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Paleoenvironmental reconstruction of the Last Glacial Maximum, inferred from insect fossils from a tephra buried soil at Tempest Lake, Seward Peninsula, Alaska

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ABSTRACT

Sediments and vegetation dated 21,570 cal yr BP were buried under tephra on the northern Seward Peninsula. This buried surface has yielded plant macrofossils in growth position, as well as numerous insect fossils, excellently preserved in permafrost. It appears that many of the insects were buried alive by the volcanic ash. The species composition and ecological affinities of this fossil fauna are typical of Alaskan Late Pleistocene steppe–tundra environments. The assemblages are dominated by the weevil *Lepidophorus lineaticollis*, one of the most common species in Eastern Beringian Pleistocene fossil assemblages. Many other members of the ancient steppe–tundra insect community are preserved in these assemblages, including the pill beetle *Morychus* sp. and weevils of the genus *Coniocleonus*. In Alaska, most of these species (but not all of them) survived the Pleistocene/Holocene environmental transition, but are restricted today to relict patches of steppe-like vegetation. Faunal diversity is low, in spite of the recovery of more than 1000 individual insects and mites including more than 600 beetles. This reflects the small number of species adapted to the cold, dry environments of the LGM in Eastern Beringia. They represent an ecosystem which no longer exists.

1. Introduction

The northern Seward Peninsula (Alaska), currently a part of the Bering Land Bridge National Park, is one of the most remarkable areas of Quaternary vulcanism in permafrost areas. According to the report summarizing 40 yr of geological observations here (Hopkins, 1988), the Cape Espenberg–Devil Mountain volcanic field consists of five small shield volcanoes and five maars. These structures repeatedly erupted during the Late Cenozoic, producing eruptions that generated large amounts of volcanic tephra during the Middle and Late Pleistocene and the Holocene.

One of the more recent eruptions occurred during the LGM (Last Glacial Maximum) interval, ca 18,000 ^{14}C yr, or about 21,600 cal yr BP. It resulted in the formation of Devil Mountain Lake craters and a widely distributed Devil Mountain Lake tephra (DMLt), which covered the surface of about 2500 km^2 with a thickness up to a few meters (Begét et al., 1996; Höfle et al., 2000). Over this large area, the DMLt buried the tundra-vegetated soil, preserving plants, insects and other organisms in perfect condition in permafrost. Later, the contact between the buried soil and tephra was exposed by erosion related to expansion of thermokarst lakes. The buried soil, named the Kitluk Paleosol (KP), became the object of multidisciplinary research supported by the U.S. National Park Service (NPS) during the summers of 1993, 1994, and 1995. The field team excavated the buried surface at 18 sites located on the banks of nine thermokarst lakes. The results of studies of the soil profiles and properties, former active layer conditions, pollen and plant macrofossils and insects have been published in a series of works (Goetcheus et al., 1994; Höfle and Ping, 1996; Höfle et al., 2000; Goetcheus and Birks, 2001; Goetcheus, 2001; Elias, 2000, 2001).

However, the sampling technique used (see “Methods”) yielded only small numbers of insect fossils (less than 100 beetle individuals from seven sites, i.e. 1–10 individuals per sample). During the summer of 2003 an international group including Paul Matheus (USA), John Storer (Canada), and Svetlana Kuzmina and Andrei Sher (Russia) visited the Tempest Lake site in the Devil Mountain Lake region. The site was chosen for study because an undisturbed geological section was exposed along the lake shore, whereas other nearby lake sites had sediments disturbed by solifluction or covered by modern vegetation. One of the principal aims of the group was to screen bulk samples from the site to obtain a large number of insect fossils, sufficient for estimates of the ecological structure of the beetle assemblages.

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2. Study area

Tempest Lake is situated near the northern coast of the Seward Peninsula at 66° 28′ 53″ N and 164° 24′ 13″ W (Fig. 1A). The modern vegetation is typical lowland shrub tundra, dominated by dwarf shrubs, including *Salix*, *Betula nana* L., *Ledum palustre* ssp. *decumbens* (Ait.) Hultén, and *Vaccinium uliginosum* L., as well as sedges, forbs and mosses. The modern vegetation cover is quite dense; the soil ranges from moist to wet, and drier, open soils are rare, even on south-facing slopes. The modern beetle fauna of the Tempest Lake area is not very rich in species; we collected ground beetles such as *Pterostichus* (*Cryobius*) spp., *Bembidion* spp., *Nebria* spp. and a weevil in the genus *Dorytomus*. Since the site visit was in early summer, normally a good time for beetle collecting, such poor species diversity is probably due to the uniformity of wetland vegetation with uninterrupted moss cover, a type of habitat not preferred by many kinds of beetles. For comparison, the modern beetle fauna found along the coast near Kotzebue is much more diverse. In this coastal region dry, open ground is common.

The study region was blanketed by a thick tephra layer from the Devil Mountain Lake eruption (DMLt) at 18,000 ^{14}C BP (calibrated age

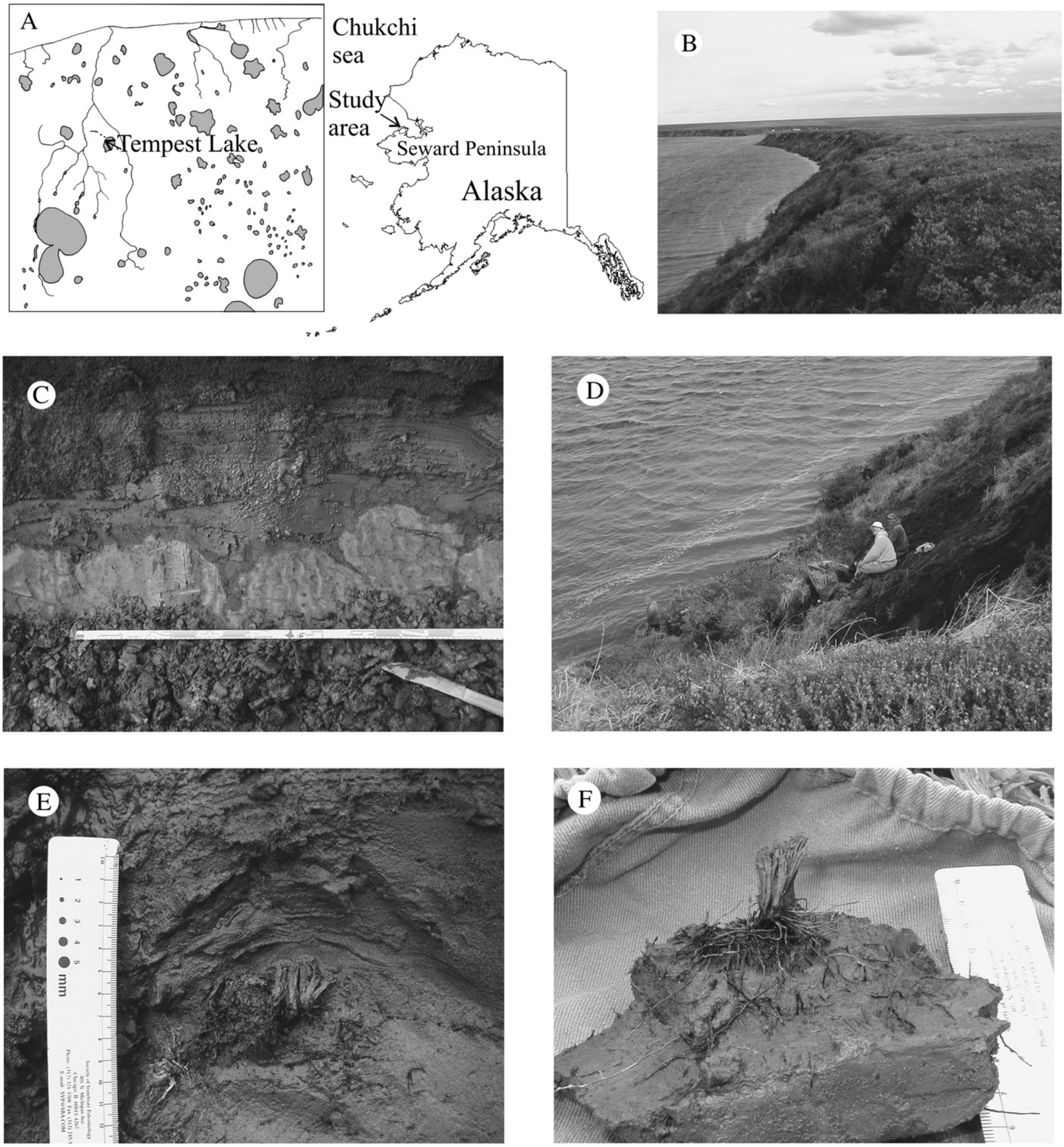

Fig. 1. A — Map of the study area (after Goetcheus and Birks, 2001); B — the Tempest Lake section, 2003; C — view of the buried surface; D — sampling; E — fossil sedge *in-situ*; F — fossil sedge. Photos by AS.

