confusion, because it used in Russia both for modern as well as Pleistocene communities (Sher, 1990). The term as used here refers to communities with a mixture of steppe and tundra plant and animal species (Tugarinov, 1929). However, these modern patches of tundra-steppe, as well as described in America tundra-steppe transition (Edwards and Armbruster, 1989), like the other relict steppe areas, only occupy small pieces of land. Hence they are not equal to the Pleistocene tundra-steppe (Sher, 1971, 1976; Kiselev, 1981; Vereshchagin and Baryshnikov, 1992; Alfimov et al., 2003) or steppe-tundra (Cwynar and Ritchie, 1980; Hibbert, 1982; Elias et al., 2000) or mammoth steppe (Guthrie, 2001), or arctic-steppe (Matthews, 1976; Stanley, 1980). Moreover, probably modern and ancient communities have little correlation with each other. The common feature is the similarity in the recorded plant and animal species, especially insects, whose fossil remains often allow identification to the species level.

2.1. Study area

In northeast Asia we examined relict steppe areas in the valleys of the Yana (Fig. 1, I–III), Indigirka (Fig. 1, V), Kolyma (Fig. 1, V,VI), Anadyr (Fig. 1, VII), Amguema (Fig. 1, IX), and Palyavaam (Fig. 1, VIII) Rivers and their tributaries, as well as on the coast of the Sea of Okhotsk near Magadan (Fig. 1, IV) and Wrangel Island (Fig. 1, X). In the Yana River basin we collected insects in steppe areas on the left bank in the vicinity of Verkhoyansk. On the Indigirka River we examined the Oymyakon Depression where steppe slopes occur on the right bank near the mouth of the Kuydusun River, downstream and upstream of the village of Oymyakon. We also collected invertebrates in the steppe areas in the Nera River valley (a right tributary of the Indigirka River) from its mouth to the village of Artyk, and downstream on the Indigirka River from the village of Ust-Nera: in the vicinity of Tyubelyakh village, at the Ebe site, near the mouth of the Inyali River – a lefthand tributary of the Indigirka River, and on the left bank of the Indigirka River opposite the village

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[3] The sum of positive temperature (SPT) includes all daily temperature above zero in the year.

[4] from Latin: "half cold-adapted plants", the specific scanty steppe community that includes cold and dry adapted plants.

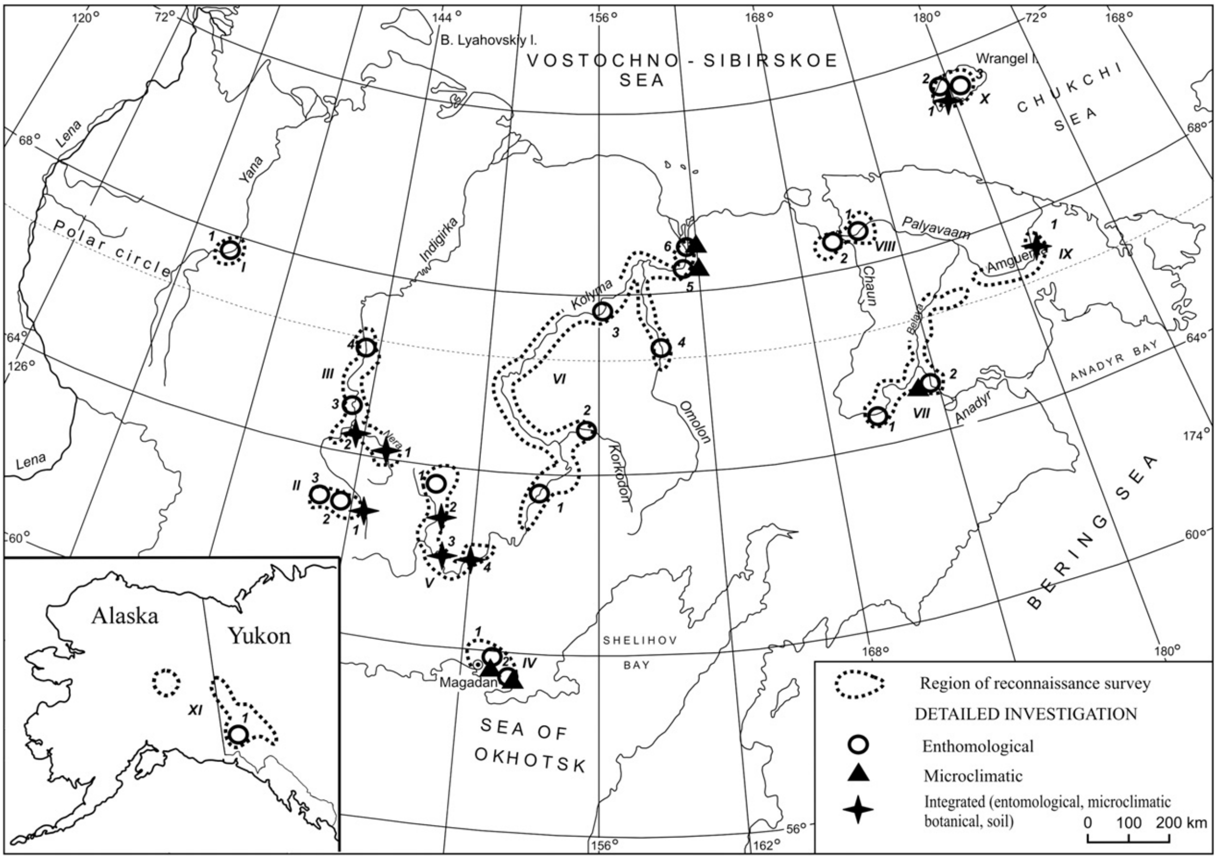

Fig. 1. Map of the study region for xerophilous insect communities on the Northerneast Asia. The general study areas are marked by Roman numerals; the areas of detailed work are marked by Arabic numerals. I – upstream of Yana River (1-Verkhoyansk town); II – Oymyakon depression (1, Tomtor village; 2, Agayakan weather station); III – middle stream of Indigirka River (1, Balagannakh village; 2, Ust'-Nera town; 3, Tybelyakh village, 4, Moma village); IV – Okhotsk Sea coast (1, Nyuklya village; 2, Atargan village); V – Kolyma River upstream (1, Byrkandya village; 2, Susuman town; 3, Orotuk village; 4, Vetrenny village); VI – Kolyma River middle and lower reaches (1, Zamkovaya Mountain; 2, Korkodon River near Bulun River mouth; 3, Konzaboy site; 4, Ust'-Oloy weather station; 5, Panteleikha River, 6, Krai Lesa and Krutaya Dresva sites); VII – Anadyr' River middle stream (1, Algan River mouth; 2, Utyosiki village); VIII – Chaun Depression (1, Palyavaam River mouth; 2, Neytlin Mountain); IX – Amguema River basin (1, Amguema Bridge); X – Wrangel Island (1, Somnitelnaya Bay; 2, Gusinaya River middle Stream; 3, Mamontovaya River middle stream); XI – Alaska and Yukon (Fairbanks area, Yukon River valley from Eagle to Whitehorse and Kluane Lake, 1, Cultus Bay).

of Moma (Khonnu). The long term observations including weather recording have been done only of the slope relict steppes of the right bank of the Nera River, approximately 30 km upstream of the mouth.

In the Kolyma River basin we examined large steppe slopes (Fig. 2-1,3) near the confluence of the Berelekh and Susumanka Rivers. We also collected insects in the Orotuk Depression on the left bank opposite the mouth of the Khattynakh River and below the mouth of the Chigichinakh River, as well as on the left bank opposite the mouth of the Detrin River, in the Kolyma River valley from the village of Srednekan to Zamkovaya Mountain, 1.5 km upstream of the mouth of the Panteleikha River near the village of Cherskii, Krai Lesa and Krutaya Dresva sites and in the valley of the Korkodon River (righthand tributary of the Kolyma River).

On the Chukchi Peninsula (Chukotka) we examined steppe areas on the right bank of the Palyavaam River near the point that the river exits the mountains. We also worked on Neitlin Mountain in the Chaun Depression, in the Amguema and Anadyr River basins, on the right bank of the Main River near the mouth of the Algan River, in the Bolshaya Osinovaya and Belaya River valleys, and on the right bank of the Anadyr River near the former village of Utyosiki. In addition, we examined steppe areas on Wrangel Island (Berman, 1986)

We made a detailed study of hemicryophytic (sedge) steppes mainly in the vicinity of the "Aborigin" Station (Fig. 2-2) and on the right bank of the Kolyma River between the mouths of the Obo and Bolshoi Sibirdik Rivers. We also re-examined previous study sites along the Burkandya River (tributary of the Berelekh River in its upper reaches), and in many of the localities on the Chukchi Peninsula listed above.

In northwest North America (Fig. 1 XI), together with colleagues Drs. M. Edwards and S. Armbruster from the Institute of Arctic Biology, University of Alaska, Fairbanks, we examined localities on steppe slopes near Fairbanks and in the Yukon River valley from the Canadian border (village of Eagle) downstream for approximately 100 km (Douglas, 1974; Young, 1976; Yurtsev, 1984a,b; Lausi and Nimis, 1991). In the Yukon Territory we studied relict steppe areas in the mountains surrounding Kluane Lake (Fig. 1XI (1), Fig. 2-4) and in the vicinity of Whitehorse and Carmacks. A steppe area near Kluane Lake (Cultus Bay) was studied in greatest detail. Here steppe and arid mountain tundra habitats are locally as abundant as forests. We examined 12 stations over altitudes ranging from 800 to 1600 m above sea level.

3. Methods

This paper is based on material collected by Berman and colleagues over a period of more than 40 years in Eastern Siberia (from Tuva and Altai to Wrangel Island) and occasionally in Alaska and the Yukon. In addition we used modern and fossil insects collected by Kuzmina in 1984–2004 in the Russian Arctic, and later (2003–2009) in Alaska and Canada. The insects were collected

Fig. 2. Map of modern steppe areas: 1. Thermophytic steppe in the upper Kolyma River basin near Susuman town; 2. Hemicryophytic steppe in the upper Kolyma River basin (elevation 1100 m); 3. Steppe area with *Agropyron jacutorum* (=*Elytrigia jacutorum*), in the upper Kolyma River basin; 4. Steppe area with Artemisia frugida and *Carex filifolia* at the Cultus Bay, Kluane Lake, Yukon.

using a variety of techniques: by hand, with a net, with pitfall traps, and using a thermophotoeclector[5] with model area 50 × 50 cm. For pitfall traps we used plastic containers with a lid, dug into the ground to the rim level. The lids were propped up approximately 1 cm above the trap to protect them from rain and also to attract insects by providing a shelter. All these methods are traditional (Yakobson, 1908) and well known in the field of entomology (Tsurikov and Tsurikov, 2001).

Modern and fossil insect identification was based on a number of guide books (Lindroth, 1969; Gur'eva and Kryzhanovsky, 1965; Ter-Minasyan, 1988; Lerh, 1989; Medvedev and Dubeshko, 1992; Bienkowski, 1999; Bright and Bouchard, 2008) and museum collections of Zoological Institute in St. Petersburg and Moscow University and fossil collections of Paleontological Institute in Moscow. Some West Beringian fossil insects were studied using modern insect collections of the E. H. Strickland Entomological Museum of University of Alberta and the Canadian National Insect Collection in Ottawa.

The soil temperature was measured during several warm seasons from the 1980s to the most recent decade. In the last 20 years we used data loggers, but earlier measurements were based on thermometry resistance bridges and sets of standard meteorological thermometers for current, maximum and minimum temperature measurements. We used ONSET (HOBO family), with intern and extern probes and iBDL loggers. Measurements in the 0–20 cm soil layer were usually taken 8 or 12 times per day during 2–3 summer months or during the whole warm season. Based on these data we assess different characteristics of seasonal temperature characteristics of soils.

