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Late Tertiary origins of the Arctic beetle fauna

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Abstract

During the past 30 years, Quaternary insect paleontologists working in the Arctic have studied rare deposits of fossil insects that date back millions of years. Some of these fossils may be as old as the Late Miocene. The fossils have been preserved mostly in permafrost environments, and their state of preservation is often exceptional. The vast majority of identifiable beetle specimens appear to match modern, extant species. This morphological constancy through time appears to reflect constancy of physiological adaptations, as well. The latter aspect is demonstrated indirectly through the ecological compatibility of species found in the ancient fossil assemblages. While most of the species themselves appear to have remained constant, the biological communities in which they lived have shifted dramatically through time. Based on both insect and plant fossil data, Late Tertiary environments of the Arctic were substantially warmer than they are today, supporting the growth of coniferous forests, up to the shores of the ancient Arctic Ocean. By about 2 million years ago (my) or shortly thereafter, Arctic tundra communities came into existence in parts of Beringia. Arctic insect faunal diversity declined markedly with the onset of Quaternary cooling.

Keywords: Tertiary; Quaternary; Beetles; Arctic; Paleoecology; Evolution

1. Introduction

During the past 30 years, paleoentomologists working in the northern high latitudes have studied a small number of organic deposits containing insect fossils that date back millions of years. The fossil assemblages represent Late Tertiary environments that preceded the earliest glaciations of the Quaternary, as well as Early Quaternary environments, representing the onset of glacial–interglacial cycles. These fossil assemblages provide rare glimpses into the history of the Arctic, and the origins of the modern insect fauna of this vast region. Because regional environments were substantially different in the Late Tertiary, there are no modern analogues for the fossil assemblages of this interval. Nevertheless, it is possible to discern ecological and taxonomic patterns in these faunas that began in the Late Tertiary and carried through the Pleistocene glaciations, ending in the modern fauna. In this paper, we trace these patterns through a series of fossil beetle faunas, from the Miocene to the Early Quaternary.

These fossil insect faunas bridge a paleontological gap between the actual exoskeletal remains preserved in the unconsolidated sediments of the Pleistocene, and the mineral replacements and trace fossils preserved in

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bedrock, from the Tertiary back to the Paleozoic. The Late Tertiary and Early Quaternary fossils discussed here range in age from perhaps 8 to 1.8 million years ago (my), yet they are the same kind of chitinous exoskeletal remains found in much younger (Pleistocene and Holocene) deposits. All of the fossil assemblages discussed here have been preserved in permafrost. Once removed from frozen sediments, these fossils are as well preserved as Holocene fossils from lower latitudes.

Fossil sites containing chitinous insect remains more than 1 million years old are extremely rare. Their long-term preservation was made possible by permafrost, but permanently frozen ground occurs almost exclusively in the high latitudes, and many high latitude regions were repeatedly glaciated in the Quaternary. Repeated glaciations obliterated nearly all organic terrestrial deposits in the Arctic during the Pleistocene. However, there were some regions in the Arctic that remained unglaciated through much if not all of the Pleistocene. Chief among these was the region known as Beringia, which included the unglaciated lowlands of northeastern Russia, Alaska, and the Yukon Territory, linked together by the Bering Land Bridge. The first signs of Arctic permafrost come from Early Quaternary, or slightly older deposits. The Miocene sediments discussed in this paper were unfrozen for at least a few million years, prior to the development of permafrost in northeastern Siberia.

A number of sites in the Canadian High Arctic islands and Greenland have also yielded Late Tertiary insect fossils. Most of the high Arctic was glaciated in the Pleistocene, but unconsolidated Late Tertiary and Early Quaternary deposits were nevertheless preserved at these sites. Notable among these are the Beaufort Formation deposits of the Queen Elizabeth Islands in high Arctic Canada. This formation consists of unconsolidated sands, gravels, and organic sediments. On Meighen Island, the Beaufort Formation is overlain by glacial till and glacially striated cobbles (Matthews, 1974a). But this could have resulted from expansion of the local ice cap during the Holocene and not glaciation of the entire region. Similarly, High Terrace Sediments on the Fosheim Peninsula of Ellesmere Island, Canada, are overlain by glacial deposits (Matthews and Fyles, 2000). The High Terrace Sediments consist of unconsolidated sands, gravels, and peats. Finally, the Kap København Formation in northernmost Greenland is an unconsolidated deposit of sand, silt and clay with beds of organic detritus. There is post-depositional disturbance of the sediments, ascribed to pressure from an overriding glacier (Funder et al., 1984).