21,570 cal yr BP). Despite some differences in radiocarbon ages associated with this eruptive event (Goetcheus and Birks 2001), there was probably just one great eruption within a period of weeks or months (Begét and Mann, 1992), or perhaps within just a few hours to a few days (Begét et al., 1996). This event took place in late winter or early spring (Goetcheus and Birks, 2001), or, alternatively, in the late fall, immediately prior to freeze-up (Höfle et al., 2000). The vegetation buried by the tephra consists of mosses, shrubs (*Salix arctica* Pall. and other dwarf willows), grasses and sedges (dominated by *Kobresia myosuroides* Vill.) and herbs and forbs, including *Draba* (Goetcheus and Birks, 2001). Mosses covered more than half the land surface. *K. myosuroides* is a xerophilous sedge species, adapted to open ground habitats and common in ancient arctic-steppe communities. In Alaska today it is found growing on dry, mostly calcareous slopes, on gravel bars, and on lichen tundra (Hultén, 1968). *Draba* is tolerant of soil disturbance, and it occurs in Alaska today in localities where animal disturbance by grazing, manuring, and burrowing is strong (Walker, 1990). In Alaska, most species of *Draba* are found today on dry mountain slopes, in rocky places such as scree slopes, or on dry tundra (Hultén, 1968). Taken together, the plant macrofossils from the buried surface are indicative of dry tundra and arctic-steppe environments, different from any modern tundra plant communities (Goetcheus and Birks, 2001).

3. Methods

The main difference in the sampling strategy between the NPS team and our work was that in 1993–1995 the top of the buried surface was sampled following the removal of the tephra layer, and each sample was taken from an area of about 5×10 cm^2 of the buried soil, not deeper than 2 cm. Thus, each sample was about 100 cm^3 in volume. That allowed precise location of the identified insect species within the microrelief of the buried soil (Goetcheus, 2001, Figs. 4–6), but the general number of fossils was very low, as was their taxonomic diversity. That is why we tried the bulk sampling traditionally used in the western (Siberian) part of Beringia.

The Tempest Lake — 2003 site (Fig. 1, B) was cleared of modern vegetation and slumped sediments before sampling. At first glance, the bluff appeared to consist of 7 m of loose, dark volcanic soil. After cleaning, it became apparent that while the upper 3 m of the section were of volcanic origin (well-sorted and stratified volcanic glass and pumice, generally of dark grey color), the underlying part of the outcrop consisted of unstratified loess-like silt of light grey–beige color. The contact between the two units looked like the surface of earthen hummocks sprinkled with ash, which penetrated deep into the fissures between the hummocks. The uneven contact was emphasized by the sharply contrasting colors of the two units (Fig. 1, C). The sediment building the hummocks was quite uniform, and did not show any features of soil profile, but on top and sometimes on the sides of hummocks we found sedge-like tillering plants in living position (Fig. 1, E). Interestingly, although all the buried plants were pressed down to the horizontal position at the root stem, all the grass leaves were not longer than 2–3 cm, giving the impression that they had been evenly cut or bitten-off, perhaps by grazers (Fig. 1, F).

The hummock-building sediment was sampled to the depth of about 20–30 cm after repeated defrosting, and was transported downslope to the lake for wet-screening (Fig. 1, D). More than 100 kg of sediment was screened through a 0.4 mm mesh sieve. Beside insects, the residue contained large numbers of sedge remains, willow branches and roots.

The screened sample from the Tempest Lake site was dried and large plant remains were separated in the field. Fossil insects were later picked from the enriched residue in the laboratory, under a low-power stereo binocular microscope. This dry sorting technique is the traditional approach among the Russian researchers of Cenozoic fossil insects (Medvedev, 1968).

The small insect samples collected by the NPS team in the 1990s have been studied by SE. These samples came from two sites at Tempest Lake (Plane and Tern), Eh'cho Lake, Ulu Lake, Reindeer Lake, Lake Rhonda, Swan Lake, Egg Lake and the banks of the Nugnugaluktuk River (Fig. 1). These were wet-sieved in the laboratory, then picked in ethanol under the microscope. The remains of small insects were recovered by careful wet-sieving of small bulk samples, as has been done here for the S. Elias samples (Table 1). Dry-sorted samples taken by screening large volumes of sediment tend to contain fewer remains of small insects, but larger numbers of large, heavy-bodied insects, such as weevils. This difference in fossil assemblages may be due to the larger screen size used in the bulk sampling.

The interpretation of the insect data has been carried out by two methods, allowing us to reconstruct general paleoenvironmental conditions and past temperatures. Environmental reconstructions were made on the basis of ecological group analysis (Kiselyov, 1973). Such an approach was developed to allow quantitative estimation of the environmental significance of each fossil assemblage based both on the ecological preferences of particular taxa and their abundance in the sample. We estimated the minimum number of individuals (MNI) for each taxon, based on the maximum number of individual sclerites (head capsules, pronota, and elytra) of a taxon in a sample.

Ecological groupings of insects found in Pleistocene fossil assemblages have been described by Matthews (1974, 1982, 1983) for Eastern Beringian faunas, and by Kiselyov (1973, 1981) for Western Beringian faunas; the latter was further developed by Kuzmina (2001), Sher et al., 2005, Kuzmina and Sher (2006) and Sher and Kuzmina (2007). Each beetle, ant and true bug taxon has been given an ecological classification that allows the combination of individual taxa into ecological groups.

Matthews' (1983) classification system is a mixture of different types of groups. Some of his groups are based on taxonomy (e.g., the *Lepidophorus*–*Morychus* group), while others are based on ecological attributes (e.g., the Hygrophilous and Aquatic groups). Matthews (1974) had also developed a more complicated scheme in which beetle taxa were divided into primary groups on the basis of their distribution, then into subgroups on the basis of their ecological preferences, then into a third level of groups, based on vegetation type.

The Russian schemes (e.g., in Kuzmina and Sher, 2006) use an ecological classification. In this article we have followed a classification scheme based on simple ecological terms. It differs from the West Beringian system where subdivisions have had to be defined in order to classify more complex steppe and tundra communities.

We use the following ecological codes here:

s–t — species indicative of Pleistocene steppe–tundra environments in Alaska, that are rare and exotic in modern tundra ecosystems. Examples include the pill beetle genus *Morychus*, some dung beetles of the genus *Aphodius*, and most of the weevils in the genus *Coniocleonus*, as well as the sage feeding weevil, *Connatichela artemisiae* Anderson. The genus *Coniocleonus* was reassigned to *Stephanocleonus* by R. Anderson (1987, 1989). This is a contentious issue among taxonomists. B. Korotyaev (in Berman et al., 2001a) has argued that the genus *Coniocleonus* must remain separate. This is very important for understanding the differences between Western and Eastern Beringia steppe–tundra. *Stephanocleonus sensu* Korotyaev was common in Western Beringia during the Pleistocene, and has never been found in America, either in the modern fauna, or as a fossil. This genus of weevils lives today only in thermophilous steppe habitats (Berman et al., 2001a) where there is a high level of soil warmth in summer.

dt — insects associated with dry, open habitats in tundra and in a part of the forest zone. This is a large group. The principal species, abundant in many Eastern Beringian Pleistocene assemblages, is the weevil *Lepidophorus lineaticollis* Kirby. The group also includes

Table 1
Taxonomic list of insects and other arthropods identified from Late Pleistocene insect fossil assemblages in the Devil Mountain region, Alaska, in minimum number of individuals per sample