In the lower reaches of the Kolyma River we used standard techniques for MCR climate reconstruction based on fossil insect assemblages (Atkinson et al., 1987; Elias, 1994) with one important addition (Alfimov et al., 2003; Alfimov and Berman, 2009). The standard method excludes phytophagous insects because their range depends on that of the host plant, and it is argued that plants may respond more slowly to climate change than predatory beetles (Coope, 1977). However, we argue that this is true mostly for forested regions. Most of fossil leaf beetles and weevils known from West Beringia (Kiselev, 1981; Kiselev and Nazarov, 2009) fed on grasses and these beetles' ranges could be more restricted than that of their host plants, thus reflecting climate features.

Last Glacial Maximum (LGM) climate deviations in northeast Asia are not so significant as in another regions (CLIMAP Project Members, 1994; Yanace and Abe-Ouchi, 2007; Allen et al., 2008 and others). This allowed us to determine the position of the boundaries of thermophytic tundra-steppe, based on the values of modern gradients of mean July and January air temperatures in different parts of the region. We consider that this approach creates more a detailed and reliable reconstruction for certain regions, in comparison with global circulation models, where the typical grid size is about 300 km (Allen et al., 2008). Because our aim is the reconstruction of the temperature field of the terrain, we used the results of LGM climate modelling for the northern Pacific (CLIMAP

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[5] The analogue of Berlese funnel, but square – a box where soil or leaf duff is placed, heated above what forces the insect to crawl down and fall to a collecting container.

Project Members, 1994 and others) as a starting point. This region is the closest one for which numerous paleoclimatic reconstructions give similar results.

We estimated the temperatures of collecting localities based on climate data from the closest meteorological stations. We did not use a gridded climate model (Elias, 1994) because most beetle specimens in Russian museum collections do not have collecting locality coordinates. However, often these specimens were collected not far from meteorological stations.

4. Results

4.1. The main beetle groups, studied in azonal steppes

Our collections (D. Berman group) from azonal steppes are kept in the museum of Zoological Institute in St. Petersburg, Russia. For East Beringia steppes, these collections and the collections of O. Khruleva from Wrangel Island are the main source of the modern beetle studies, including the new species descriptions that have made by B. Korotyaev, O. Kryzhanovsky and other experts.

4.1.1. Curculionidae

The weevil fauna (Curculionidae and Apionidae) of northeast Asia has been studied reasonably well, mainly because of the work of Korotyaev and Egorov (1977), Korotyaev (1976, 1977, 1987a,b), Korotyaev and Ter-Minasyan (1977) and Khruleva and Korotyaev (1999). A total of 108 species have been recorded (Korotyaev, 1987a). In addition, 112 species are known from northern USA and Canada (Alaska, Yukon and Northwest Territories) (Bousquet, 1991), including 66 species from the Yukon (Anderson, 1997; Berman et al., 2001b). Our data are shown in Table 1–4[6]. Of the 108 weevil species recognised in northeast Asia, thermophytic and hemicryophytic steppe groups contain in total 36 species (Berman, 1974; Berman and Mordkovich, 1979; Korotyaev, 1980). With the exception of *Coniocleonus zherichini*, *Ceutorhynchus barkalovi*, *Prisistus olgae*, *Mesotrichapion wrangelianum*, and *Lepidophorus lineaticollis*, almost all these species inhabit steppe and mountain steppe regions of southern East Siberia and have clearly disjunct geographic ranges in northeast Asia.

Based on their habitat preferences, the following species may be considered cryoxerophilic: *Coniocleonus cinerascens*, *Coniocleonus cineritius*, *C. zherichini*, *Hypera diversipunctata*, *Hypera ornata*, and *Sitona borealis*. The species *Tychius albolineatus* and *Baris artemisiae* prefer meadow and steppe-like meadow habitats.

4.1.2. Carabidae

The ground beetle species are presented in the Tables 5–7. At present more than 160 species of ground beetles are recorded from northeast Asia (Lerh, 1989; Kryzhanovsky et al, 1995). Of these, 16 species (Table 5) display a disjunct distribution pattern, with their main range in the zonal and mountain steppes of southern Siberia, Mongolia, and Kazakhstan (Berman and Mordkovich, 1979). In the relict steppe areas in the upper reaches of the Indigirka River we collected 14 of these species. *Curtonotus harpaloides* has been collected in the Verkhoyansk region, and the *Harpalus lederi* is known from the Kolyma River basin. *Cymindis arctica*, conventionally regarded as an endemic species of the steppes of the Indigirka River (Kryzhanovsky and Emets, 1979), was collected in steppe habitats, along with *Poecilus nordenskioldi* from tundra northern taiga areas (Berman, 1974). Both species are significant elements of the Pleistocene fossil faunas of West Beringia (in Kiselev (1981),
P. nordenskioldi was reported as *Poecilus (Derus) samojedorum*). *C. arctica* belongs to the subgenus *Mastes*, which is best represented in desert and steppe regions of Middle and Central Asia (Emets, 1974). The genus *Poecilus* is also mostly desert-steppe and Asian, while *Poecilus fortipes* occurs in zonal steppes and in the relict areas in the upper reaches of the Indigirka and Kolyma Rivers. Two species, *P. nordenskioldi* and *Poecilus nearcticus* are recorded only from the subarctic[7].

Thus, at least part of these steppe-origin species with disjunct and restrict modern ranges are relicts of a much more widely distributed ancient steppe-tundra insect community.

4.1.3. Chrysomelidae

In the thermophytic steppes of northeast Asia we have identified eight steppe species of leaf beetles. Six of these were collected in the upper reaches of the Indigirka River: *Cassida nobilis*, *Chrysolina exanthematica exanthematica*, *Chrysolina aeruginosa*, *Chrysolina perforata*, *Chrysolina brunnicornis bermani*, and *Labistostomis bipunctata indigirensis*. We found *Colaphellus alpinus* in the lower course of the Kolyma River, near the village of Cherskii, and *Longitarsus violentus* is known from the upper course of the Kolyma (40 km northeast of the village of Seimchan), (Matis, 1986). Six of the eight leaf beetle species are widely distributed in the Northern Eurasian steppes. *Labistostomis bipunctata indigirensis* and *C. brunnicornis bermani* are endemics of the Indigirka relict steppes (Medvedev and Dubeshko, 1992). The latter taxon is extremely abundant in the steppe areas in the vicinity of the village of Balagannakh on the Indigirka River, constituting approximately a third of all beetles collected, with numbers reaching 16 individuals per square meter.

Four of these species have been found in Pleistocene deposits in Western Beringia: *Chrysolina exanthematica*, *C. perforata*, *C. aeruginosa*, *C. alpinus*, as well as two southern Siberian steppe species: *Galeruca daurica* and *Chrysolina rufilabris* (Kiselev, 1981; Kiselev and Nazarov, 2009). They are found only in strongly pronounced thermophilous tundra-steppe fossil assemblages. The fossil remains identified by Kiselev as *Chrysolina perforata* require reidentification, based on a recent revision (Sher et al., 2006; Kiselev and Nazarov, 2009). Similar remains have been identified as *C. arctica*, a species described from Wrangel Island (Chernov et al., 1993).

4.1.4. Other insects

Many groups of insects (true bugs, ants, butterflies, leafhoppers and other) have been studied from relict steppe localities (Vinokurov, 1979; Berman et al., 1983, 1984, 1995, 2001a). Part of the huge beetle collection is not yet completely described; unidentified specimens from some families, such as Elateridae, could provide very useful information. Special attention was paid to the pill beetle *M. viridis* whose distribution is strongly correlated

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[6] Tables 1 and 2 do not include *Ceutorhynchus viridanus*, found only in relict steppe patches in the upper reaches of the Yana River (Korotyaev, 1980).

[7] Poecilus nearcticus has been collected from the Northwest Territories of Canada, near the mouth of the Anderson River (Lindroth, 1969). This species is also known from the Palaearctic by single specimens from the tundra of the Polar Urals and the Taimyr Peninsula (O.L. Kryzhanovsky pers. comm.), and also from the vicinity of Zhigansk, from the basin of the Amga River and the upper course of the Indigirka River (collection of Zoological Institute, Russian Academy of Sciences). It was later found on Ajon Island by S.V. Kiselev; a specimen from the vicinity of Verkhoyansk is housed in the Zoological Institute, Russian Academy of Sciences. One of us (SK) collected this beetle from dry tundra habitat near the Keremesit River in the lower reaches of the Indigirka River, and from dry tundra near the Titaluk River, on the North Slope of Alaska. This beetle was widely distributed across the whole of Beringia in the Pleistocene (Kiselev, 1981; Kiselev and Nazarov, 2009; Sher et al., 2006; Nelson and Carter, 1987; Matthews and Telka, 1997; Zazula et al., 2006). Fossil finds are common.

Table 1
Weevils of the xeromorphous communities of northeastern Asia and north-western America.

Species, area	Ecology	Indigirka River basin	Kolyma River Basin	Chukotka	Fossil (Pleistocene)	Yukon Territory Canada
NEARCTIC						
Connatichela artemisiae And.	s?				−+	+
Lepidophorus thulius (Kiss.)	cr-s				++	+
Sitona aquilonius Bright	cr-s				−+	+
Mesotrichapion cyanitinctum (Fall)	me				−+	+
Ceutorhynchus oregonensis Dietz	s				−−	+
Ceutorhynchus subpubescens LeC.	s				−+	+
Ceutorhynchus sp.	s?				++?	+
HOLARCTIC						
Hypera diversipunctata Schr.	cr-s	+	+	+	++	+
Coniocleonus zherichini T.-M. et Kor.	cr-s	+	+?	+	++	+
Tychius tectus LeC.	me-s	+	+	+	++	+
Sitona lineelus (Bon.)	me	+	+		++	+
Eutrichapion viciae (Payk.)	me	+	+		−−	+
Ceutorhynchus querceti (Gyll.)	me	+	+		−−	+
Ceutorhynchus rapae Gyll.	me	+	+		−−	+
Ceutorhynchus barkalovi Kor.	cr-s			+	−−	+
Prisistus olgae Kor.	cr-s			+	+−	+
Lepidophorus lineaticollis Kby.	cr-s			+	−+	+
PALAEARCTIC						
Arcto-alpine						
Hypera ornata (Cap.)	cr-s	+	+	+	+−	+
Transpalaearctic						
Baris artemisiae (Herbst)	me	+	+		−−	
Mesotrichapion amethystinum (Mill.)	me	+	+		+?−	
Phyllobius virideaeris Laich.	me	+	+	+	+−	
East Siberian						
Sitona borealis Kor.	cr-s	+	+	+	+−	
Dactylotus tshuktsha Lukjan.	me	+	+	+	−−	
Phyllobius hochhuthi Motsch.	me	+			+−	
Southern Siberian						
Coniocleonus astragali T.-M. et Kor.	cr-s	+	+	+	+−	
Coniocleonus cinerascens (Hochh.)	cr-s	+	+	+	+−	
Coniocleonus ferrugineus (Fahr.)	s	+	+		+−	
Coniocleonus cineritius (Gyll.)	cr-s	+	+		−−	
Ceutorhynchus seniculus Ch. Bris.	s	+	+	+		
Tychius albolineatus Ziegl. in Dejean	me	+	+			
Otiorhynchus cribrosicollis Boh.	s	+	+		+?−	
Coniocleonus vinokurovi T.-M. et Kor.	s	+			+−	
Stephanocleonus foveifrons Chevr.	s	+	+		+−	
Stephanocleonus fossulatus (F-W.)	s	+			+−	
Stephanocleonus eruditus Faust	s	+			+−	
Conditional -endemic						
Mesotrichapion wrangelianum Kor.	cr-s			+	+−	
Pseudaplemonus bermani Kor.	cr-s			+	−−	
Apion amguemai Kor.	cr-s			+	−−	
Phyllobius kolymensis Kor. et Egor.	me		+		+−	
Total 36 species		**25**	**20(21)**	**16**	**24(26)**	**17**

s – steppe; cr-s – hemicryophytic steppe; me – meadow; me-s – meadow-steppe; "+" or "−" presence or absence of the species (for fossils: left in West Beringia, right in East Beringia).

with steppe areas. This beetle is found on the moss *Polytrichum piliferum* (the host plant) in association with xerophilous sedges, mainly *Carex argunensis*. It is occasionally recorded from thermophytic steppe, and very commonly from hemicryophytic steppes, only in the West Beringia (Berman, 1990, 1992; Berman et al., 2001a).