1.1. Dating of fossil assemblages

One of the most difficult aspects of this research has been establishing the chronologies of the fossil assemblages. While radiometric dating has been used to establish the age of a few samples (notably the Lava Camp assemblages from Alaska), most of the assemblages discussed here have only been dated on the basis of site stratigraphy. These assemblages necessarily have only approximate age estimates. The ages discussed below represent the most recent geologic interpretations of the sites, but the chronologies will almost certainly be refined or changed as more geologic research is done in the study regions.

2. Research in Alaska and Canada

The work of John Matthews on the topic of Late Tertiary and Early Quaternary insect faunas from Alaska and northern Canada spans 25 years and 19 publications. Nine faunal assemblages dating from about 5.7 to 1.8 my have thus far been analyzed (Table 1). The sites range from just south of the Arctic Circle at the Lost Chicken site, to north of 80° latitude at the Meighen Island and Wolf Valley sites. The individual sites are discussed below, roughly in chronologic order, starting with the oldest site.

2.1. Lava Camp Mine, Alaska

The Lava Camp Mine site is located on the Seward Peninsula of Alaska (Fig. 1, No. 2). The fossil insect fauna was described by Hopkins et al. (1971). A fossil forest bed at this site was capped by a lava flow that has been dated by potassium–argon, yielding an age of 5.7 my ± 0.2 my. The forest bed was preserved in a section of alluvium. The alluvial sequence evidently consists of basal gravel deposited in an open river channel and an overlying mass of finer sediment deposited on a forested flood plain. The fossil flora includes at least 10 species of conifers, including species found today in the forests of the Pacific Northwest region, such as Sitka spruce and western hemlock. The floral assemblage is thus indicative of relatively warm, maritime climate. The Lava Camp Mine fossil insect fauna was quite rich, containing 84 insect and arachnid taxa (Matthews and Telka, 1997). MCR analysis of the beetle fauna yielded TMAX and TMIN estimates as much as 2 °C warmer than modern values (Elias and Matthews, 2002). White et al. (1997, 1999) considered the Lava Camp assemblage to represent a cool climate during the Messinian (latest

Table 1
Fossil insect assemblages discussed in text

Site	Age (millions of years ago)	Insect fauna	References
(1) Ary-Mas, NE Siberia, Russia	Miocene	41 beetle taxa, indicative of coniferous woodland	This paper
(2) Lava Camp Mine, Alaska	5.7±0.2 my (Late Miocene)	83 insect and arachnid taxa, including several extinct species; fauna indicative of coniferous forest	(Hopkins et al., 1971; White et al., 1997, 1999; Elias and Matthews, 2002)
(3) Niguanak, Alaska	Early Pliocene?	47 insect and arachnid taxa, including extinct species, *Diacheila matthewsi*. Fauna not yet fully analyzed, but has some Asian affinities	(Matthews and Telka, 1997; Elias and Matthews, 2002)
(4) Ballast Brook, Banks Island, NWT, Canada	5–3 my	39 insect and arachnid taxa, indicative of boreal environment	(Fyles et al., 1994; Elias and Matthews, 2002)
(5) Strathcona Beaver Peat, Ellesmere Island, NWT, Canada	>3.3 my	86 insect and arachnid taxa, including both arctic and boreal elements; some species with Asian affinities	(Matthews and Telka, 1997; Elias and Matthews, 2002)
(6) Meighen Island sites, NWT, Canada	3 my	198 insect and arachnid taxa, including both boreal and arctic tundra species. Faunal affinities with eastern North America and Asia	(Matthews and Telka, 1997; Elias and Matthews, 2002)
(7) Lost Chicken, Alaska	3 my	83 insect and arachnid taxa, including blind weevil, *Otibazo*, found today in Japan; boreal fauna with several extinct species	(Matthews and Telka, 1997; Elias and Matthews, 2002)
(8) Bluefish, Yukon Territory	<3 my (Late Pliocene)	26 insect and arachnid taxa, including *Notiophilus aeneus*, now confined to eastern N. America, and extinct species, *Helophorus meighensis*	(Matthews and Ovenden, 1990; Matthews and Telka, 1997; Elias and Matthews, 2002)
(9) Krestovka, NE Siberia, Russia	Late Pliocene (Kutuyakh Fm.)	22 beetle taxa; mixture of boreal and arctic fauna; some elements of steppe tundra fauna already present	Kiselyov, 1981
	Late Pliocene to Early Quaternary (Olyorian Suite)	51 beetle taxa; most found today in arctic tundra regions; some taxa with steppe affinities	(Kiselyov, 1981)
(10) Chukochya River, NE Siberia, Russia	Late Pliocene to Early Quaternary (Olyorian Suite)	80 beetle species; most found today in arctic tundra regions; some taxa with steppe affinities	(Kiselyov, 1981)
(11) Alazea, NE Siberia, Russia	Late Pliocene to Early Quaternary (Olyorian Suite)	56 beetle species; most found today in arctic tundra regions; some taxa with steppe affinities	(Kuzmina, 1989)
(12) Sededema, NE Siberia, Russia	Late Pliocene to Early Quaternary (Olyorian Suite)	55 beetle species; most found today in arctic tundra regions; some taxa with steppe affinities	(Kiselyov, 1981)
(13) Kap København, Greenland	2.5–2 my (Early Quaternary)	154 insect and arachnid taxa, indicative of northern tree line environments	(Böcher, 1995; Elias and Matthews, 2002)
(14) Wolf Valley, Ellesmere Island, NWT, Canada	2–1.7 my	21 insect and arachnid taxa, indicative of northern tree line environments	(Matthews and Fyles, 2000; Elias and Matthews, 2002)
(15) Cape Deceit, Alaska	1.8 my	86 insect and arachnid taxa, indicative of northern treeline environments; some elements of tundra fauna seen for first time in Eastern Berngian region	(Matthews, 1974a,b; McDougall, 1995; Matthews and Telka, 1997; Elias and Matthews, 2002)