		Sample								
		TL03	TL	LR	UL	LE	RL	SL	EL	NR
Taxon	EcoCode									
Order Coleoptera										
Carabidae										
Carabus truncaticollis Esch.	mt	1	–	–	–	–	–	–	–	–
Stereocerus haematopus (Dej.)	dt	5	–	–	–	–	–	–	–	–
Pterostichus (Cryobius) arcticola Chaud.	mt	2	–	–	–	–	–	–	–	–
P. (Cryobius) kotzebuei Ball	mt	13	–	–	–	–	–	–	–	–
P. (Cryobius) tareumiut Ball	mt	10	1	–	–	–	–	–	–	–
P. (Cryobius) nivalis (Salhb.)	mt	–	–	–	–	1	–	1	–	–
P. (Cryobius) parasimilis Ball	mt	–	13	–	–	–	–	–	–	–
Pterostichus (Cryobius) spp.	mt	19	1	3	1	1	1	3	–	4
Amara alpina Payk.	dt	15	–	–	–	–	1	–	–	–
Amara sp.	dt?	–	–	–	–	–	–	–	–	1
Dytiscidae										
Hydroporus sp.	r&a	–	–	–	–	–	–	–	–	1
Agabus arcticus Payk.	r&a	–	–	–	–	1	–	–	–	1
Staphylinidae										
Olophrum sp.	pl	–	–	–	–	–	–	–	–	2
Holoboreaphilus nordenskioeldi Makl.	mt	–	–	–	–	1	–	–	–	–
Eucnecosum brachypterum (Grav.)	pl	–	–	1	–	–	–	1	–	–
Micralymma brevilingue Schiodte	dt	1	1	1	2	3	–	1	–	1
Tachinus brevipennis Sahlb.	mt	–	1	–	2	3	–	1	1	1
Stenus sp.	r&a	–	–	–	–	–	–	–	–	1
Hydrophilidae										
Helophorus sp.	r&a	–	–	–	–	–	–	–	–	3
Byrrhidae										
Simplocaria tessellata LeC.	dt	–	–	–	1	–	–	–	–	–
Curimopsis albonotata (LeC.)	dt	3	–	–	–	–	–	–	–	–
Morychus cf. *aeneolus* LeC.	dt	–	2	–	–	–	1	–	–	–
Morychus sp.	s-t	108	–	–	–	1	–	–	–	–
Scarabaeidae										
Aphodius spp.	s-t?	–	1	–	–	–	–	1	–	–
Chrysomelidae										
Chrysolina basilaris (Say)	mt?	2	–	–	–	–	–	–	–	–
Chrysolina subsulcata Mnnh.	ar	23	–	–	–	–	–	–	–	–
Chrysolina septentrionalis Men.	mt	22	–	–	–	–	–	–	–	–
Chrysomela cf. *septentrionalis* (Men.)	mt	–	–	–	–	3	–	–	–	–
Chrysomela cf. *crotchi* Brown	sh	–	3	1	–	–	–	4	–	–
Chrysomela sp.	sh	–	2	–	1	3	–	–	–	–
Phaedon oviformis (LeC.)	mt	–	–	–	–	1	–	–	–	–
Altica sp.	oth	–	–	–	–	–	–	–	–	1
Apionidae										
Mesotrichapion alaskanum (Fall)	dt	–	3	1	–	–	2	1	–	–
Mesotrichapion cyanitinctum (Fall)	dt	5	–	–	–	–	–	–	–	–
Apionidae gen? spp.	dt?	–	2	–	1	1	1	3	1	–
Curculionidae										
Sitona aquilonius Bright	dt	1	–	–	–	–	–	–	–	–
Lepidophorus lineaticollis Kby.	dt	252	19	4	3	5	4	1	–	–
Coniocleonus confusus (And.)	s-t	3	–	–	–	–	–	–	–	–
Coniocleonus parshus (And.)	s-t	2	–	–	–	–	–	–	–	–
Lepyrus nordenskioeldi Faust	sh	2	–	–	–	–	–	–	–	–
Lepyrus gemellus Kby.	sh	–	–	1	–	–	–	–	1	1
Notaris sp.	r&a	–	–	–	–	–	–	2	–	–
Ceutorhynchus subpubescens LeC.	s-t	1	–	–	–	–	–	–	–	–
Order Heteroptera										
Saldidae										
Chiloxanthus sp.	r&a	1	–	–	–	–	–	–	–	–
Order Homoptera										
Cicadellidae										
Genus et sp. indet.		–	4	–	–	11	1	–	–	–
Order Diptera										
Chironomidae										
Genus et sp. indet.		–	–	–	–	1	–	–	–	–
Fam., gen. indet (pupae)		16	24	2	3	12	–	–	–	–
Order Hymenoptera										
Suborder Apocrita (Parasitica)										
Fam., gen. indet.		5	–	–	–	–	–	–	–	–
Order Trichoptera										
Molannidae										
Molanna sp.		–	–	–	–	–	–	–	–	15
Limnephilidae										
Genus et sp. indet.		–	–	–	–	–	–	–	–	10
Order Lepidoptera										
Fam., gen. indet. (larvae)		1	–	–	–	–	–	–	–	–
Insect varia larvae		13	–	–	–	–	–	–	–	–
Class Arachnida, order Sarcoptiformes										
Suborder Oribatei										
Genus et sp. indet.		–	39	58	48	108	67	–	–	–

Site names: TL03 = Tempest Lake 2003 sample; LR = Lake Rhonda; UL = Ulu Lake; LE = Lake Eh'cho; RL = Reindeer Lake; SL = Swan Lake; EL = Egg Lake; NR = Nugnugaluktuk River.

many other weevils such as *Coniocleonus zherichini* Ter-Minassian et Korotyaev, *Sitona aquilonius* Bright, *Hypera* spp., and the ground beetles *Amara alpina* Zett., *Stereocerus haematopus* (Dejean) and others.

mt — insects associated with mesic to moist tundra habitats, mostly found today in the arctic tundra but also in patches in northern forests. These communities include meadows and bogs. The most abundant beetles of this group that are found in Pleistocene assemblages are ground beetles in the *Cryobius* subgenus of the genus *Pterostichus*. The mesic tundra group includes some rove beetles, such as *Tachinus brevipennis* (Sahlb.) and *Holoboreaphilus nordenskioeldi* Mäklin, the leaf beetles *Chrysolina septentrionalis* Men. and *Phaedon* spp., and others.

ar — arctic insects. This group consists of cold-resistant beetles, living today in the northern tundra and polar desert, such as the leaf beetle *Chrysolina subsulcata* Mannh. (Makarova et al., 2007).

sh — insects that live and feed on shrubs, mostly willows, such as weevils of the genus *Lepyrus*, and some leaf beetles of the genus *Chrysomela*.

pl — plant litter inhabitants including many species of rove beetles.

oth — other insects, with indeterminate ecological status, such as inexactly identified specimens.

r&a — riparian and aquatic insects. This group includes aquatic beetles in the families Hydrophilidae and Dytiscidae, as well as caddisfly (Trichoptera) larvae and riparian insects of different families. These include the ground beetle genera *Bembidion*, *Nebria*, and *Elaphrus*, the rove beetle genus *Stenus*, the weevil genus *Notaris*, and shore bugs (Saldidae). North American species of *Notaris* include *N. aethiops* (Fab.), a wetland species associated with *Typha*, and *N. bimaculatus* (Fab.), a wetland species associated with reeds and rushes (Anderson, 1997).

There is also a forest group in this scheme, but this group is altogether absent from the Seward Peninsula faunas.

The mean temperatures of the warmest and coldest months were reconstructed using the Mutual Climatic Range (MCR) method (Atkinson et al., 1986, 1987, Elias, 1994). This method has already been developed for use in both Eastern Beringia (Elias, 2000, 2001) and Western Beringia (Alfimov et al., 2003). It should, however, be noted that the Russian approach to the MCR method is different from the classical (European–American) one. The main difference is that Russians include phytophagous species in their analyses (ignored in the classical approach), as they consider that the plant eating species are important indicators of past temperature in Western Beringia (Alfimov et al., 2003).