4.2. Beetles of Indigirka steppe

4.2.1. Curculionidae

The weevil fauna of the thermophytic steppe of the Indigirka River basin (Fig. 1: II, III) stands out among all the faunas of xeromorphic communities we have examined, as having the greatest species diversity (21 of 25 species in Table 1). The highly diverse weevil fauna of this area benefits from the presence of Daurian–Mongolian steppe species of the genera *Stephanocleonus* and *Otiorhynchus*, as well as cryoxerophilous species of the genus *Coniocleonus*. *Stephanocleonus foveifrons*, *Stephanocleonus fossulatus* and *Stephanocleonus eruditus* are known from the mountainous steppe of the Altai and Tuva regions, and northern Mongolia, whereas the modern range of *Otiorhynhus cribrosicollis* embraces central and northern Mongolia, and the steppes of southern Siberia from Baikal to Blagoveshchensk.

Apart from the aforementioned areas, the range of *Coniocleonus ferrugineus* includes isolated localities in central Kazakhstan, the Taimyr Peninsula, and the lower reaches of the Lena River. Two other species of *Coniocleonus* have complex ranges. *Coniocleonus cinerascens* occurs in the mountainous steppe of northern Mongolia, Buryatia, Altai, Khakasia, and Tuva, and a few individuals have been collected on the Indigirka River (our material) and in the

Table 2
Weevils in the xeromorphic communities of northeastern Asia (maximum amount for 100 pit-trap/day; + single and rare).

Species	Indigirka		Kolyma			
	Thermophytic steppe		Meso-phytic meadows	Hemi-cryophytic steppe	Tundra-steppe	Mountain dry tundra
Phillobius hochhuthi Motsch.	+	–	–	–	–	–
Coniocleonus zherichini T.-M. et Kor.	?	–	+	–	–	–
Coniocleonus astragali T.-M. et Kor.	?	–	–	–	+	–
Stephanocleonus foviefrons Chevr.	+	–	–	–	–	–
Stephanocleonus eruditus Faust	7.7	–	–	–	–	–
Baris artemisiae (Herbst)	+	–	+	–	–	–
Tychius albolineatus Ziegl. in Dejean	+	–	+*	–	–	–
Ceutorhynchus seniculus Ch. Bris.	+	–	+	–	–	–
Otiorhynchus cribrosicollis Boh.	7.7	–	+	–	–	–
Stephanocleonus fossulatus (F-W.)	34.4	+	–	–	–	–
Sitona lineelus (Bon.)	+	0.1	+	–	–	–
Ceutorhynchus rapae Gyll.	+	0.1	+	–	–	–
Phillobius viridiaeris Laich.	3.0	0.2	0.1*	–	–	–
Phyllobius kolymensis Kor. et Egor.	–	0.3	49*	0.4	–	–
Coniocleonus ferrugineus (Fahr.)	3.3	0.3	–	1	0.7	–
Hypera ornata (Cap.)	7.0	+	0.3*	4.5	56.4	3.8
Sitona borealis Kor.	+	+	+	3.5	3.6	0.4
Hypera diversipunctata Schr.	+	?	0.3*	7.7	2.2	0.3
Dactylotus tshuktsha Lukjan.	+	0.1	2.5*	9.5	0.6	1.7
Lepyrus nordenskioldi Faust	+	+	0.3*	4.5	1.8	0.6
Tychius tectus LeC.	+	?	+	4.7	0.3	0.1
Coniocleonus cineritius (Gyll.)	+	–	–	1.5	0.8	–
Coniocleonus cinerascens (Hochh.)	+	–	–	+	–	–
Pissodes gyllenhali Gyll.	–	–	–	0.4	–	–
Total	21	10	13	11	8	6

* On the meadows with sandy soil.

vicinity of Pevek (Korotyaev, 1977). *Coniocleonus astragali* is known from the Chui steppe of southeastern Altai, and from the basins of the Indigirka and Kolyma Rivers, from the Verkhoyansk Range, from Kamchatka and from Wrangel Island (Khruleva and Korotyaev, 1999). The thermophytic steppe weevils of the Indigirka River also include broadly xerophilous species (*H. ornata*, *H. diversipunctata*, *S. borealis*), and some species of mesoxyrophilic meadow and meadow-steppe species (*Tychius tectus*, *T. albolineatus*, and *B. artemisiae*).

Steppe and meso-xerophilous species within the Curculionidae are distinctly separated on the basis of habitat preference. The steppe areas are inhabited almost exclusively by steppe species. Of 707 weevils captured in traps in July–August on the thermophytic steppe slope in the Nera River valley, almost 95% represent three Daurian–Mongolian species (*S. fossulatus*, *S. eruditus* and *O. cribrosicollis*) and the eastern Siberian *C. ferrugineus*. Interestingly, the dominant group is represented by only a few species, whereas the superdominant *S. fossulatus* represents 63% of all specimens collected in all areas. This species is associated with the sagebrush *A. gmelinii*. Only twelve out of 445 individuals were collected in areas with other sagebrushes, and it was not present in other areas examined. Moreover, the above species are not found outside thermophytic steppe. Conversely, most cryoxerophilous and meadow species cannot exist on most areas of thermophytic steppe because of the extremely high surface temperatures and aridity.

Table 3
Maximum amount of weevils in the steppes and tundra-steppes of the upper Kolyma River basin, 1986–1987 years (individuals for 100 pit-traps/day).

Species	Hemi-cryophytic steppe	Tundra-steppe
Coniocleonus ferrugineus (Fahr.)	1	0.6
Hypera diversipunctata Schr.	7.7	2.2
Sitona borealis Kor.	3.5	3.6
Hypera ornata (Cap.)	15.4	56.4
Lepyrus nordenskioldi Faust	15.4	1.8
Coniocleonus cinerascens (Hochh.)	1	–
Coniocleonus cineritius (Gyll.)	1.5	0.8
Tychius tectus LeC.	4.7	0.3
Phyllobius kolymensis Kor. et Egor.	0.4	–
Pissodes gyllenhali Gyll.	0.4	–
Dactylotus tshuktsha Lukjan.	8	0.6

4.2.2. Carabidae

We collected various mesic-adapted ground beetles in this area, including *Curtonotus alpinus* (=*Amara* (*Curtonotus*) *alpina*), *Miscodera arctica*, *Carabus macleayi* and *Carabus canaliculatus*. These were found on the margins of steppe patches. On steppe slopes we collected *Harpalus pusillus*, *Curtonotus tumidus*, and *Curtonotus fodinae*, in combination with *C. arctica* and *P. nordenskioldi*. These beetles dominate the fauna on various steppe slopes. Their total number in sagebrush habitats reached 45 individuals per square meter.

Pitfall trapped specimens show a similar dominance pattern. Of 6454 individuals collected of 15 species, *C. tumidus* specimens comprise 46% of all collected specimens), followed by *C. fodinae*, *H. pusillus* and *P. nordenskioldi*, each constituting 11–16%. Smaller numbers of *C. arctica*, *Amara infuscata*, *Harpalus brevicornis* and *Harpalus fuscipalpis* were collected (2.5–5%). Most steppe species, and also *C. arctica* and *P. nordenskioldi*, have not yet been found outside the relict steppe area in this region.

4.3. Beetles of the Kolyma steppe

4.3.1. Curculionidae

In the thermophytic steppes of the Kolyma River drainage, the species diversity of true steppe weevils is low. The only *Stephanocleonus* present is *S. fossulatus*. This weevil is also found on *A. gmelinii*, an isolated population of which is recorded only on a steppe slope near the village of Orotuk. *O. cribrosicollis* is not found here, and the genus *Coniocleonus* is represented only by *C. ferrugineus*. The Kolyma areas of thermophytic steppes are inhabited by typical meadow and meadow-steppe species, which are few in number. The cryoxerophilous species that are widespread in northeast Asia are either absent here, or very scarce. For comparison, Table 2 shows data on mesophytic meadow weevils,

Table 4
Weevils of the steppe slope Kluane Lake, Cultus Bay (number of weevils caught in pit-traps from 10 to 22 July 1993).

Species	Altitude above sea level (m)											
	821	912	1094	1155	1246	1337	1398	1459	1490	1520	1550	1611
Sitona aquilonius Bright	1											
Connatichela artemisiae And.	3	5	5									
Lepidophorus lineaticollis Kby.	5	6	62	56	55	36	176	36	4	25	18	24
Tychius tectus LeC.						1	2					
Hypera diversipunctata Schr.								1			1	
Prisistus olgae Kor.												1

including those of sandy dunes in the Kolyma River valley near the village of Vetrenyi. It shows that their species diversity reaches a maximum here, and *Phyllobius kolymensis*, an endemic species for the Kolyma River region, is extremely abundant.

4.3.2. Carabidae

In the Kolyma River basin only nine species of steppe-associated Carabidae have been found. Their main range is in the steppes of southern Siberia (Table 5). Only *A. infuscata*, *H. pusillus* and *H. lederi* are very abundant here. *H. lederi and H. pusillus* also occur in dry areas in forest clearings, recently burnt dry lands, and hemicryophytic steppe. Only *H. lederi* was found on steppe-like alpine tundra.

4.4. Beetles of other steppe-like associations of Kolyma River basin

4.4.1. Curculionidae

In contrast to the hemicryophytic steppes and steppe-tundra, the number of mesic-adapted species is very high in most localities. This is despite the harsh microclimate (dry and cold) and due to the abundance of forbs, primarily those of the Fabaceae family *Astragalus* and *Oxytropis*. All the species recorded from hemicryophytic steppes, except *P. kolymensis*, are also found above tree line, into the alpine tundra, in the ecotone between steppe and alpine tundra communities dominated by *Dryas octopetala* and *C. argunensis* (Berman, 1992).