Miocene), based on the palynological signature of the fossil assemblage.

2.2. Niguanak, Alaska

The Niguanak site is on the Alaskan North Slope, near the Alaska–Canada border (Fig. 1, No. 3). The stratigraphy of the site has yet to be described in the literature. The fossil insect fauna was described by Matthews and Telka (1997). The fossil beetle assemblage has not been precisely dated, but based on associated paleobotanical remains, it is at least Late Pliocene in age, and may be as old as the Early Pliocene. The fossil floras are indicative of coniferous forest, including such warmth-loving taxa as *Tsuga* and *Lonicera*. However, the assemblage also contains

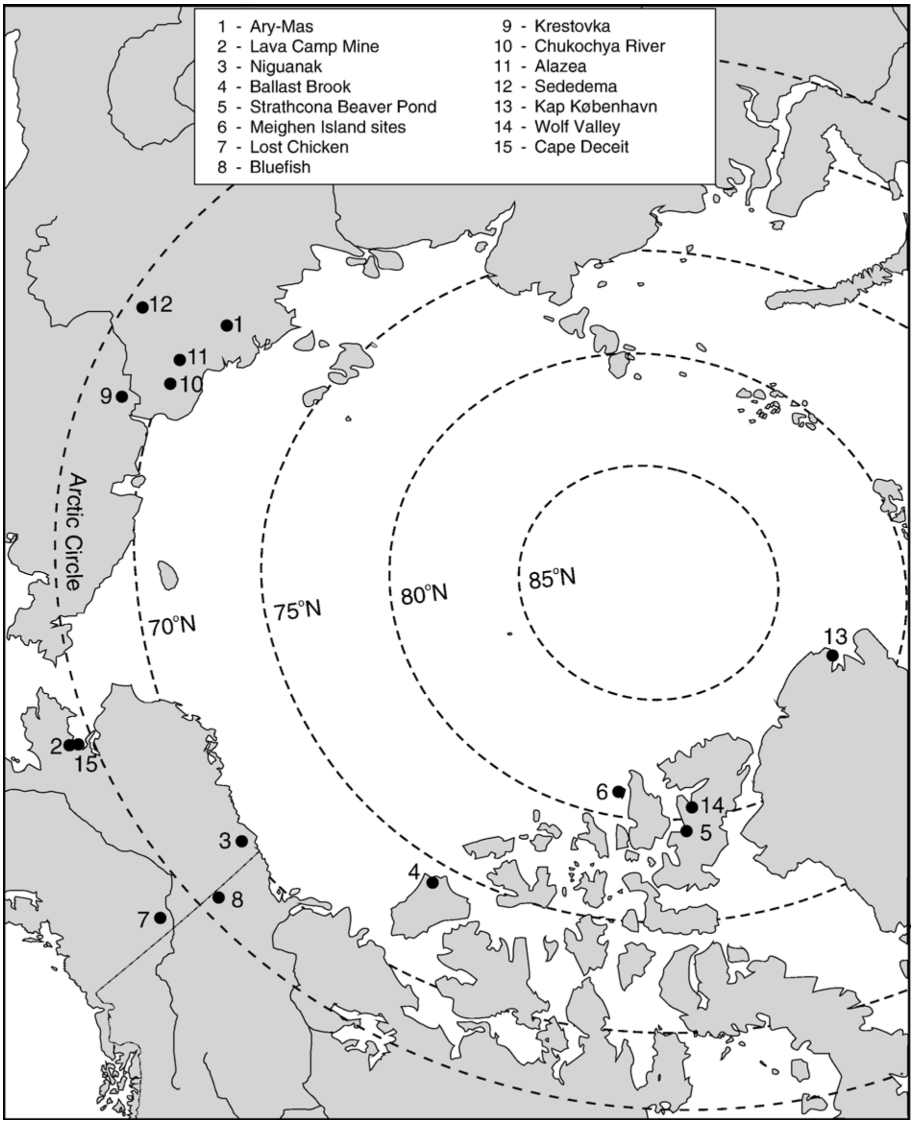

Fig. 1. Map of the Arctic, showing fossil sites discussed in text.

Dryas leaves which seem to contradict the warming implied by *Tsuga* and *Lonicera*. TMAX at the site today is about 4 °C. MCR analysis of the fossil beetle assemblage yielded a TMAX estimate of 7–10 °C (Elias and Matthews, 2002). The fossil assemblage contained 47 taxa of insects and arachnids, including the extinct ground beetle, *Diacheila matthewsi*. The fauna has not yet been fully analyzed, but has some Asian affinities (Matthews and Telka, 1997).

2.3. Ballast Brook, Banks Island, NWT, Canada

The fossil insect assemblage discussed here comes from the Beaufort Formation exposure (sample 3-73) at Ballast Brook, Banks Island (Fig. 1, No. 4). The insect fossils were extracted from a peat unit (Unit 4) that has been interpreted as a flood-plain pond deposit (Fyles et al., 1994). This sample yielded the greatest number of identified insect fossils (39 taxa). No exact age has been obtained from the Beaufort Formation deposits on Banks Island, but Fyles et al. (1994) suggest that it falls within the range of 5–3 my. The fossil plant assemblage associated with the Beaufort Formation at Ballast Brook is indicative of coniferous forest, similar