4. Results

We analyzed a total of 47 insect samples from eight sites: Tempest Lake (three different sections), Lake Rhonda, Ulu Lake, Eh'cho Lake, Reindeer Lake, Swan Lake, Egg Lake and the Nugnugaluktuk River. The insect remains extracted from these samples have truly remarkable preservation; in fact they are even better preserved than those from other permafrost sites in Alaska and Siberia. Some specimens still have major body parts connected, such as elytra still attached to abdomens, bodies with legs, and heads with antennae (Fig. 2). The best studied site is Tempest Lake, where one large and twelve smaller samples were taken. Thirteen samples were taken from an exposure at Eh'cho Lake, and other sites yielded 2–3 samples each (Table 1). The samples from the same locality were pooled in Table 1.

The most abundant species in our samples is the weevil *Lepidophorus lineaticollis*. This beetle makes up half of the specimens from the large sample taken from Tempest Lake, and it is present in the all other Tempest Lake samples except one; it occurs in all the Lake Rhonda site samples, and most of the Ulu Lake and Reindeer Lake site samples. Other members of dry tundra (dt) group are less abundant. There are the ground beetles *Amara alpina* and *Stereocerus haematopus*, the rove beetle *Micralymma brevilingue* Schiodt, the pill beetles *Curimopsis albonotata* (LeC.) and *Simplocaria tessellata* LeC., and the weevils *Mesotrichapion alaskanum* (Fall), *M. cyanitinctum* (Fall), and *Sitona aquilonius*. All the species discussed here could potentially live in modern shrub tundra, in patches of open ground with scattered xerophilous vegetation.

The remains of a pill beetle *Morychus* cf. *aeneolus* (LeC.) may represent aberrant specimens of an undescribed species of *Morychus*. The identification of *Morychus rutilans* Mots. in Matthews and Telka's (1997) list of Eastern Beringian fossil insects was due to a misunderstanding of the taxonomic status of *Morychus viridis* Kuzm et Kor.

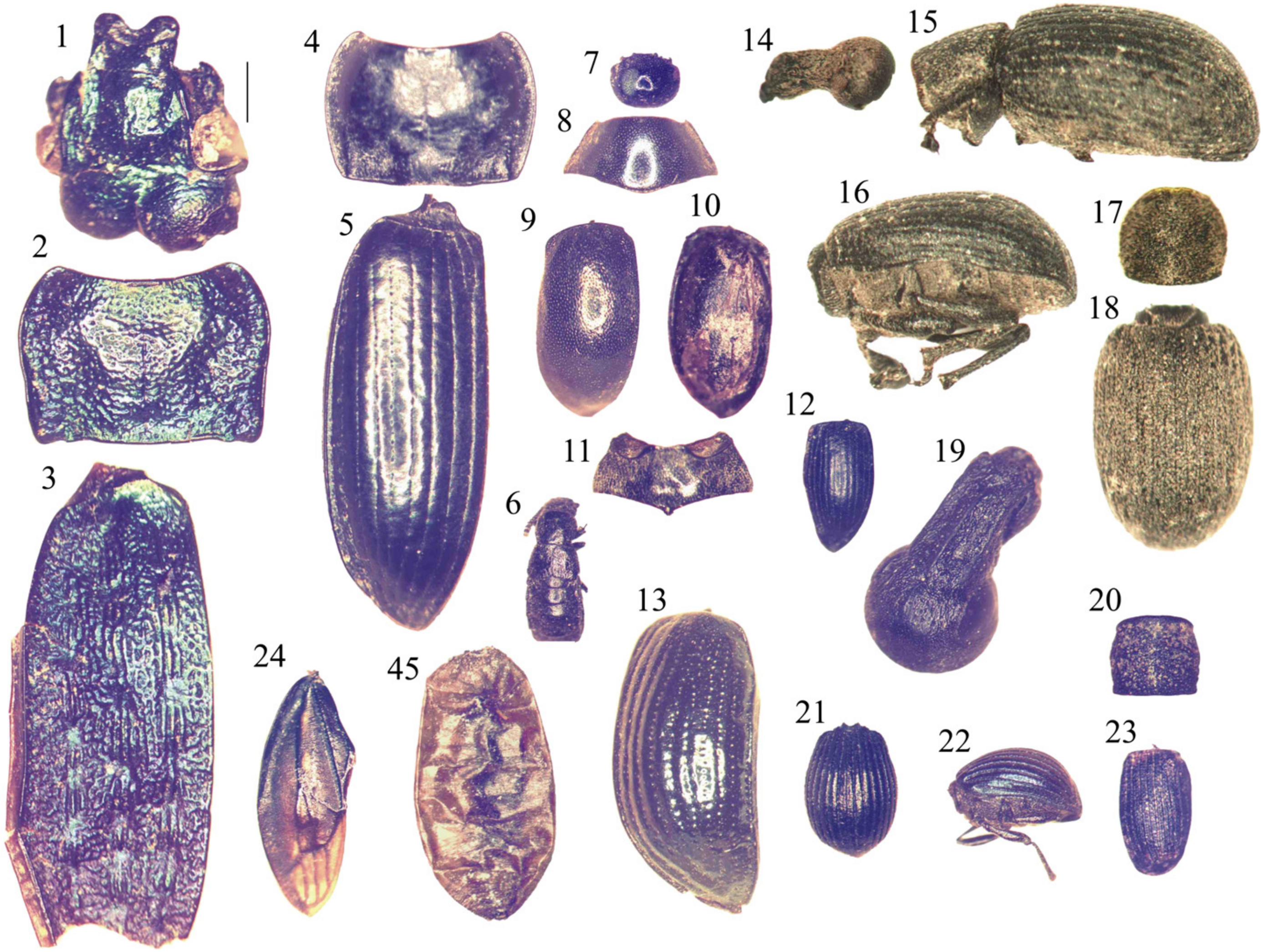

Fig. 2. Fossil insects from the Large Tempest Lake sample 1–3: *Carabus truncaticollis*, 1 — head, 2 — pronotum, 3 — left elytron; 4–5: *Stereocerus haematopus*, 4 — pronotum, 5 — left elytron; 6 — *Micralymma brevilingue*, near-complete specimen; 7–11: *Morychus* sp., 7 — head, 8 — pronotum, 9 — left elytron, 10 — underside of elytron showing remains of a wing, 11 — metathorax; 12 — *Curimopsis albonotata*, left elytron; 13 — *Chrysolina septentrionalis*, right elytron; 14–18: *Lepidophorus lineaticollis*, 14 — head, 15 to 18: partially articulated specimens; 19 — *Coniocleonus parshus*, head; 20 — *Sitona aquilonius*, pronotum; 21, 22 — *Mesotrichapion cyanitinctum*, whole body without head and pronotum; 23 — *Ceutorhynchus subpubescens*, right elytron; 24 — *Chiloxanthus* sp., left elytron, 25 — fly pupa.

Sergei Kiselyov, a Russian fossil beetle expert, sent some modern individuals of *M. viridis* from Chukotka to Paul J. Johnson, who was revising North American byrrhids at that time. Johnson was confident that these specimens belonged to *Byrrhobolus rutilans* Mots. This taxonomic revision took place before *M. viridis* had been described. Subsequently, Johnson (1985) revised the status of *B. rutilans*. In reality, *B. rutilans* is a completely different species, known today from the Altai region. Johnson later revised the status of the genus *Byrrhobolus*, making it a subgenus of *Morychus* (Kuzmina and Korotyaev, 1987). In our opinion, the American fossil *Morychus* is an undescribed species, different from the Siberian species *M. viridis* and from *M. rutilans* in the Matthews and Telka (1997) list.

The steppe–tundra (s–t) group is of secondary importance in the faunal assemblages. The dominant taxon of this group is the pill beetle *Morychus* sp. This beetle makes up one-fourth of the specimens in the large sample from Tempest Lake and it also occurs occasionally in the other site assemblages, mostly from Tempest Lake. The large sample from Tempest Lake also contains other members of the steppe–tundra group, including the weevils *Coniocleonus confusus* (Anderson), *C. parshus* (Anderson), and *Ceutorhynchus subpubescens* LeC. A few samples contain specimens of the dung beetle *Aphodius* sp.