Table 5
Ground beetles of xeromorphic communities of Indigirka and Kolyma River basins (maximum beetles for 100 pit-traps/day).

species	Species ecology	Indigirka	Kolyma					
		Thermophytic steppe	Thermophytic steppe	Mesophytic meadows*	Forest after fire **	Cryophytic steppe	Tundra-steppe	Mountain dry tundra
Harpalus viridanus Motsch.?	s	+	–	–	–	–	–	–
Harpalus obtusus amputatoides Mlynar	s	+	–	–	–	–	–	–
Harpalus amariformis Bates	s	1.2	–	–	–	–	–	–
Amara similata (Gyll.)	s	4	–	–	–	–	–	–
Cymindis arctica Em. et Kryzh.	s	4.8	–	–	–	–	–	–
Poecilus nordenskioldi J. Sahlb.	t	18.3	–	–	–	–	–	–
Harpalus fuscipalpis Sturm	s	2.5	–	–	–	–	–	+
Harpalus salinus Dej.	s	+	+	–	–	–	–	–
Harpalus vittatus Gebl.	s	+	+	+	–	–	–	–
Curtonotus fodinae (Man.)	s	22.4	+	+	–	–	–	–
Curtonotus tumidus (Mor.)	s	34.4	+	+	–	–	–	–
Harpalus brevicornis Germ.	s	2.8	+	+	–	–	–	–
Amara infuscata Putz.	s	3.3	65.8	9	–	–	–	–
Poecilus fortipes (Chaud.)	s	+	+	+	+	–	–	–
Harpalus pusillus (Motsch.)	s	11	55	86.9	+	9.4	–	–
Harpalus lederi Tsch.	s	?	18.7	1.6	1	5.5	16.7	–
Amara interstitialis Dej.	f–t	+	+	1.4	+	+	+	–
Harpalus torridoides Reitt.	f?	–	26.7	3.5	+	6.7	2.7	–
Harpalus major Motsch.	f	–	7.3	4	+	+	–	+
Cymindis vaporariorum (L.)	f	–	2.5	+	1.4	+	1	1.5
Harpalus solitaris Dej.	f	–	4.2	+	2.1	+	3	+
Curtonotus hyperboreus (Dej.)	f	–	+	3	10.6	1.2	+	+
Notiophilus aquaticus L	f–t	–	+	4.5	+	3.7	+	+
Carabus macleayi Dej.	f	–	+	+	4	2.9	+	+
Carabus odoratus Motsch.	f–t	–	+	–	5	3.3	3.4	–
Dicheirotrichus mannerheimi (R.Sahlb.)	f	–	+	+	–	5.7	3.4	+
Carabus canaliculatus Adams	f	–	+	15	1.4	–	–	–
Curtonotus torridus (Panz.)	f–t	–	–	2.1	–	–	–	+
Pterostichus adstrictus Esch.	f	–	–	1	–	–	–	–
Miscodera arctica Payk.	f	–	–	3	1	–	+	–
Amara brunnea Gyll.	f	–	–	–	6	–	+	+
Pterostichus eximius Mor.	f	–	–	–	12	–	–	–
Carabus kolymensis Lafer	m	–	–	–	–	6.7	9.4	24.1
Pterostichus sp. 1	m	–	–	–	–	14.2	6.7	–
Curtonotus kurnakovi (Bud. et Kryzh.)	m	–	–	–	–	–	2.5	+
Carabus truncaticollis Esch.	t	–	–	–	–	–	–	6.9
Pterostichus sublaevis (Say.)	t	–	–	–	–	–	–	+
Pterostichus (Cryobius) spp.	?	–	–	–	–	–	–	27.5

* grassy habitats on sandy soil; ** xeromorphous birch, aspen, larch forests. "+" – single and rare beetles s – steppe; f – forest; f-t – forest and tundra; t – tundra; m – mountains. Curtonotus hyperboreus (Dej.) is Amara (Curtonotus) hyperborea Dej., Curtonotus torridus (Pan.) is Amara (Curtonotus) torrida Pan. in East Beringia references.

Table 6
Ground beetles of the hemicryophitic steppe and tundra-steppe of the upper Kolyma River basin (maximum beetles for 100 pit-traps/day for season).

Species	Hemicryophytic steppe	Tundra-steppe
Harpalus pusillus (Motsch.)	19.4	–
Pterostichus eximius Mor.	14.2	6.7
Carabus kolymensis Lafer	6.7	23.7
Harpalus torridoides Reitt.	6.7	2.2
Notiophilus aquaticus L	5.4	1.0
Carabus odoratus Motsch.	3.4	1.8
Harpalus lederi Tsch.	5.5	16.7
Dicheirotrichus mannerheimi (R.Sahlb.)	5.7	3.4
Curtonotus hyperboreus (Dej.)	1.2	+
Harpalus major Motsch.	1.0	–
Harpalus solitaris Dej.	+	3.0
Cymindis vaporariorum (L.)	2.0	1.0
Curtonotus kurnakovi (Bud. et Krysh.)	–	2.5
Amara kingdoni Bal.	+	+
Carabus macleayi Dej.	2.0	–
Amara brunnea Gyll.	–	+
Miscodera arctica Payk.	–	+
Curtonotus torridus (Panz.)	–	–
Amara interstitialis Dej.	+	+
Amara quenseli (Schön.)	+	–
Trachypachus zetterstedti (Gyl.)	2.7	–
Pterostichus (Cryobius) sp. 3	–	3.8
Pterostichus (Cryobius) sp. 1	–	+
Pterostichus sublaevis (Say.)	–	+

Cryoxerophilous species are abundant in both hemicryophytic steppes, and in steppe-tundra, (Table 3), with mesic-adapted species such as *Lepyrus nordenskioeldi* and *Dactylotus tschuktsha* reaching high numbers. As seen in Tables 2 and 3 there are no fundamental differences in abundance or composition of weevil faunas between hemicryophytic steppes and ecotonal habitats. Thus, the insect faunal diversity of hemicryophytic steppe and ecotones examined in the Kolyma River basin is extremely impoverished compared to the fauna of the thermophytic steppes of the Indigirka River. Among characteristic taxa, only three species of Cleoninae are recorded in the former region (two more are found in the Chukchi Peninsula).

4.4.2. *Carabidae*

In relict steppe areas in the upper course of the Kolyma River that are dominated by the sedge *C. argunensis*, most of the ground beetle fauna (Table 6) consists of moderately dry-adapted species that are widespread in the northern taiga. These beetles are usually found in grassy openings, and on dry mountain slopes. Only two species truly characterize this habitat: *Pterostichus eximius* and *Carabus kolymensis*. These are considered endemic species; the latter is found above alpine tree line. However, in the areas of hemicryophytic steppes it extends down onto river terraces. It reaches its highest abundance in high mountain (1750 m above sea level) tundra-steppe communities. The ground beetle fauna of hemicryophytic steppe and steppe-tundra habitats are similar in composition.

4.4.3. *Other beetles*

The main feature of the beetle fauna of the hemicryophytic steppe is extremely high concentration of the pill beetle *M. viridis* – sometimes more than 100 larvae per m^2.

4.5. *Beetles of the Chukchi Peninsula*

Elements of hemicryophytic steppes and steppe-tundra, along with some of their characteristic weevil species, reach the Chukchi Peninsula. Small areas of relict steppe are widely dispersed in the tundra landscape. Small flooded meadows with legume vegetation (on edges of floodplain terraces, formed by well drained pebbles alluvium) are inhabited by fourteen xerophilous species restricted today to the Chukchi Peninsula (see Table 1). This number of species exceeds that of the background tundra weevil fauna. Chukotka is the only one region in the West Beringia where the widespread East Beringian weevil *L. lineaticollis* has ever been recorded. It is known from many sites on the Chukchi Peninsula in Northeastern Asia: along the Chegitun River, on Ratmanov Island, at Emma Bay, and near the villages of Uelen, Chaplino, Provideniya, Sireniki, and Anadyr (Berman et al., 2001a). Near Anadyr, the southern-most site in the range, *L. lineaticollis* has been found in meadows with tall (ca. 50 cm), dense grass, including sites at the damp bottoms of drained thermokarst lakes with willow vegetation (Bukhkalo, pers. comm.).

Table 7
Ground beetles from the steppe slope near Kluane Lake, Cultus Bay, (number of beetles caught in pit-traps from 10 to 22 July 1993).

species	Altitude above sea level (m)											
	821	912	1094	1155	1246	1337	1398	1459	1490	1520	1550	1611
Harpalus nigritarsis Sahlb.	1	–	–	–	–	–	–	–	–	–	–	–
Cicindela sp.2	1	–	–	–	–	–	–	–	–	–	–	–
Cicindela sp.1	1	–	–	2	3	–	–	–	–	–	–	–
Amara obesa Say	36	9	–	19	14	15	2	–	–	–	–	–
Harpalus opacipennis Hald.	37	4	–	–	–	4	1	1	–	–	–	–
Carabus taedatus Fabr.	3	2	2	2	28	7	7	5	2	4	–	1
Pterostichus brevicornis (Kir.)?	1	–	–	–	–	2	3	1	1	–		–
Curtonotus hyperboreus (Dej.)	–	2	–	–	–	–	–	–	–	–	–	–
Cymindis cribricollis Dej.	–	–	1	–	2	30	89	16	3	19	6	7
Harpalus fulvilabris Man.	–	–	1	–	–	–	–	–	–	–	–	–
Harpalus fuscipalpis Sturm	–	–	–	1	–	–	–	–	–	–	–	–
Curtonotus torridus (Pan.)	–	–	–	–	1	–	3	7	2	2	4	2
Amara quenseli (Schön.)	–	–	–	–	4	–	–	–	–	–	–	–
Carabus chamissonis F.	–	–	–	–	–	1	–	1	2	2	14	7
Syntomus americanus (Dej.)	–	–	–	–	–	–	1	–	–	–	–	–
Bembidion dauricum Motsch.	–	–	–	–	–	–	1	–	–	1	–	–
Cymindis unicolor Kirby	–	–	–	–	–	–	–	1	–	–	–	–
Pterostichus pinguedineus Esch.	–	–	–	–	–	–	–	–	10	–	–	–
Dyschirius sp.	–	–	–	–	–	–	–	–	1	–	–	–
Notiophilus borealis Harris	–	–	–	–	–	–	–	–	1	–	–	1
Amara (Leiocnemis) sp.1	–	–	–	–	–	–	–	–	–	–	–	1

Footnotes see Table 4; *Curtonotus hyperboreus* (Dej.) is *Amara (Curtonotus) hyperborea* Dej., *Curtonotus torridus* (Pan.) is *Amara (Curtonotus) torrida* Pan. in East Beringia references.

No steppe-adapted species of Carabidae have been found on the Chukchi Peninsula. (Berman, 1983; Marusik, 1993; Berman et al., unpublished data).

4.6. Beetles of the East Beringian steppe

4.6.1. Curculionidae

In north-western America, on steppe slopes in the upper reaches of the Yukon River, 10 species were collected of which four are Holarctic in distribution. These are associated with meadow vegetation (*Sitona lineellus*, *Ceutorhynchus querceti*) and to varying extents dry habitats (*H. diversipunctata*, *T. tectus*). The two of Nearctic species: *Mesotrichapion cyanitinctum* and *Sitona aquilonius* are possibly synonyms of the Russian species *Mesotrichapion amethystinum* and *S. borealis*, according to B. Korotyaev (Berman et al., 2001b). *L. lineaticollis* and *P. olgae* are Amphi-Beringian species. Our record of *P. olgae*, originally described from Wrangel Island (Korotyaev, 1987b), is the first record for North America. On Wrangel Island (Khruleva and Korotyaev, 1999) it has been collected from tundra-steppe with sedge-herbaceous vegetation and dry tundra, although the host plant is unknown. On Kluane Lake, in the southwest Yukon region, the single specimen was found in a pitfall trap in dry tundra at 1611 m (Table 4).

The range and ecology of the weevil *L. lineaticollis* are particularly important to understand. Its presence in significant numbers in many Pleistocene deposits is an extremely important phenomenon in the Late Pleistocene history of East Beringia (Matthews and Telka, 1997). *L. lineaticollis* is widespread in Alaska, the Yukon, western Northwest Territories, and in northern British Columbia (Anderson, 1997). In the Yukon this species mainly occurs in steppe areas, but it is also widespread on the tundra, where it can inhabit environments ranging from dry to wet. It has also been collected from under alder leaf litter (Matthews, 1975, 1983; Matthews and Telka, 1997; Kuzmina et al., 2008). Based on our observations in the Yukon, *L. lineaticollis* is also common on disturbed ground in the forest, where there are roads, logging activity, etc. Our specimens from the Kluane Lake area allow us to evaluate the dependence of *L. lineaticollis* on the heat supply in its habitat. Table 4 shows that *L. lineaticollis* was found along the entire transect, and its abundance has a pronounced peak at an altitude of 1400 m. The SPT of the soil surface in the profile decreases more than two folds at this elevation, from 2380 to 1040°. The higher value is similar to the heat capacity of the soil of thermophytic steppes in the upper Kolyma basin, but the lower one is similar to that of typical tundra of the Chukchi Peninsula. The position of peak abundance of this species, corresponding to the ecotone between steppe and alpine tundra, seems to indicate that the species has selected an environment with moderate soil temperatures. Although this interpretation is attractive, it should be noted that it could be due to the phenology of the transect. As spring temperatures rise up the transect, so do mass hatchings of beetle larvae. The inconsistency of existing data on this species calls for more detailed examination of its ecology.