to modern forests in the subarctic regions of Canada. There are indications that the site was near northern treeline at the time of fossil deposition. Matthews (written communication, 3/06) has recently revised his opinion on the probable environment at the time of deposition of the Beaufort Formation and other Late Tertiary sites on Ellesmere and Prince Patrick Island. Based on the plant macrofossils (and a few of the insect fossils), it now seems more likely that the coniferous environment at the time of deposition was more like the modern Acadian forest of maritime Canada. Modern TMAX at this high arctic site is only about 2.4 °C. The estimated TMAX for the fossil beetle assemblage was 14–14.5 °C—substantially warmer than today. Likewise, the estimated TMIN was more than 20 °C warmer than the modern TMIN (Elias and Matthews, 2002).

2.4. Strathcona Beaver Peat, Ellesmere Island, NWT, Canada

This deposit comes from a site near Strathcona Fiord on Ellesmere Island (Fig. 1, No. 5). The vertebrate fossil fauna and plant macrofossil data suggest that this deposit predates the Meighen Island deposits, so the age of the Beaver Peat fossils is thought to be greater than 3.3 my (Matthews and Telka, 1997). The deposit has been interpreted as a mass of semi-autochthonous peat, sufficiently compact to form a vertical wall within an alluvial deposit. This is a high arctic site, where modern TMAX is only about 2.4 °C, and TMIN is about −41 °C. The fossil assemblage contained 86 insect and arachnid taxa. MCR analysis of this fauna indicates that TMAX was about 10 °C warmer than today, and that TMIN was about 14 °C warmer than today. The fossil flora contains a mixture of boreal and tundra elements, and northern treeline may have been near the site at the time of fossil deposition. Thus, the level of warming indicated by the flora is a good agreement with that indicated by the beetle fauna (Elias and Matthews, 2002).