Insects associated with more-or-less wet habitats play a less important role in these faunal assemblages, compared with the xerophilous taxa. The mesic tundra (mt) group is best represented by the ground beetles of the *Pterostichus* (*Cryobius*) group, including *Pterostichus arcticola* (Chaud.), *P. kotzebuei* Ball, *P. tareumiut* Ball, *P. nivalis* (Sahlb.), and *P. parasimilis* Ball, and some specimens of the *Cryobius* subgenus that could not be specifically identified. They are more abundant in the Tempest Lake and Lake Rhonda sites. Beside these beetles, the mesic tundra group includes the rove beetle *Holoboreaphilus nordenskioeldi* (Mäklin) (only one specimen from the Eh'cho Lake site), *Tachinus brevipennis* (Sahlb.) (occurs occasionally), and the leaf beetles *Chrysolina septentrionalis* (Men.) (common in the large Tempest Lake sample and rare in other samples), *C. basilaris* Say (a single specimen from the Tempest Lake site), and *Phaedon oviformis* LeC. (a single specimen from the Eh'cho Lake site). Arctic species are represented by the leaf beetle *Chrysolina subsulcata* Mannh., which is numerous in the large Tempest Lake sample.

The shrubs group is poorly represented in these faunas. We only found single specimens of the willow weevils *Lepyrus nordenskioeldi* Faust and *L. gemellus* Kirby. Other members of this group include the leaf beetles *Chrysomela* cf. *crotchi* Brown, and *Chrysomela* sp.

Likewise the plant litter group is poorly represented. We only found a few specimens of the rove beetle genus *Olophrum* sp. from the Nugnugalukluk River site, and we found the rove beetle *Eucnecosum brachypterum* (Grav.) in samples from Lake Rhonda and the Nugnugaluktuk River.

Specimens from the Riparian and Aquatic group are limited to the Nugnugaluktuk River samples. Single specimens of truly aquatic insects (one water beetle and one chironomid midge larva) have been recovered from the Eh'cho site, but three water beetle species and numerous caddisfly larvae were recovered from the Nugnugaluktuk River site. Adult water beetles are known to leave the water and fly to other water bodies, while caddisfly larvae remain in the water until they become winged adults. This evidence suggests that the buried surface at the Nugnugaluktuk site was aquatic in nature, probably a system of shallow streams with sandy bottoms, as preferred by the caddis larva of *Molanna* sp. and was likewise suitable for some caddis larvae in the family Limnephilidae. Other than at this site, there are almost no aquatic insects in our fossil records from this region.

It seems likely that all other samples represent terrestrial surfaces that were buried by the tephra. Further evidence supporting this hypothesis comes from the presence of fossil leafhoppers (Cicadellidae) in our samples. This group is uncommon in modern tundra communities; their presence in our fossil assemblages is most likely linked to grassy steppe–tundra vegetation. Interestingly, Matthews (1974) found large numbers (149 individuals) of the Cicadelid species *Hardya youngi* in his sample S-1 from Cape Deceipt, about 50 km southeast of Tempest Lake on the northern coast of the Seward Peninsula. This assemblage is also thought to be of LGM age.

5. Discussion

The insect assemblages from our study sites are generally indicative of dry, cold steppe–tundra environments. We conclude that this was the nature of the landscape buried by the tephra about 21,600 yr ago. The composition of our fossil assemblages is unlike any modern insect communities. More specifically, the proportion of ecological groups found in our fossil assemblages could not be found in any modern fauna. First of all, the combination of steppe–tundra and arctic groups does not occur today, even though it typified large regions of steppe–tundra during the Pleistocene. Some insects, for instance the weevils *Coniocleonus confusus* and *C. parshus*, now live far south of the Seward Peninsula.

Our unidentified specimens of *Morychus* may represent an extinct steppe–tundra pill beetle. The fossil *Morychus* from the Seward Peninsula apparently belongs to the same species as the *Morychus* specimens found in Pleistocene faunal assemblages from other sites in Alaska and the Yukon. SK has examined fossil specimens in the collections of the Geological Survey of Canada (originally collected by John Mattews and Alice Telka from Alaskan and Yukon fossil localities), in addition to fossils she collected from the North Slope of Alaska and from five sites along the Yukon River. There is no doubt that they all belong to the same species, but no match has been found among the modern *Morychus* species of North America or Asia. The closest relative of this fossil *Morychus* is the Western Beringian species, *M. viridis*, which played a similar ecological role in Siberian Pleistocene faunas. The fossil American *Morychus* species differs from all modern North American *Morychus* (including the apparently close relatives, *M. aeneolus* (LeC.) and *M. oblongus* (LeC.)) by its size, body shape, and wing development. It differs from the Siberian *Morychus viridis* Kuzmina et Korotyaev by its wing development and the shape of the elytral shoulder. *M. viridis* is a short-winged form (wing shorter than elytron) with a flattened shoulder and hind angles of the pronotum (Berman and Zhigulskaja, 1989). The American fossil *Morychus* has a less-flatted elytral shoulder with a track of tubercles on the underside which indicates a better-developed wing. The Tempest Lake fauna contains a well preserved *Morychus* elytron with a preserved wing that is the same length as the elytron (Fig. 2).

The ecology of *Morychus viridis* is well studied (Berman, 1990; Berman et al., 2001a). It is found in specific habitats in northeast Asia today, where the soil is very dry and remains free from winter snow cover. It is associated with the dry-adapted sedge *Carex argunensis* Turcz., and lives where this sedge forms a dense sod. Its larvae feed on the moss *Polytrichum piliferum* Hedwig that grows in sparse patches of sedge clumps. At the northernmost extent of its modern range on Wrangel Island, it lives in similar habitats with other species of xerophilous sedges (O. Khruleva, pers. comm.). We envision a similar role in the ancient steppe–tundra ecosystem for the unidentified species of American *Morychus* found in Eastern Beringian fossil assemblages. It probably lived on patches of dry soil with thin moss cover, surrounded by *Kobresia* sedge plants. *Kobresia myosuroides* (false elk-sedge) dominated the ground cover at all of the Seward Peninsula sites buried by the LGM tephra (Goetcheus and Birks, 2001).

The abundance of the weevil *Lepidophorus lineaticollis* in our samples is evidently linked with the ancient steppe–tundra environment, but this species is also quite common today in open, dry, warm patches in the tundra, such as south-facing slopes, and on sandy soil with thin moss cover. It has also been found in the boreal forests of Alaska and the Yukon, in patches of open ground with scattered vegetation, on patches of steppe, and on sandy river banks far back from the water's edge. According to Anderson (1997) it has also been found on moist tundra and under alder leaf litter. Nevertheless, despite its variable ecological preferences, we consider this to be an indicator of Pleistocene steppe–tundra environment, as did Matthews (1982, 1983). Indeed, dominance of *L. lineaticollis* in many of our fossil assemblages could be explained by the existence of dry steppe–tundra conditions where soils were warm in summer. An investigation of the habitat preferences of *L. lineaticollis* shows the number of beetles increases dramatically with elevation in the Kluane Lake region of the southern Yukon Territory. Here the forest zone gives way to mountain steppe at an elevation of 1400 m above sea level, and the abundance of this weevil sharply increased (up to 3–4 times) just in this transition zone (Berman and Alfimov, 2000). Annual soil degree days (SDD) in the mountain steppe zone vary from 1040 to 2380C°/day, which corresponds to the variation between shrub tundra and the relict steppe in the upper Kolyma River basin in northeastern Siberia. This latter region is a modern refugium for thermophilous insect species that formed part of the Beringian steppe–tundra community during the Pleistocene (Berman et al., 2001a).

Mesic tundra beetles may seem out of place in an LGM steppe–tundra environment, but no Beringian landscape was completely covered by one kind of vegetation (Schweger, 1982; Yurtsev, 2001). Topographic diversity leads to mosaics in soil moisture and vegetation cover. Apparently the mesic tundra fauna of Eastern Beringia was able to exploit the damp patches of the northern Seward Peninsula, even during the cold, dry interval of the LGM. *Pterostichus* (*Cryobius*) spp. are common inhabitants of modern mesic tundra in Alaska and the Yukon (Ball, 1963; Lindroth, 1963). These beetles are typically found under mosses, along river banks, and under deciduous leaf litter, but some species are also occasionally found in rather dry habitats. These typical tundra beetles like to warm themselves on dry patches of ground. On the Pleistocene steppe–tundra, they might have lived in topographic depressions where increased moisture would have supported more dense vegetation cover, such as mosses, shrub birch and willows.