Connatichela artemisiae is a weevil endemic to the Yukon and Alaska (Anderson, 1984). We collected it in traps on the lower slopes adjacent to Kluane Lake; we also found it in similar habitats in the vicinity of Carmacks. We also collected many *C. artemisiae* on the steppe slope on the right bank of the Yukon River near Whitehorse at the end of June. The beetles came to the surface to mate. Here the land surface is covered by scattered low sagebrush (*A. frigida*) bushes and xerophilous grasses and sedges; the beetles were concentrated on the ground under *Artemisia* leaves. Single living specimens *C. artemisiae* were collected from the surface of a sedimentary exposure at the Chester Bluff site, not far from Eagle, Alaska; the beetles crawled down the slope 50 cm below the top surface of the exposure, in the middle of an unvegetated, very hot and dry bluff surrounded by *Artemisia* scrub. This weevil seems to be the only true steppe indicator in East Beringia.

The third important American species is the weevil *Lepidophorus thulius*, formerly called *Vitavitus thulius* (revised by Bright and Bouchard, 2008). Several specimens of *L. thulius* were collected at the base of the slope near Kluane Lake, in spruce-grass-moss forests near a steppe-like area on the slope. Modern specimens of *L. thulius* are recorded from the Anderson River Delta (to the east of the mouth of the Mackenzie River) and from the region of the Thelon River, Northwest Territories, but, despite a careful search, it has not been found on riparian landscapes of the Yukon (Morgan et al., 1983). However, this species was collected in the western Yukon on dry tundra and on south-facing slopes where steppe occurs with sagebrush (Anderson, 1997). The tree line lies at the mouth of the Anderson River, whereas at the Thelon River region these beetles are found in a combination of northern taiga and sparse woodland habitats (Dr. S. Smith, pers. comm.). Other collecting localities, such as Blue fish Caves (Yukon) are also in the forest zone (Anderson, 1997).

Fossil beetles, both in West and East Beringia (Kiselev, 1981; Nelson and Carter, 1987; Matthews and Telka, 1997; Sher et al., 2006; Zazula et al., 2006, 2007) are mostly representative of steppe-tundra environments. However, forest vegetation and steppe-tundra environments are not mutually exclusive. Almost all large insect samples indicating steppe-tundra environments contain single tree-related species. Fossils of *L. thulius* are not very widespread in West Beringia. They have only been found in 42 out of 687 studied faunal assemblages (Sher et al., 2006). It is much more common in East Beringia fossil assemblages indicative of steppe-tundra (Matthews and Telka, 1997, S. Kuzmina, unpublished data). Some West Beringian fossil assemblages with *L. thulius* probably represent very cold environments, as they do not include any forest insects (for example the Krasivoe site (Kiselev and Nazarov, 2009) and the Utkinsky Kamen site (Kiselev, 1981)).

Apart from the species we collected, Anderson (1997) indicates four additional species found in xerophilous communities of Yukon Territory. All these species belong to the genus *Ceutorhynchus*. One of these, *C. barkalovi*, is an arctic and alpine species, known from southeastern Tuva, Khamar-Daban, Taimyr, Wrangel Island and the upper course of the Yukon; three others are distributed to a varying degree in eastern and central North America.

The steppe fauna weevil communities of northwest North America are less diverse than these communities in northeast Asia. This fauna mainly contains widely distributed Holarctic species, only three Beringian species and five American species (one of these is endemic to the Yukon and Alaska, while another is known from the North-western Territories and the Yukon). It is noteworthy that the North American fauna includes not one Asian species indicative of true steppe environments. *T. tectus* is the only representative of the meadow-steppe fauna that is common to Eurasia and North America (Caldara, 1990; Korotyaev, 1990). It is widely distributed in different meadow-steppe habitats, but it is distributed on the most part of its area on floodplain dry meadows.

4.6.2. Carabidae

The steppe component of the ground beetle fauna of Northwest North America has not previously been thoroughly discussed (Ball and Currie, 1997). On the steppe slopes we examined (Table 7) over two-thirds of all Carabidae are represented by American, mainly widespread xerophilous species. These are *Amara obesa*, *Carabus taedatus*, *Carabus chamissonis*, *Harpalus opacipennis*, *Harpalus fulvilabris*, *H. nigritarsis*, *H. fuscipalpis*, *Cymindis cribricollis*, *C. unicolor*, *Syntomus americanus*, and two species of dry-adapted *Cicindela*. We also found *A. obesa* on the steppe slopes of the Kathul Mountain site, Alaska (Yukon River valley near the Canadian border), and at the Bonanza Creek site near Fairbanks. *Amara (Curtonotus) carinata* was collected from the same site). The first five of these species form a core group. Each species occurs within its own elevational range; only *C. taedatus* is found across the entire elevational transect of study sites. The dominant group includes a single Holarctic species *Amara (Curtonotus*) cf. *torrida*, a boreal species, connected with open, dry biotopes. The other Holarctic species represent an ecologically eclectic group: the above mentioned steppe species *H. fuscipalpis*, forest or tundra species with clearly pronounced xerophilous affinities (*Amara (Curtonotus) hyperborea, Bembidion dauricum*, and *Amara quenseli*), mesic forest and tundra species (*Pterostichus brevicornis*, *Pterostichus pinquedineus)*, and *Nebria borealis*, a tundra species that apparently ranges throughout the whole Beringian region.

5. Discussion

5.1. Diversity of the modern azonal steppes

Relict modern thermophytic steppe areas should be considered steppe ecosystems, separated from the steppe regions. Because the isolation happened at least from the Early Holocene with the collapse of the Beringian steppe-tundra ecosystem and the separated ranges are so remote from the main steppe ecosystems (resulting in provincial differences), the thermophytic steppes of northeast Asia are certainly different from the mountainous steppes of southern Siberia, and also from lowland plain steppes (Yurtsev, 1981). Studied steppe areas that exist due to microclimate, isolation and remoteness from the main range, are inevitably different from the zonal plain steppes. The vegetation differences between azonal steppes of Asia and North America and between zonal and azonal steppes inside each continent are described in botanical studies (Yurtsev, 1981, 1982, 2001b; Ritchie, 1984; Murray, 1987; Lausi and Nimis, 1991; Vetter, 2000).

The main difference in entomofauna between azonal and zonal thermophilous steppes in Asia is the absence in the northern azonal steppes of darkling beetles (Tenebrionidae), which are the most abundant element of the steppes of Central Asia. These are detritus-feeding beetles. Tenebrionidae are also absent in the Pleistocene faunas of Beringia. This is quite difficult to explain by climatic factors, because the modern range of steppe darkling beetles has seasonal temperatures that are similar to those reconstructed for the lower course of the Kolyma River in the Late Pleistocene. Likewise, northeast Asian assemblages (modern and fossil) do not contain the longhorn beetle (Cerambycidae) genus *Eodorcadion*, or comb-clawed beetles (Alleculidae) that are likewise typical of southern Asian steppes. Among other beetles species diversity is lower in azonal steppes. For example, 3 species of the genus *Stephanocleonus* (Table 1) are found in azonal steppe sites, compared with 56 *Stephanocleonus* species recorded in southern Siberia steppes (Chabanenko, 2009). There are also differences in other insect orders (Berman et al., 2001a), but we do not address these aspects here.

The modern existence of relict steppe areas is quite surprising, given their small size and geographic isolation. The functioning of the isolated patches of steppe and the main steppe ecosystems are fundamentally different. In zonal steppe, disturbances such as fires are not major barriers to dispersal, as insects can easily repopulate the disturbed ground from the surrounding areas. This does not work in azonal steppes where the surrounding area is covered by another kind of vegetation. Migrants from surrounding tundra and forest communities avoid steppe patches because of the strong microclimate gradient; tundra and forest insects can visit these areas, but they never live there. So, the isolated steppe patches have only their own repopulation resources. As with steppe vegetation (Yurtsev, 1981), the species diversity of true steppe insects decreases from the Indigirka River basin to the Kolyma River basin by approximately one-third, and it decreases further towards the Chukchi Peninsula (Table 8). There is a considerable drop in mean July air temperatures from the upper Indigirka River to the Chukchi Peninsula, but due to the continental climate of the Central Chukchi Peninsula, this region supports a unique assemblage of xerophilous weevils.

The insect fauna of East Beringia azonal steppes is poor compared with West Beringia. The beetle fauna of Asia azonal steppes has both endemic species and species with disjunctive ranges (Berman et al., 2001a). American azonal steppes have only one specific steppe beetle species – the weevil *C. artemisiae* that is endemic of Yukon and southern Alaska (Anderson, 1984, 1997; Bright and Bouchard, 2008). However, among other insects of East Beringian steppes not only endemics, but also species with disjunctive ranges (Yukon and prairies) have been recorded. They are observed, for instance, in Lepidoptera (Lafontaine and Wood, 1988; Mikkola et al, 1991) and Heteroptera (Scudder, 1993). The origin of such disjunctions is explained from two points of view: they could occupy the Yukon steppe areas in postglacial times, moving from the south (Lafontaine and Wood, 1988; Fimamore, 1997); or they survived in the Yukon from the Pleistocene (Scudder, 1993, 1997).

5.2. Similarity and differences of modern relict steppe and the Pleistocene steppe-tundra

The small size of relict steppe patches is probably responsible for the low number of endemic taxa in northeast Asia. Allopatric speciation in these disjunct communities could have been interrupted many times by the periods of aridity allowing the expansion of steppe areas during dry glacial intervals, or interglacial periods when moist tundra was dominant, as it is today in arctic Siberia. On the other hand, numerous steppe patches would have served as sources of steppe biota that could rapidly colonize the surrounding landscapes when cold, dry climate became dominant, as opposed to a gradual slow expansion of biota from the steppe zones of the south (there was no obstacles for meridian migration in West Beringia (Velichko, 1973, 1993). In North America, south-north migrations were limited by ice sheet isolation (Cwynar and Ritchie, 1980) and, in this case, re-colonisation from the local steppe areas could play an extremely important role during Pleistocene climatic fluctuations.

Endemics of the northern azonal steppes, such as the ground beetle *C. arctica* from West Beringia and *C. artemisiae* from East Beringia are known from the Pleistocene record as common elements of the fossil entomofauna (Kiselev, 1981; Kiselev and Nazarov, 2009; Matthews and Telka, 1997; Zazula et al., 2006). Moreover, *C. arctica* had been found in fossil assemblages[8] before it was described from our collections on the Indigirka relict steppes (Kryzhanovsky and Emets, 1979). Recently, both species exist only on northern azonal steppe areas. This is the only modern evidence of the relationship between them and the Pleistocene steppe-tundra faunas.

A beetle most commonly known in West Beringia Pleistocene deposits, the pill beetle *M. viridis*, has been found in relict (thermophytic and hemicryophytic) steppe areas in Asia, but nowhere else (Berman, 1990, 1992).

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[8] Kiselev, 1974 recorded a fossil Cymindis sp., and later these fossils were re-identified as *C. arctica* (Kiselev, 1981).

Table 8
Species diversity of steppe and hemicryophytic steppe insects on northeastern Asia (number of species).