2.5. Meighen Island, NWT, Canada

The Meighen Island sites (Fig. 1, No. 6) have been dated at about 3 my (Fyles et al., 1991), making them about the same age as the Lost Chicken site in Alaska (see below). These deposits are part of the Beaufort Formation. Thin organic lenses are interbedded with alluvial sands and gravels, interpreted as representing an ancient floodplain (Matthews, 1974a). The fossil assemblages have been described by Matthews and Telka (1997). The site is situated far north of modern treeline, at 80°N latitude. The Meighen Island samples yielded extremely abundant, diverse insect fossil assemblages, comprising 198 taxa of insects and arachnids. MCR analysis of the assemblages indicated levels of warming of summer and winter temperatures almost identical to those inferred from the Strathcona Fiord site (Elias and Matthews, 2002). The paleobotanical evidence from the Meighen Island deposits is indicative of northern treeline vegetation. The level of climatic warming needed to allow coniferous forests to grow at this latitude is essentially the same as that indicated by the MCR analysis of the beetle assemblages.

Elsewhere in the Canadian Arctic, several large assemblages of Tertiary fossils have recently been found on Prince Patrick Island and Late Tertiary insects have also been found on Bylot Island by a research group from Laval University. The Bylot Island fossils may be of about the same age as Kap København, discussed below. They do not look to be as old as the fauna from Meighen Island (J.V. Matthews, written communication, 3/06).

2.6. Lost Chicken Mine, Alaska

The Lost Chicken site (Fig. 1, No. 7) is near the Yukon border in east-central Alaska. The Lost Chicken Mine is a working placer mine along the Taylor Highway. It includes exposures of plant- and insect-bearing fluvial sediments and peats of upper Pliocene age, as indicated by the Lost Chicken tephra layer, with a glass isothermal fission-track age of 2.9 ± 0.4 my (Matthews et al., 2003). These deposits are thought to represent slow deposition of organic matter in wetlands marginal to streams or in abandoned channels. The plant macrofossils found in this deposit include larch (*Larix laricina*), a pine similar to lodgepole pine (*Pinus contorta*), and several warmth-loving plants, such as elderberry (*Sambucus*). The fossil flora is indicative of warm, wet climate that was far less continental than it is today. The fossil insect fauna from the Lost Chicken site has been described by Matthews and Telka (1997). It contained 83 insect and arachnid taxa. The beetle fauna yielded an MCR estimate for TMAX that is essentially the same as the modern TMAX at the site (15.3 °C). The paleobotanical data indicates that mean winter temperatures were substantially milder than they are today. The MCR reconstruction of TMIN yielded a result of −27.75 to −19.25 °C. This is a rather broad estimate, as are many TMIN reconstructions based on the MCR method (Elias et al., 1996). Modern TMIN at the site is −25.4 °C. Thus, the MCR TMIN estimate ranges from more than 2 °C colder than modern, to more than 6 °C warmer than modern. The latter estimate appears agree reasonably well with the paleobotanical evidence.

2.7. Bluefish, Yukon Territory, Canada

The Bluefish site lies near the Alaskan border in the northwestern region of the Yukon Territory (Fig. 1, No. 8). The Bluefish assemblage is not precisely dated, and the stratigraphy of the site has not yet been published, but the fossil insect fauna was considered by Matthews and Telka (1997) to be more modern than that of the Lost Chicken site in Alaska, dated around 3 my. The Bluefish plant fossil assemblages include species indicative of substantially warmer, less continental climate than exists in the Yukon today. The insect fauna was relatively small, containing only 26 insect and arachnid taxa. MCR analysis of this fauna indicates mean summer temperatures that were very near the modern level, and mean winter temperatures that were as much as 8 °C warmer than modern (Elias and Matthews, 2002).

2.8. Wolf Valley, Ellesmere Island, NWT

The Wolf Valley site lies near Cañon Fiord on Ellesmere Island (Fig. 1, No. 14). The fossil insects were described by Matthews and Fyles (2000). The fossil insect specimens come from lenses of organic detritus or peat, forming part of river terrace deposits (Matthews and Fyles, 2000). The fossil plant record is indicative of treeline conditions, so the climate is inferred to have been warmer than it is today. The Wolf Valley samples are not precisely dated, but they may correlate with the fauna and flora from the Kap København Formation in Greenland, estimated to be 2–1.7 my. On the other hand, they may correspond to the Early Quaternary Fishcreekian Transgression of the northern Alaskan coast (McDougall, 1995), which occurred between 1.7 and 1.2 my (Matthews and Fyles, 2000). The fossil insect fauna contained just 21 taxa. MCR analysis of this fauna suggests that mean summer temperatures were 5–7 °C warmer than they are today. TMAX near modern Arctic treeline in Canada averages about 10 °C, which agrees with the upper end of the TMAX reconstruction based on the beetle fauna. The TMIN estimate from the beetle fauna was 8–13 °C warmer than modern. Both the fossil flora and insect fauna are suggestive of climatic conditions substantially cooler than those associated with the Beaufort Formation (3 my), and likewise somewhat cooler than those inferred from Kap København in Greenland.