Another mesic tundra species, the rove beetle *Holoboreaphilus nordenskioeldi*, is one of the most hygrophilous species in our fossil assemblages. This species prefers wet, often boggy habitats in tundra and the northern edge of boreal forest (Campbell, 1978). In a steppe–tundra landscape it could have lived in small boggy patches or frost cracks.

Tachinus brevipennis and *Chrysolina septentrionalis* are as common today on the Alaskan arctic tundra as they were in Pleistocene steppe–tundra communities. Both species are highly cold adapted, and widely distributed on the modern arctic tundra. Only single specimens of *T. brevipennis* were found in most of our fossil assemblages. Numerous specimens of *C. septentrionalis* were recovered from the large sample from Tempest Lake, and single specimens were recovered from Eh'cho Lake samples. This paucity is probably due to taphonomic bias in the samples. *C. septentrionalis* is a large, heavy-bodied beetle, and it might not have been found in small samples because of its size. This species feeds on Brassicaceae which are well represented (Brassicaceae undifferentiated, *Draba* sp., *Eutrema edwardsii* R. Br.) in the buried soil plant list (Goetcheus and Birks, 2001).

Shrub-associated insects are quite rare in our fossil assemblages. All of the species we identified feed on willows. We might have expected greater numbers of these insects in our samples, because shrub willow was very likely part of the steppe–tundra vegetation mosaic, growing near water bodies or in depressions (Guthrie, 1990). However, during the LGM, Seward Peninsula willows were represented mostly by small dwarf shrubs such as *Salix arctica* (Goetcheus and Birks, 2001). This prostrate willow would hardly be a good host plant for the willow weevils of the genus *Lepyrus* or for the willow feeding leaf beetles of the genus *Chrysomela*. The presence of these beetles in our fossil assemblages suggests that at least some medium-sized willow shrubs were part of the northern Seward Peninsula LGM vegetation.

Today the leaf beetle *Chrysolina subsulcata* lives only in the northern parts of the Arctic tundra, including polar desert. It was also a common member of the Pleistocene steppe–tundra community. The remarkable numbers of specimens of this species in the Tempest Lake fauna suggests quite cold conditions. We also found another species in this genus: *Chrysolina septentrionis*. The closest relative of *C. septentrionalis* is *C. tundralis* Jacobson (Bienkowski, 2004). The principal modern range of the latter species is in northern Siberia, mostly on the tundra, but individual specimens have been collected from steppe regions much farther south, such as the Lipetsk region south of Moscow, about 53° N.

The proportion of different ecological groups (Fig. 3), as reconstructed from the insect data, is quite similar to the reconstructions based on plant macrofossil evidence (Goetcheus and Birks, 2001). The botanical evidence also indicates an LGM environment dominated by steppe–tundra vegetation with sedges, grasses and herbs, interspersed with open ground with thin moss cover. The wide distribution of dry tundra vegetation during the LGM on the loess soils of plains may have been fostered by a climatic regime featuring low humidity and enhanced evaporation. Cold steppe vegetation, dominated by xerophilous sedges including *Kobresia*, herbs and thin moss cover, exists only in relict patches today, even though it was typical in the Beringian Pleistocene. For instance, it occurs in the cold, windswept alpine tundra of the Rocky Mountains. This kind of vegetation requires low humidity, high levels of summer warming, and little or no snow cover in winter. Strong winds may have enhanced soil evaporation. Active loess deposition may also have enhanced soil dryness. Today, relict patches of steppe grow mostly on detrital soils, but in the Pleistocene it was widely distributed on loessic soil as well. Although mesic and moist tundra vegetation dominates the Seward Peninsula today, these communities played a secondary role during the LGM. The paleobotanical reconstruction confirms the presence of dwarf shrubs, herbs and thin moss cover.

During the LGM, most of the landscape of the northern Seward Peninsula was relatively open ground with small herbs and arctic willows. The insect fauna of this habitat lives today in the high arctic (arctic tundra is characterized by more-or-less open ground); these species are probably better adapted to live on dry steppe–tundra than on modern moist tundra with thick moss cover.

The main feature of the lifestyle of cold-adapted Arctic insects is the prolongation of larval development for several years (Chernov, 1978). This allows them to build up a store of chemical energy to fuel their eventual metamorphosis. The short growing season in the Arctic makes it essential for Arctic beetles to find patches of open soil on which to warm themselves. This behaviour is quite difficult to achieve in a carpet of wet mosses.

In our view, the modern insect communities of northeast Asia and northwestern North America represent new combinations of species that came together after the collapse of the steppe–tundra ecosystem. Hence the modern ranges of species previously found together on the steppe–tundra do not overlap today, but they could do again, if the steppe–tundra were to reform in another glacial interval. This has probably happened repeatedly in the past. Components of the steppe–tundra beetle fauna were living at Cape Deceit during at least the last 400,000 yr (Matthews, 1974). These taxa include *Lepidophorus lineaticollis* and *Morychus*. Also, Matthews (1974) found the weevil *Vitavitus thulius* Kissinger in assemblages from the Cape Deceit Formation, dating approximately to 1.8 mya. This weevil lives today on dry tundra in the Yukon, and in steppe environments farther south (Anderson, 1997). While this species was not recovered from our LGM-age samples, it has been found in Middle Pleistocene faunal assemblages from the Alaskan interior (Elias et al., unpublished data), and from the Late Pliocene fauna at the Lost Chicken site in east-central Alaska (Matthews and Telka, 1997).

5.1. MCR temperature reconstructions

The beetle faunas that lived in the study region at the time when the Devil Mountain tephra buried the landscape are indicative of climatic conditions apparently somewhat colder than today. Our