Group of insects	Indigirka River basin	Kolyma River basin	Chukotka
Carabidae	14	9	–
Weevils (Curculionidae and Apionidae	15	10	14
Meadow-steppe weevils	1	1	1
Steppe weevils	7	3	1
Cryoxerophilous weevils	7	6	12

Table 9
Ecology-faunistic associations of weevils (Curculionidae and Apionidae) on northeastern Asia and number of Holarctic species among them (after Korotyaev, 1977 with add-ins).

Ecology-faunistic associations	Number of species*	Holarctic species
Zonal tundra	5	4
Mountain tundra	15	6
Taiga forest	13	2
Valley forest	18	–
Floodplain willow bush	19	8
Riparian herbaceous	7	2
Meadow	23	10
Steppe	7	–
Tundra-steppe	12	4
Sea cost	2	2

* Some ecological flexible species are included to multiplicity associations (*Lepyrus nordenskioldi*, *Hypera ornata* and others).

A fundamental difference between the relict steppe faunas and the Pleistocene insect faunas (Sher et al., 2006; Matthews and Telka, 1997) of West and East Beringia is the absence in the modern steppe faunas of tundra beetles species such as the ground beetles *Pterostichus agonus*, *Pterostichus costatus*, *Pterostichus sublaevis*, *Stereocerus haemotopus*, *C. alpinus*, *Diacheila polita* and others. All these are now known from the north of the Boreal zone (Lindroth, 1969; Lerh, 1989; Ball and Currie, 1997) where they are found in the permafrost larch sparse woodlands and on marshes, i.e. sometimes not far from steppe areas (based on our modern collections) in the coldest biotopes: on northern slopes, and on slope wash substrates of all aspects where permafrost is very close to the surface. Their ecological requirements are completely incompatible with conditions of thermophytic steppes on southern slopes. But the Pleistocene steppe-tundra environment was suitable for both steppe and tundra insect species, even though they have absolutely different ecological preferences and have never occur in the same places today.

5.3. Fauna of some groups in common between Northeastern Asia and North-western America

An examination of lists of Holarctic species in various taxonomic groups allowed us to analyze the insect faunal exchange between West and East Beringia (see also Elias et al., 2000; Elias and Crocker, 2008). Our analyses suggest possible environmental conditions at the times of these exchanges.

5.3.1. Curculionidae

Of 108 weevil species known from northeast Asia, only 26 have Holarctic distributions (Korotyaev, 1980, 1990; our data, Table 9). These include four moderately xerophilous meadow species, one meadow-steppe species, and five cold-dry adapted (cryoxerophilous) species. There are no Asiatic steppe weevils in America and the single Yukon steppe weevil, *C. artemisiae*, (Anderson, 1997) is absent in Asia. Presence of one species common to both parts of Beringia meadow-steppe weevil (*T. tectus)* is exception to the rule – this particular species is tolerant of meadow environments and can also live on river floodplains (Korotyaev, 1990; Caldara, 1990). The modern weevil fauna of northeast Siberia shows that the Pleistocene environment of the Bering Land Bridge allowed the migration of the meadow and cryoxerophilous species, but was impenetrable for true steppe species.

5.3.2. Carabidae

Both sides of Bering Strait have a limited number of modern steppe ground beetle species in common, or even beetles of steppe-origin, such as *Poecilus* spp. In fact there are only four such species: *Harpalus vittatus*, *Harpalus obtusus*, *H. fuscipalpis* and *P. nearcticus*. The ground beetle *H. vittatus* has been subdivided into three subspecies with different ranges. *H. vittatus vittatus* lives today in southern Siberia from the Altai Mountains and Transbaikalia to Mongolia. Two other subspecies of *H. vittatus* are described from Western Beringia: *H. vittatus kiselevi* is found in Lena and Yana River basins. The second subspecies, *H. vittatus alaskensis* is found in the basins of the Indigirka Kolyma Rivers and in Alaska, where it was previously described as *Harpalus alaskensis* on the basis of a single specimen (Lindroth, 1969)[9]. The range of *H. obtusus obtusus* includes southern Siberia, Mongolia, and northern China. *H. obtusus amputatoides* was described from the basins of the Lena. This beetle has not been found in the modern fauna of the eastern part of northeast Asia. *H. obtusus amputatus*[10] is widely distributed in North America, ranging from grassland habitats of Alaska and the northern parts of the Yukon and Northwest Territories of Canada to the central plains of the lower 48 states (Lindroth, 1969; Kataev, 1987, 1990). *H. fuscipalpis* is widespread in Europe, in the south of the former Soviet Union, in Mongolia, China, northern India, and is widespread in North America (Kataev, 1987). We collected an abundance of this species on the Indigirka River, and a few specimens in the upper reaches of the Kolyma River, on the edge of the Bolshoi Annachag Range.

Modern finds of *P. nearcticus* show that although its subgenus is rooted in the steppe, the species itself is not a steppe taxon. A similar interpretation may be applied to the northern subspecies of the steppe beetles *H. vittatus* and *H. obtusus*. It is noteworthy that even the most characteristic of the Asian hemicryophytic steppe carabid beetle species (*H. lederi*, *P. eximius*, *Carabus odoratus* and *C. kolymensis*) are not found in North America. On the other hand, American xerophilous carabid species such as *C. chamissonis* and *C. taedatus* have never been able to penetrate west of the Bering Land Bridge into the Chukchi Peninsula.

5.4. Insects as temperature and environment indicators in West Beringia

The study of the modern distribution and ecology of the steppe insects (including the Phytophagous families: Curculionidae and Chrysomelidae) found in Pleistocene deposits allow us to reconstruct some features of glacial-era Pleistocene climate of West Beringia (Kiselev, 1981; Berman, 1983; Alfimov and Berman, 2001;

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[9] The distribution of the fossil *Harpalus vittatus* subspecies is slightly different. Most of fossil specimens of *Harpalus vittatus* in West Beringia belong to *H. vittatus kiselevi* Kataev and single specimens belong to two other subspecies (Kataev, 1990; Kiselev and Nazarov, 2009); while all East Beringian fossils belong only to *H. vittatus alaskensis* (recorded as *H. alaskensis* in Matthews and Telka, 1997; Zazula et al., 2007).

[10] This subspecies (recorded as *Harpalus amputatus*) was present in the East Beringia fossil record (Matthews and Telka, 1997).

Alfimov et al., 2003; Sher et al., 2002)[11]. Strict stenothermic species (i.e. species restricted to a narrow range of temperatures) are the most useful indicators of Pleistocene climate. Using these indicators, it is possible to quite reliably reconstruct microclimate, and through that, the past climate of territories where fossil insects are found.

Thermophilous weevils of the genus *Stephanocleonus* and one of the dominant species of hemicryophytic steppes, the pill beetle *M. viridis* (Berman, 1990, 1992; Berman and Alfimov, 1998) are among the numerous, easily collected, and relatively well studied species. Within the main part of the range of the weevil genus *Stephanocleonus* in southern Siberia and in northeast Asia, the air temperatures differ very significantly (18–20 °C in July in the Tuva region and 13–15 °C in the Kolyma and Indigirka river basins). However, in northeast Asia, the distribution of steppe weevil species is apparently limited not by summer or winter air temperatures *per se*, but by the SDD (soil degree days) of the upper layers of soil (i.e. positive degree days), in which the larvae develop.

In the upper reaches of the Indigirka River, in the habitats of the beetles discussed, on dry steep slopes of southern aspect, facing the valleys of large rivers, SDD on the soil at a depth of 5 cm is approximately equal 2400 °C whereas the mean July temperatures are 22–24° and maximum temperatures are 58–62°. (Berman and Alfimov, 1993). Such high heat supply in the subarctic regions at latitudes of 63–67° is only possible in an environment with a highly transparent atmosphere and low precipitation, which is typical of continental climates. The increase in the temperature gradients between the ground surface and the air is the most important factor determining the distribution of thermophilous weevils (Alfimov, 1998). Here, the degree of climatic continentality is 2.2–2.4 according to Ivanov (1959), which is 85–90% of the maximum values recorded on Earth. Because of the disproportional (in relation to the air) increase in the soil temperature, the heat supply of the upper layer of the soil in the thermophytic steppes on southern slopes in the valleys of the Kolyma and Indigirka Rivers approximates that of the steppes of southern Siberia and Central Asia, where the degree of climatic continentality is 10–15% lower.

Records of the *Stephanocleonus* remains from Pleistocene cold periods, in particular during the last glaciation in the lower reaches of the Kolyma River (Kiselev, 1981) and during the LGM in even the northernmost regions, such as the Lena River delta, (Sher et al., 2005; Wetterich et al., 2008), allow reconstructions of the environment and climate of those times. The fundamental principle of this reconstruction is that the soil temperature in the Pleistocene habitats of *Stephanocleonus* should have been at no lower than those presently recorded in the upper reaches of these rivers. This reconstruction contradicts the majority of LGM paleoclimate reconstructions based on general circulation models, paleobotanical and other data. In the majority of cases, the reconstructed air temperatures in the Kolyma–Indigirka Plain are about 0–4°. (Budyko et al., 1992; Velichko, 1993; Kutzbach et al., 1998; Kim et al., 2008 and others) which would exclude the possibility of the existence of thermophilous weevil species, even in the warmest biotopes. However, our reconstruction of LGM TMAX in this region, based on the thermal requirements of these weevils and taking into account the degree of continentality, air temperature on a regional scale, and soil temperatures of the warmest biotopes, yielded quite different results (Alfimov, 1998). However our reconstruction of LGM TMAX in this region, based on the thermal requirements of these weevils and taking into account climate continentality, (Alfimov, 1998), yielded quite different results. Given the most conservative scenario, that the weevils were restricted to the slopes of southern aspect, the TMAX values needed to generate soil degree days in the range of 2200–2300° would have had to be at least 11–12°.

This climatic reconstruction is also somewhat contradictory to our own estimates based on the ecological requirements of another stenothermic beetle, *M. viridis* (Berman, 1990, 1992, 2001). Based on the wide range of this species in the fossil record of West Beringia, and its ubiquity in regional fossil records, it would appear that *M. viridis* should be capable of survival in a range of climatic conditions. However, studies of modern specimens suggest it has a narrow range of environmental tolerances. At present *M. viridis* is almost exclusively found in hemicryophytic and tundra-steppes patches in the upper reaches of the Kolyma River, at all altitudes. We have also found it on thermophytic steppe habitats in the Kolyma and Indigirka River valleys, as well as in tundra-steppe areas in the Amguema and Anadyr valleys, and in the mountains surrounding the Chaun depression. A general range of SPT of the soil in these localities is 720–2000°, but the range of soil water content and vegetation cover is very narrow. We do not know with any certainty whether the environmental tolerances of this beetle were the same during the Pleistocene as they are today. Some limiting factor could have been different in the past. For example, in the modern environment the strong wind is a necessary factor, because it removes the deep snow cover that typifies the areas surrounding *M. viridis* habitats. Perhaps snow cover was substantially less during Pleistocene cold intervals. Thus, *M. viridis*, while certainly a xerophilous species, tolerates a much broader range of summer temperatures, and it is less thermophilous than *Stephanocleonus*.

In contrast to other xerophiles, *M. viridis* reliably indicates several other climatic features, including little snow cover, dry summers, and sparse vegetation. It is associated with a vegetation cover of grasses, the xerophilous sedge *C. argunensis* or ecologically similar species, and most importantly the presence of the moss *P. piliferum*. Our conclusion that this species requires little snow cover (either through scarce snow fall or strong winds that sweep snow from the landscape), dry summers and variations in heat capacity do not contradict some previous environmental reconstructions of Beringia (Tugarinov, 1929; Sher, 1967; Guthrie, 1968). These climatic characteristics can be extrapolated relatively broadly, since they would dominate the environments of large lowland regions. Evidently, reconstructions of the environment based on the ecological requirements of thermophytic weevils and *M. viridis*, have both similarities (dry summers), and differences (SPT of the soil requirements of *M. viridis* and *Stephanocleonus*). There are further difficulties in reconstructing past winter environments. *M. viridis* can survive highly severe winters, but the range of winter conditions found in the modern relict steppe habitats of *Stephanocleonus* are highly variable.