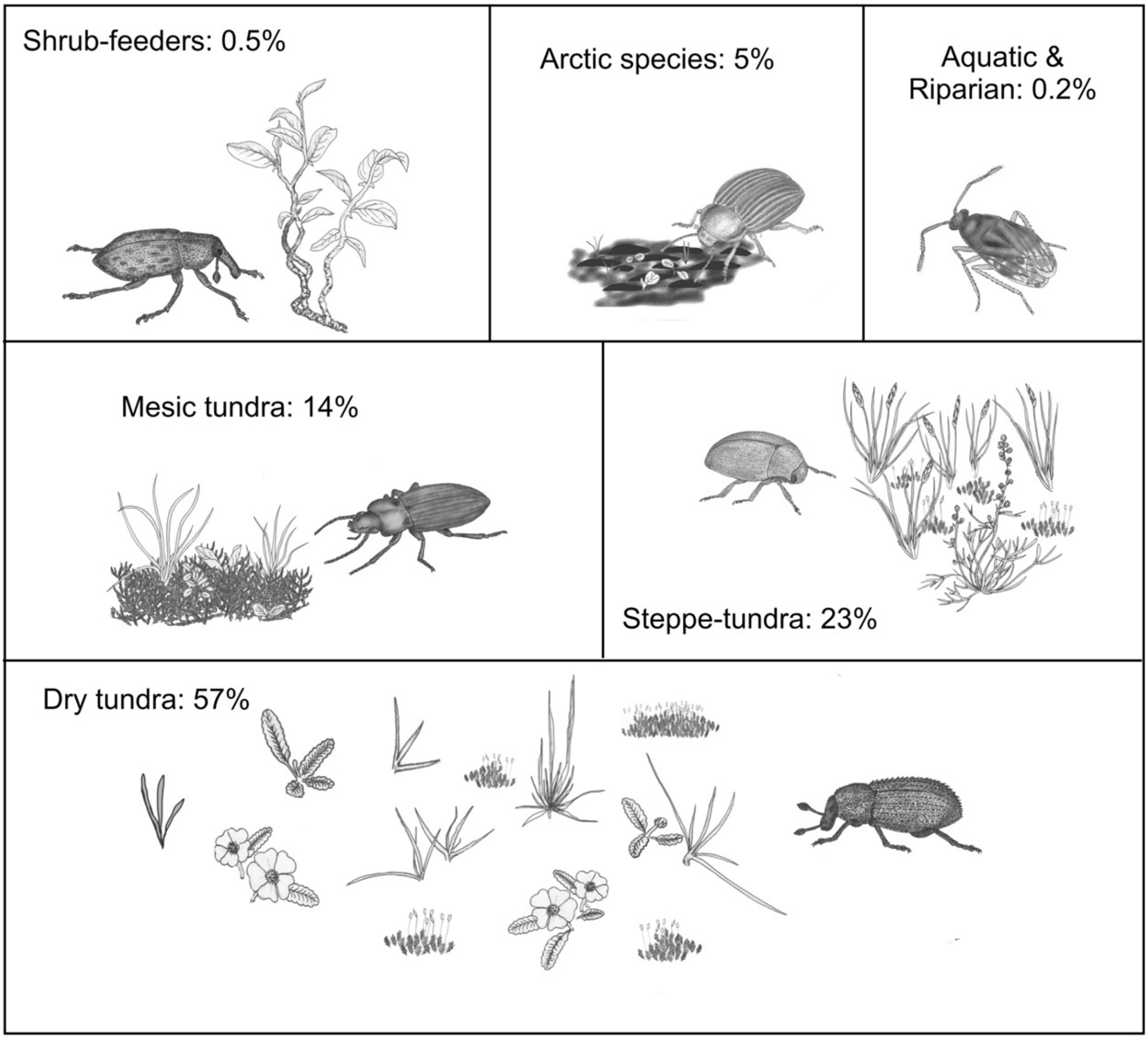

Fig. 3. Ecological structure of large Tempest Lake sample of ecological groups: sh — shrubs, r&a — riparian and aquatic, ar —arctic, mt — mesic and wet tundra, s–t — steppe–tundra, dt — dry tundra.

estimate of the mean July temperature (TMAX), based on the mutual climatic range of the predators and scavengers living there at that time, is 7.5–9.5 °C. The modern TMAX in this region is unknown, because there are no meteorological stations nearby. The closest long-term meteorological station is at Kotzebue, which lies about 0° 25′ north of the study sites. TMAX at Kotzebue is 12.6 °C, which is about 3–5 °C warmer than the reconstructed LGM TMAX for the study region. However, more short-term climate data are available for Wales, Alaska, which lies south west of our study region on the Bering Sea coast of the Seward Peninsula. Modern TMAX at Wales is only 8.4 °C. In comparison with the modern climate at Wales, Alaska, our MCR estimate of TMAX during the LGM straddles the modern value by about 1 °C on either side.

Our estimate of the mean temperature of the coldest month of the year (TMIN) is −32 to −24.5 °C. Modern TMIN at Kotzebue is −19.7 °C, but as discussed in Elias et al. (1999), it is inappropriate to compare TMIN estimates for regions which are now situated along the Alaskan coastline with glacial-age TMIN values for these regions, because the Bering Land Bridge was exposed at that time, so the maritime climatic effects of today did not affect the study region during the LGM, when it was in the middle of a very large continental region.

The only other LGM beetle fauna from Eastern Beringia comes from the Colorado Creek site, in southwestern Alaska (Elias, 2001). This site is dated at approximately 18,250 cal yr BP. Here, the TMAX estimate was 11.5–12.5 °C, and the TMIN estimate was −21 to −19 °C. The TMAX estimate is 2.3–3.3 °C colder than the modern value, and the TMIN estimate is 2.1–1.6 °C warmer than today. The LGM temperature reconstructions for these two regions of western Alaska suggest that regional temperatures were not radically different from today during the LGM. The main features of regional LGM climate that would distinguish it from the modern climate were thus likely to be decreased precipitation, lower relative humidity, lower snow cover and perhaps increased wind speeds. These were the climatic factors that fostered the steppe–tundra ecosystem.

The LGM insect fauna from our study region has both similarities and differences from other Late Pleistocene insect faunas in Eastern and Western Beringia. Late Wisconsinan insect faunas from the Titaluk River (North Slope of Alaska), Old Crow Basin (Northern Yukon), and some additional sites in Yukon Territory, aged from 32 to 13 ka BP are dominated mostly by xerophilous beetles living in treeless landscapes. The dominant species are the weevil *Lepidophorus lineaticollis* and the pill beetle *Morychus* sp. (Matthews and Telka, 1997). Some weevils of the genus *Coniocleonus* (listed as *Stephanocleonus* in Matthews and Telka, 1997) were also present. The arctic leaf beetle *Chrysolina subsulcata*, found in the Seward Peninsula samples, was absent from these other sites. This could be due, in part, to a lack of specific

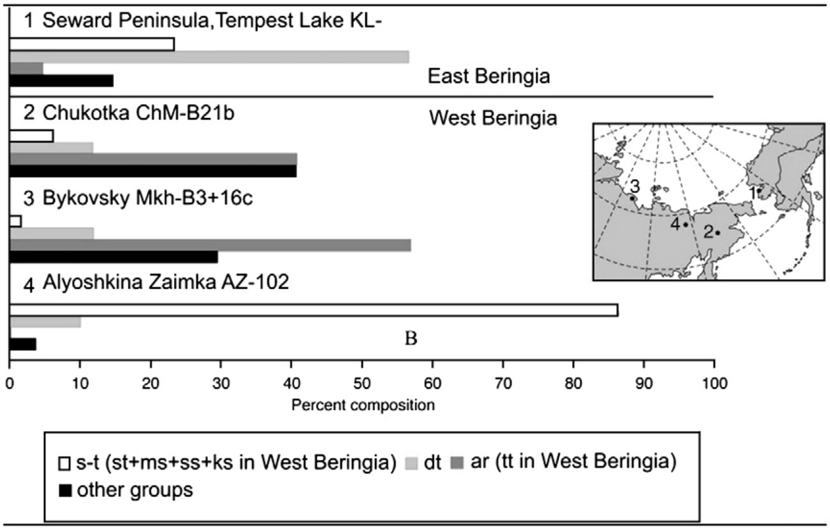

Fig. 4. Ecological structure comparison of the selected LGM faunas from East and West Beringia: s–t — steppe–tundra in East Beringia classification corresponded to sum of groups (st — steppe, ms — meadow steppe, ss — hemicryophytous or "sedge" steppe and ks — xerophylous insects) in West Beringia; dt — dry tundra, the group ar — arctic insects is named in West Beringia tt (insect of typical and arctic tundra).

identifications of *Chrysolina* specimens by other workers. Matthews and Telka's (1997) list simply shows '*Chrysolina* spp.' In any case, it does not appear that *C. subsulcata* was an important species in other Late Wisconsinan assemblages.

Beetle faunas from the LGM in Western Beringia have been studied in several areas (Fig. 4): in the Lena Delta (Bykovsky Peninsula, Sher et al., 2005), on the Kolyma Lowland (Alyoshkina Zaimka, Kiselyov, 1981) and on the south of the Chukotka Peninsula (Kuzmina and Sher, unpublished). The latter site is situated along the Main River, at 64° 35′ N, a little south of our study sites on the Seward Peninsula. The insect fauna dated from about the LGM is characterized by high percentages of arctic insects (up to 41%), fewer numbers of dry tundra species, and an absence of the steppe group. The earlier and later insect assemblages are more similar in ecological structure to our Seward Peninsula faunas: the dry tundra group dominates, the arctic insect component is not very significant, but the number of steppe–tundra indicators is lower in Chukotka. Despite this ecological similarity, the species compositions are different. There are no *Lepidophorus* remains in the Chukotka samples; the species of *Morychus* pill beetle is different; the arctic group is represented by the weevil *Isochnus arcticus* (Kor.), which is absent from Seward Peninsula assemblages. However, the two faunas do share some species in common, namely *Amara (Curtonotus) alpina* Payk, *Stereocerus haematopus*, and *Lepyrus nordenskioeldi*.

The Bykovsky section (71° 53′ N) is situated far north of both the Chukotka and Seward Peninsula sites. The LGM insect fauna from Bykovsky is completely dominated by arctic insects, such as *Isochnus arcticus*, while other groups are only represented by single individuals. Pre-LGM assemblages are dominated by the mesic tundra group, while post-LGM assemblages are dominated by steppe insects. Thus, the northern site shows a significantly stronger influence of cold climate during the LGM and its environmental history is not fully analogous to the more southerly sites on either side of the land bridge.