5.5. *Reconstruction of climate suitable for tundra and steppe insect species*

Pleistocene fossil assemblages from both West and East Beringia include not only steppe, but also tundra insect species. Their association has repeatedly been discussed in the literature (Kiselev, 1981; Matthews, 1982; Elias, 1994; Sher and Kuzmina, 2000; Alfimov and Berman, 2004; Kiselev and Nazarov, 2009) and was connected with the mosaic of habitat types (from steppe to wetland) on permafrost landscapes. This combination of insect species is presently not found anywhere. Therefore it is impossible to use full modern analogues to reconstruct Pleistocene environments. The Mutual Climatic Range (MCR) method has been used to reconstruct Late Pleistocene climates in West Beringia (Alfimov et al., 2003). The lower temperature boundary was determined

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[11] Similar works in East Beringia based on steppe beetles including phytophagous taxa have not yet been completed.

by the ecological requirements of thermophilous weevils. The highest lower limit (+12 °C) of TMAX was set by the requirements of *S. eruditus*. Three other species of this genus in high mountain regions of Tuva and Mongolia can exist where TMAX is only 9–10 °C.

Based on the thermal tolerances of the tundra rove beetle *Tachinus arcticus*, the upper limit of TMAX for assemblages in which this species occurs is 13 °C. This beetle lives today throughout the whole tundra zone of Asia, and scarcely occurs outside the tundra (Ullrich and Campbell, 1974).

Finally, the last tundra species commonly found in these depositions is the water scavenger beetle *Helophorus splendidus*. This species inhabits small pools from the Gyda Peninsula to the western Chukchi Peninsula and from Okhotsk Sea coast to the continental regions of the upper reaches of the Kolyma River. The upper TMAX limit of its climate envelope (13.6 °C) is similar to that of *T. arcticus*.

Based on the climate envelopes of these beetles, we estimate that Late Pleistocene TMAX in parts of West Beringia was at least 12 °C, a value that is at least 1 °C higher than modern TMAX in this region. Using reconstructed calibrated temperatures [i.e. temperatures corrected to compensate for the main errors of the method (Alfimov and Berman, 2009)], the resulting values show that in the lower reaches of the Kolyma River during the last glaciation, July was warmer than today by at least 3 °C. Thus, the study using the MCR method not only confirmed the result that we obtained by estimating the heat requirements of thermophilous weevils (Berman, 1983; Berman and Alfimov, 1998), but also showed somewhat higher summer temperatures for the LGM.

As discussed above, we reconstruct a highly continental climate for much of West Beringia during the Late Pleistocene. In order to reconstruct the style of climate that would allow the co-occurrence of tundra and steppe insects, it is necessary to factor in contrasting microclimates. Such climatic variability could only be found under mosaic conditions of relief at the meso- and micro-scales (Alfimov, 1988; Berman and Alfimov, 1993; Sher and Kuzmina, 2000; Berman et al., 2001a).

5.6. Fossil insect evidence

The fossil insect faunas of West and East Beringia each had their own dominant species. Steppe-tundra faunas from East Beringia are most often dominated by *L. lineaticollis*, whereas steppe-tundra faunas from Western Beringia are often dominated by *M. viridis*. The ancient steppe-tundra fauna from West and East Beringia exhibited relatively low species diversity – significantly lower than that of the modern taiga and southern tundra. The fossil Beringian assemblages trend towards dominance by just one or a few species, and also contain large numbers of species that today are quite rare. For instance, pill beetles usually play a minor role in modern regional faunas. The only habitats where pill beetles such as *M. viridis* are dominant are areas of relict steppe, such as the hemicryophytic steppe. In the Pleistocene, this species was superdominant in West Beringian steppe-tundra assemblages, often comprising 90% of the total number of individuals in a fauna (Kiselev, 1981; Kiselev and Nazarov, 2009).

In East Beringia, an apparently extinct close relative of the above species, (certainly different than Asiatic *M. viridis* and than *M. aeneolus*, currently occurring in Alaska and Yukon), was often important, but it rarely accounted for more than 10% of the specimens in fossil assemblages (Matthews and Telka, 1997; Nelson and Carter, 1987; Kuzmina et al., 2008; Zazula et al., 2006). In the modern landscapes of Eurasia and even more so in North America, *Morychus* beetles are usually only found by experienced entomologists who know exactly where to look. Such rare taxa would seem unlikely to be preserved in fossil assemblages, and in fact they are very rarely found in fossil faunas from the mid-Holocene onwards (Kiselev and Nazarov, 2009; Kuzmina and Sher, 2006; Andreev et al., 2009; Matthews and Telka, 1997). The Pleistocene species of *Morychus* apparently evolved independently in West and East Beringia. After widespread tundra-steppe landscapes disappeared, *M. viridis* was restricted to the isolated areas of hemicryophytic steppe that are found today in northeast Asia, while the American species apparently did not find such a favourable environment. We did not find the equivalent relict habitats along the Yukon River and its tributaries, despite careful searching. Moreover, the moss *P. piliferum* (a host plant of *M. viridis*) is not a very important element in the moss flora of East Beringia today (Barbara Murrey, pers. comm.).

It is noteworthy that fossil faunas from throughout Beringia contained weevils of the subfamily Cleoninae. In the modern and fossil faunas of West Beringia they are more numerous and diverse, which is apparently due to the Asian origin of the group. Cleoninae are extremely rare in the North, and like *Morychus*, they can be only found by experienced entomologists. However, this group is recorded almost everywhere and over a wide chronological range in Pleistocene assemblages, suggesting their ubiquity on Pleistocene landscapes (Kiselev, 1981; Anderson, 1997; Matthews and Telka, 1997; Sher et al., 2006; Kiselev and Nazarov, 2009). West Beringian fossil assemblages also contain species of Cleoninae known recently only from southern Siberia and Mongolia. The Pleistocene faunas of East Beringia also contain similar southern migrants represented by American species (Zazula et al., 2006; Kuzmina et al., 2008; Kuzmina, unpublished data), some of them are difficult to identify and are possibly extinct[12].

Only one Asian species of the Cleoninae, *C. zherichini*, penetrated into the Nearctic. It was found in the Yukon (Keele Range, Blue fish Caves) by Anderson (1997) and described as *Stephanocleonus stenothorax*, but later synonymised under *C. zherichini*. (Anderson, 1988) *C. zherichini* is otherwise only known from the northeastern Palaearctic (Korotyaev, 1980; Ter-Minasyan, 1988). On the Chukchi Peninsula this species is found only on relict hemicryophytic steppe or steppe-tundra. Based on its habitat requirements, this is a cryoxerophilous species. It is rare in fossil assemblages from West Beringia (Kiselev and Nazarov, 2009), but more or less common in East Beringian faunas. *C. zherichini* has been found in many fossil samples from the Klondike and Old Crow regions of the Yukon (Kuzmina, unpublished data).

The fossil record of *L. lineaticollis* in West Beringia is particularly interesting, as it is only known from Miocene-age faunas at the Ary-Mas locality (however, this identification needs to be verified), in the western part of the region (Elias et al., 2006). It has not been found in Pleistocene or Holocene faunas, even in the eastern parts of the Chukchi Peninsula, even though it lives there today. Perhaps this species was accidentally introduced by man in recent years, although the mechanism for such an introduction remains unclear. In contrast to this, *L. 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 is not found in Asia today.

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[12] Matthews and Telka (1997) noticed the presence of *Stephanocleonus* sp. in East Beringia faunas. But, B. Korotyaev (Berman et al., 2001b) considers that all American *Stephanocleonus* belong to the genus *Coniocleonus*, which has been previously removed to synonymy for *Stephanocleonus* by R. Anderson (1989). B. Korotyaev (pers. comm.) has also examined some fossil Cleoninae specimens from Alaska and Yukon collected by S. Kuzmina. According to his opinion, all of them belong to North America *Coniocleonus* species. S. Kuzmina et al. (2008) has found the southern species *Coniocleonus confusus* and *C. parshus* in Late Pleistocene faunas from Alaska.

The weevil *C. artemisiae* has never been found in Asia, past or present. This strictly xerophilous species, a modern endemic of the Yukon and adjacent regions of Alaska, is commonly found in Pleistocene faunal assemblages from East Beringia (Matthews and Telka, 1997; Zazula et al., 2006, 2007); the fossils were recorded not only from the Yukon, but also from the Northwest Territories and from Alaska (Anderson, 1984). The northernmost site is on the Alaskan North Slope site of Titaluk River, in Late Pleistocene assemblages (Nelson, 1982). Obviously *C. artemisiae* was more widespread in the Pleistocene than it is today, but its range probably did not reach the Bering Land Bridge. *C. artemisiae* has not found in the areas close to the Bering Land Bridge, such as sites on the Seward Peninsula (Matthews, 1974 (revised in Matthews and Telka, 1997); Kuzmina et al., 2008).

The Eurasian weevil genus *Phyllobius* has practically not been found in fossil assemblages from North America. There is only one find in the Pliocene of Alaska (Matthews and Telka, 1997), but this identification needs verification. Apparently it has been introduced in America in recent years (Bousquet, 1991). In West Beringia fossil assemblages these weevils, including *P. kolymensis*, flourished, especially when the steppe aspects of the steppe-tundra were expanding. At least two species of the genus are thought to now be extinct (Korotyaev and Kuzmina, unpublished data). These species are only known from fossil faunas associated with xerophilous landscapes in the upper reaches of the Kolyma River (Kiselev, 1981; Kiselev and Nazarov, 2009).

Pleistocene entomofaunas throughout Beringia (Matthews and Telka, 1997; Sher et al., 2006) often contain large numbers of dung beetles in the genus *Aphodius*. These beetles are not commonly found in either the modern tundra or the northern taiga (Gordon and Skelley, 2007), and are also lacking in Holocene fossil assemblages (Kuzmina and Sher, 2006; Kuzmina, unpublished data). High concentrations of *Aphodius* are characteristics for Beringian faunal assemblages taken from ancient ground squirrel nests (Gubin et al., 2003; Zazula et al., 2011). It is possible that these dung beetles fed on ground squirrel droppings, although the abundance of ungulates (and hence their dung) must also be carefully considered. Although we cannot yet identify fossil Aphodius to species, those in Asia and America were apparently different, possibly representing a case of parallel evolution.

As expected, there are larger numbers of Holarctic species of hygrophilous tundra beetles, although there are some differences between northeast Asia and northwest North America. For instance, of the 65 species of hygrophilous tundra ground beetles (Chernov et al., 2000, 2001), only 37 species are Holarctic. The differences are the greatest in the typical tundra subgenus *Cryobius* in the genus *Pterostichus*. Of eleven species listed for the Asian Arctic, only three (*P. brevicornis*, *Pterostichus pinguedineus* and *P. ventricosus*) are Holarctic; these species have always been most abundant in the Beringian region. Together with P. *sublaevis*, *P. vermiculosus* and *Amara (Curtonotus) alpina* they inhabited the entire territory of Beringia throughout the Late Cenozoic (Sher et al., 2006; Matthews and Telka, 1997). A different pattern is displayed by the Siberian species *Pterostichus abnormis*. This species is common in fossil assemblages from West Beringia, but it apparently has never been part of the East Beringia fauna. Most fossil specimens of *Pterostichus (Cryobius)*, apart from three mentioned above from the Asian sections, have not been identified to the species level in West Beringia faunas. They are extremely variable and apparently many of them belong to the Palaearctic species *Pterostichus nigripalpis*, which is absent in America in fossil and modern faunas. Fossil *Pterostichus (Cryobius)* spp. are better known in East Beringia. These assemblages contain abundant remains of *Pterostichus arcticola*, *Pterostichus caribou*, *Pterostichus kotzebuei* and other species that have never been identified in Asian faunas (Matthews and Telka, 1997; Chernov et al., 2000, 2001; Elias, 2000; Sher et al., 2006).