The difference between the Seward Peninsula and Bykovsky faunas can be explained by the northern position of the latter. More southern and inland West Beringian sites, such as Alyoshkina Zaimka in the lower course of the Kolyma, show much more xerophilic ("steppic") insect assemblages than the Seward Peninsula LGM fauna. The lower part of the Alyoshkina sequence (sample AZ-102) is dated about 16–17 ka (Alfimov et al., 2003), so it is probably slightly younger than the peak-LGM Seward Peninsula assemblage, but it definitely pre-dates the Bykovskiy post-LGM peak of steppe insects. The dominance of steppe insects in the AZ-102 assemblage can be clearly seen in Fig. 4; moreover, unlike the fauna from the Seward Peninsula, this group includes species of true Asiatic plain and mountain steppe, such as the weevils *Stephanocleonus* spp., the leaf beetles *Chrysolina aeruginosa* (Fald.) and *C. perforate* (Gebl.), the ground beetle *Curtonotus (Amara) fodinae* Mannh., and others.

The fossil insect faunas from the Seward Peninsula offer some unique insights into the ecosystems of central Beringia during the LGM. Presumably nearly all of the specimens identified from our fossil assemblages died on the same day, providing a detailed snapshot of local environments, ranging from aquatic to upland habitats. The reconstruction discussed here is therefore unique among fossil insect reconstructions, which are usually based on samples that are 2.5–5 cm thick, representing accumulations of organic detritus spanning decades or even centuries of time. Our insect evidence, combined with the plant macrofossil evidence, indicates a productive ecosystem, dominated by dry-adapted sedges that would have provided suitable grazing for herds of large mammals. The condition of buried plant stems at the Tempest Lake (2003) site (Fig. 1, F) may offer indirect evidence of intense grazing of local plant cover during the LGM. The former abundance and diversity of large grazing mammals in this area has been repeatedly demonstrated (Guthrie, 1990, 2001).

6. Conclusions

This research contributes to the decades of discussions between the Russian and North American schools of Quaternary paleoecology. The main controversy was that Russians believed that most of the Pleistocene environments, and the LGM ones in particular, have no complete modern analogues, thus supporting extinct communities (Vangengeim, 1977; Giterman, 1985; Yurtsev, 1981; Sher, 1997). Most North American colleagues insisted that the Late Pleistocene plant communities were just a pauperized version of modern arctic vegetation (e.g., Ritchie and Cwynar, 1982; Colinvaux, 1996). The study of the Kitluk Paleosol – a live soil surface buried under the thick volcanic ash during the LGM – has demonstrated for the first time that the character of plant associations of that time can hardly be found in the modern Arctic (Goetcheus and Birks, 2001).

Analysis of fossil insects from the Tempest Lake site and accompanying sites has led us to the conclusion that the beetle fauna found there has no complete modern analogues in Alaska, or Yukon, or elsewhere. It raised, however, another question — were the Alaskan beetle assemblages, interpreted as steppe–tundra ones, similar to the classic Siberian tundra–steppe? Our research has shown that they were ecologically alike to some degree. Both showed the combination of tundra beetles (among which dry tundra habitat species prevailed, but with the admixture of high Arctic species) with relatively more thermophilic beetles, currently living farther south. Both reflected the general mosaic of habitats — from dry, open sites with steppe-like vegetation to wetter sites where the vegetation was more like what is found today on the Seward Peninsula.

The taxonomic composition of ecologically similar beetle assemblages was, however, quite different. Practically none of Siberian true steppe weevils, ground and leaf beetles were found in the Seward Peninsula assemblages, and even the moss-feeding pill beetle (*Morychus*) was represented by different species. The considerable differences between the modern insect faunas of Western and Eastern Beringia, (and also the differences in Pleistocene faunas) have recently been discussed in detail by Berman et al. (2001a). We have now been able to demonstrate this phenomenon by comparison of more-or-less synchronous fossil assemblages of LGM age. It remains unclear why invertebrates, including many beetle species, appear to have been less capable of crossing the Bering Land Bridge than were plants and mammals.

The suggestions that the bridge itself played a role in filtering out xerophilic and relatively thermophilic animals because of its higher humidity (Elias et al., 1996), or that it formed a sort of “mesic buckle” in the Holarctic tundra–steppe belt (Guthrie, 2001) have been discussed in two papers (Berman et al., 2001a,b). They have shown that some mesophilic and cold-adapted insects and other invertebrates (e.g., widely distributed earthworms) were also unable to cross the land bridge.

Evidently, this problem does not have one simple explanation. In some cases, we are most probably dealing with a kind of vicariance. For example, weevils feeding on sage (*Artemisia*) are represented in Alaska and Siberia by different genera — might competitive exclusion be the explanation? Also, what do we know of the ecology and behaviour of the Alaskan Pleistocene pill beetle *Morychus* sp. (most probably an extinct species, see above)? Its role in the biological communities which existed in rigorous environments like the Kitluk buried soil is so similar to the role of *M. viridis* in Siberian assemblages that it begs the question: could the Alaskan species have prevented *M. viridis* from dispersing to Alaska, because it occupied the niche of the former, even though it was morphologically different? Evidently, this and similar scenarios are possible, but we have drawn the following conclusions: 1) the steppe–tundra fauna definitely arose well before the LGM; 2) this fauna had deep historical roots in the different insect faunas of Eurasia and North America; 3) unravelling the steppe–tundra faunal story requires much deeper knowledge of their evolution and environmental history than we currently have.

This work revealed one more interesting aspect — the appreciable differences between roughly contemporaneous fossil insect assemblages (LGM) in the different sectors of Beringia: northeastern Siberia and western Alaska. Although we cannot be sure of their precise synchronicity along the more than 50° longitude transect (about 2500 km long), it should also be noted that most of the Siberian assemblages came from continuous sections, covering many thousands of years and yielding sequences of fossil insect assemblages of various ages. Although this issue deserves a separate analysis, we can preliminarily state the following: the westernmost and the northernmost assemblages in the Lena Delta (Bykovsky) during the LGM show an important decrease in steppe species, replaced by arctic beetles; however, they still included single fossils of some relatively thermophilic species, such as *Phaedon armoraciae* (L.), which, when MCR analysis is applied, shows that LGM summer temperatures were not lower than today (Sher et al., 2002). The post-LGM and early MIS-3 beetle assemblages from this region had a much more pronounced steppe component than LGM assemblages, despite the high latitude of the site, which we explain by the effect of high continentality.

To a much greater degree, this effect manifested itself in the Kolyma Lowland, which is supposed to have historically been the area of the most pronounced steppe component in the tundra–steppe insect assemblages (Kiselyov, 1981; Kuzmina, 2001). The Kolyma assemblages had a relatively high proportion of steppe and tundra–steppe species during the late LGM.

Surprisingly, the percentage of steppe species drops almost to zero in the South Chukotka insect assemblages, during both the LGM and pre-LGM intervals. Although the description of this sequence is still in preparation, it is evident that the South Chukotkan Late Pleistocene assemblages are markedly different from the Ayon Island assemblages (north-central Chukotka), where the percentage of true steppe insects reached about 20% (Kiselyov, 1981; Sher et al., 2006). The reason for this discrepancy is still being discussed, but if steppe species did not reach this region, how could they disperse to Alaska? This fact rather favours the climatic explanation of the observed differences between the beetle assemblages in Chukotka and Alaska.

Finally, the LGM Seward Peninsula fauna was taxonomically very different from all the published Western Beringian (Siberian) assemblages. The s–t (steppe–tundra) group here has no species in common with the Siberian assemblages, and the most prominent member of the Arctic group in Siberia, *Isochnus arcticus*, is not found here, although currently this beetle lives in Arctic Canada.

This unique 2500 km-long transect of more-or-less synchronous insect assemblages merits further study. The non-analogue community of beetles recovered from under the 21 ka old volcanic ash represents the Alaskan version of a steppe–tundra beetle assemblage, quite different from the synchronous and ecologically more-or-less similar Siberian assemblages. The reasons for these differences are shrouded in a complex biological history, yet to be understood.

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