The absence of exchange between the steppe beetle species of West and East Beringia agrees well with the theory that the BLB served as a mesic filter on the migration pathway of Beringian biota (Sher, 1971; Elias et al., 1992, 1996; Berman, 2001; Guthrie, 2001; Yurtsev, 2001a; Ager, 2003). However, the large area of the BLB does not conform to the hypothesis of a monotonous tundra landscape. Based on pollen, plant macrofossils and insect fossil evidence from different parts of this territory during the LGM, there were a variety of types of tundra on the land bridge: cold arctic, mesic, herb, birch-graminoid and shrub tundra (Elias and Crocker, 2008). A possible reason for the limited faunal exchange could be that the corresponding ecological niches were already occupied by indigenous species (Sher, 1971). This is one possible reason for the persistence of different species of *Morychus* on either side of Bering Strait. The easternmost modern finds of *M. viridis* are from the middle reaches of the Amguema River (Berman et al., 2001a); the easternmost fossil locality is in the vicinity of Anadyr, Chukotka (Kuzmina, unpublished data). The westernmost find of the extinct American species of the genus *Morychus* is the Seward Peninsula (Kuzmina et al., 2008). Thus, the distance between the ranges of these species in the Pleistocene was not very great. The reason why *L. lineaticollis*, a species tolerant of tundra conditions, did not penetrate into Asia in the Pleistocene is more difficult to explain.

5.7. *Area of distribution of the Pleistocene steppe-tundra*

The climate of West and Central Beringia (Fig. 3) should be considered one of the important factors preventing migration of some steppe species across the BLB. The MCR analysis based on fossil evidence allows us to be sure that the growing degree day values of the Asian steppe-tundras discussed in this paper were only achieved during the Last Glaciation (LG) in the lower reaches of the Kolyma River. In other parts of West Beringia the climate could have been considerably different. Unfortunately, it is difficult to reconstruct temperatures in all parts of West Beringia based on beetle evidence, because of the lack of studied faunas (past and present) in this enormous region.

The climate reconstructions based on climate modelling for the northern Pacific (CLIMAP Project Members, 1994 and others) and using modern regional temperature gradient for the mean July and January air temperatures (Alfimov and Berman, 2004) allows better understanding of the past distribution of steppe-tundra. It was shown that in the Subarctic lowlands west of Chaun Bay, the regression of sea level in the Arctic Ocean played a major role in LG climate forming. As a result LG TMAX values in this region should have increased to 11–12°. These values coincide with the estimates based on the ecology of the steppe beetle species and MCR method, which we obtained previously (Berman and Alfimov, 1998; Alfimov et al., 2003).

To the east on the BLB the combined effect of global and regional factors produced a different result (Alfimov and Berman, 2004). Even at the times of the maximum sea level drop (by 120 m) (Creager and McManus, 1967; Hopkins, 1982; Elias et al., 1996) LG TMAX in the northern part of the land bridge reached only 10 °C. It appears that the boundary of extremely continental climate did not go significantly east of 180°E, i.e. up to the upper Anadyr River basin (Fig. 2). Actually this boundary must have been located even further west, because in this scheme we do not take into account the impact of mountain glaciation. During the LGM glacial ice occupied a considerable part of the eastern mountains (Glushkova and Prokhorova, 1989), but the vast plain areas on Chukotka remained ice-free. Thus, the tundra-steppes fell short by approximately

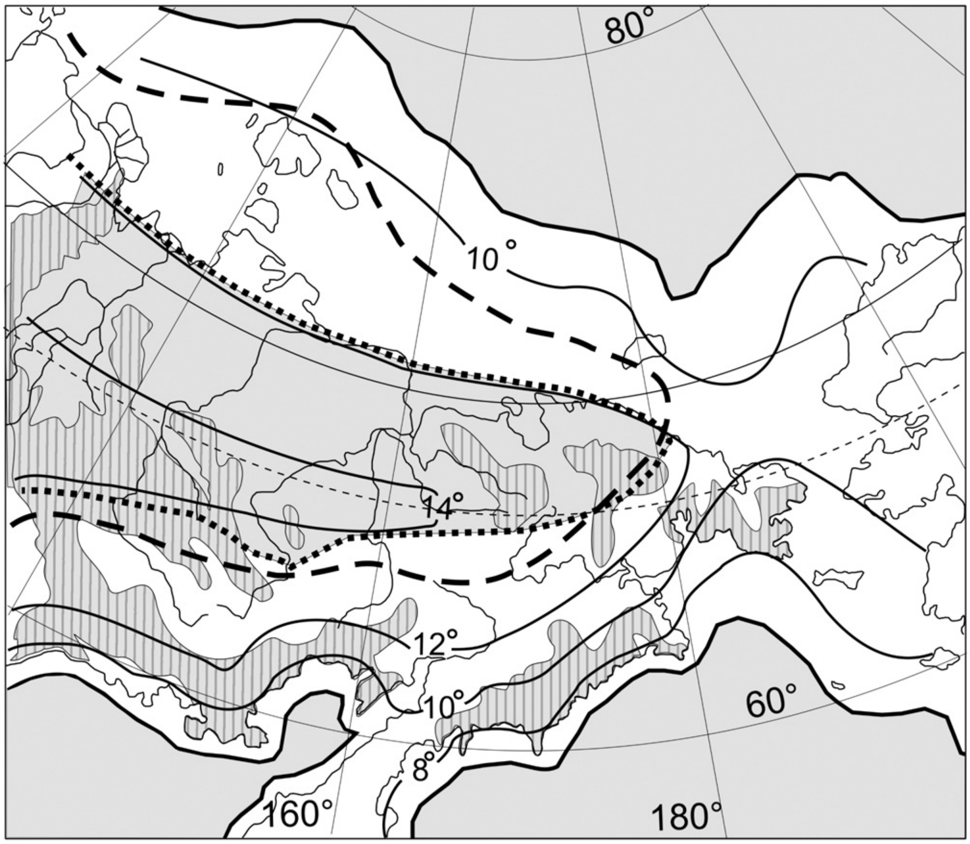

Fig. 3. Mean July temperature isotherm reconstruction (solid line), isoline of maximum climate continentality (hatched line), estimated boundaries of thermophilous steppes (filled outline) and glaciations in West Beringia (hatched outline according to Glushkova and Prokhorova, 1989 with additions) during LGM with sea level regression of 100 m.

100 km of reaching the Bering Land Bridge, and thermophilous insects could not use the Anadyr River basin as an eastern migration pathway because of insufficiently high air temperatures and low continentality of the climate. Thus, in the LG only steppe species that were tolerant of low-summer temperatures could migrate from West to East Beringia via the BLB (Yurtsev, 1974; Berman, 2001).

5.8. *Transcontinental fauna exchange in the Pleistocene*

We do not deny the traditional view that the BLB acted as a migrational filter (Elias et al., 1996, 1997; Guthrie, 2001), because its climate was more humid than that of West and East Beringia. Our reconstruction of summer temperature regime and continentality during the LGM in West Beringia (Alfimov and Berman, 2004), strongly suggests that the tundra-steppes with Asian steppe species never got as far east as the Anadyr River basin, let alone the Chukchi Peninsula. In other words, the ‘filter’ region began far to the west of the BLB, although parts of the exposed continental shelf 200–300 km offshore of the current coastline of the Arctic Ocean to the west of the Chaun Bay had temperatures suitable for steppe biota. However, we note that the Pleistocene ranges of *M. viridis* and the fossil American *Morychus* species nearly overlapped, as the former got as far east as the Chukchi Peninsula and the latter got as far west as the Seward Peninsula. Thus, during marine regressions they could have been in contact on the BLB. The main insect exchanges across Bering Strait probably occurred in pre-Quaternary times, possibly as early as the Miocene (Matthews, 1980). Petrov (1966) considered the time of the deposition of the Koinatkhun Formation on the Chukchi Peninsula and the similar Bering Formation of Alaska as the last stage of the permanent existence of thermophilous forest vegetation in Beringia. The Bering Formation is no younger than 2.2 mya (Creager and McManus, 1967). According to Petrov (1966), on the Chukchi Peninsula during the Koinatkhtun interval the vegetation changed from taiga to forest-tundra. It is possible that the exchange of thermophilous dry-adapted invertebrate taxa, potential members of steppe-meadow and azonal steppe communities inside forest zone, ended at the same time.

6. Conclusions

1. Azonal steppes of northeastern Asia and north-western America (Pleistocene Beringia) are characterized not only by specific vegetation, but also by their insect fauna; this is sharply different from the fauna of the surrounding tundra and taiga communities.
2. The insect fauna (like the flora) of azonal steppes shares species in common with the steppes of Mongolia, Kazakhstan, and Southern Siberia; the species have disjunctive ranges.
3. The existence of modern Beringian steppe habitats inside such generally cold environments as the northern taiga and tundra is only made possible by the existence of specific microclimates.
4. Some insect species recorded from modern Beringian steppes were common members of the Pleistocene steppe-tundra fauna. These include the weevils *S. eruditus* and *S. fossulatus* and the pill beetle *M. viridis* for West Beringia and the weevil *C. artemisiae* for East Beringia. This commonality allows us to compare the affinity of the modern azonal steppes and the Pleistocene steppe-tundras in Beringia.

5. Azonal steppes in West Beringia are clearly subdivided into two main types: thermophytic and hemicryophytic. The first one occupies the warmest steep dry slopes and, rarely, river floodplains. The second one occupies also dry sites, but these localities differ in their supply of summer warmth; they are essentially snowless in the winter, and they occur in open areas. The indicator beetles for the thermophytic steppe type in the West Beringia are weevils of the genus *Stephanocleonus*; the characteristic species for the hemicryophytic steppe type is the pill beetle *M. viridis*.
6. The beetles *S. eruditus*, *S. fossulatus* and *M. viridis* are useful environmental indicator species, providing strong indications of microclimate. This allows us to use them for palaeoenvironmental reconstructions. The presence of *S. eruditus* and *S. fossulatus* in fossil assemblages allows us to infer that mean July temperatures associated with these assemblages were not lower than 11–12 °C, developing within a highly continental climate with low levels of precipitation and high air transparency. The dominance of *M. viridis* in West Beringian fossil assemblages indicates a floristically poor, low productivity sedge steppe, with low humidity, but possibly broad temperature ranges.
7. Only thermophilous steppe is known to have existed in East Beringia. Asiatic steppe beetles are not recorded from East Beringia, either in modern steppe environments or from fossil steppe-tundra assemblages. This is one piece of evidence indicating restricted migrations of the thermo-xero-philous beetle fauna between Asia and America. Paleoclimate reconstructions for East Beringia have their own important steppe species, such as *Connatichela artemsiae*, but the temperature preferences of such species are poorly known. This is a task for future investigations.
8. The important differences between the insect faunas of modern azonal steppes and those of Pleistocene steppe-tundra assemblages do not allow us to consider modern azonal steppe communities as fully applicable analogues for Pleistocene steppe-tundra communities.
9. There is a trend of declining species diversity in xerophilous insect faunas from the modern steppe communities from the Indigirka River basin eastwards to Chukotka. There is a similar trend in the fossil assemblages from these regions. This helps explain the restricted migrations between West and East Beringia. The discontinuity of insect steppe communities in Asia and America may have been caused not only by unsuitable environments on the Bering Land Bridge itself, but more importantly, the Chukotka region may have been an important barrier to dispersal. We interpret this region to have been dominated by mesic environments during the last glaciation.

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