2.9. Cape Deceit, Alaska

The Cape Deceit site (Fig. 1, No. 15) lies north of the Lava Camp Mine site on the Alaskan Seward Peninsula. The fossil insect fauna was originally described by Matthews (1974b), and contained 86 taxa. The age of the Cape Deceit Formation has recently been revised to 1.8 my (McDougall, 1995; Matthews and Telka, 1997). As such it may be roughly contemporaneous with the Wolf Valley samples from Ellesmere Island. The insect fossils from this formation were extracted from peat beds, interpreted by Matthews (1974b) as autochthonous fen and bog peats. The Cape Deceit Formation paleoflora is likewise indicative of northern treeline environments. The insect fauna contains arctic tundra elements. The vegetation record suggests that temperatures were slightly warmer than they are today, because treeline is only about 100 km south of Cape Deceit. The MCR analysis of the beetle fauna from the Cape Deceit Formation yielded a TMAX estimate about 2 °C warmer than modern, and a TMIN estimate about 4–6 °C cooler than modern (Elias and Matthews, 2002). However, as discussed by Elias et al. (1999), TMIN reconstructions for coastal sites in Alaska are skewed towards colder temperatures, probably because Arctic air incursions during the winter months are sufficiently cold to kill the more maritime-adapted species that might otherwise live in coastal regions.

3. Research in Northeastern Siberia

During the 1980s, two of us (Kuzmina and Kiselyov) studied Late Tertiary and Early Quaternary insect fossil assemblages from a series of four sites in northeastern Siberia (Kiselyov, 1981; Kuzmina, 1989). The fossil assemblages were sampled from four geologic formations. The lowest of these, from the Ary-Mas site, is thought to be of Miocene age. The Begunov Formation is thought to be of Early Pliocene age. Above this lie the Kutuyakh Beds, thought to be Late Pliocene in age. The uppermost deposits in this sequence are in the Olyor Formation, now thought to represent the Pliocene–Quaternary boundary. All of the fossil sites are in lowland basins that were unglaciated during the Pleistocene. The individual sites are as follows.

3.1. Ary-Mas, NE Siberia

This site yielded a small fauna (41 beetle taxa, including 31 specific identifications). The fauna is thought to be of Miocene age (Ovander and Pybakova, 1985). The sample was taken from the upper part of a Late Miocene lacustrine-alluvial unit, which is fine-grained sand with thin beds of plant detritus. It contains five species thought to be extinct. The fauna contains numerous riparian species, most of which live in coniferous forest regions today. However, some arctic tundra species, such as *Diacheila arctica*, were found in this assemblage. Also, some open ground, temperate species were found, such as *Trachypachus holmbergi*. Taken as a whole, this fauna is indicative of open coniferous woodland or forest–tundra. Given the apparent age of the fauna, we find it remarkable that 26 out of the 31 identified species remain extant. One other remarkable feature of the Ary-Mas fauna is the presence of some Eastern Beringian components (*T. holmbergi*, *Blethisa inexpectata*, *Lepidophorus lineaticollis*) which have been found in no other deposits from northeast Asia.

3.2. Krestovka, NE Siberia

The Krestovka site, at about 70 °N, lies in the Kolyma River basin (Fig. 1, No. 9). Today, the site is situated in the taiga (boreal forest) zone. Three major deposits of Late Tertiary-age were studied here. The lower deposit comes from the Begunov Formation of the Early Pliocene (Sher et al., 1977a). This is probably an alluvial deposit that consists of pebbles with lenses of sand and plant detritus. Almost all of insect remains belong to ground beetles in the *Cryobius* group of the genus *Pterostichus*, which are typical arctic tundra inhabitants (Kiselyov, 1981). Some species indicative of shrub (the weevil *Dorytomus* sp.) and riparian (the weevil *Pelenomus velaris*) environments and wet tundra were found there. The paleobotanical data indicate a forest environment, based on the presence of conifer pollen and plant macrofossils (Sher et al., 1977a,b). When taken together, the fossil data indicate a coniferous woodland, with open patches of steppe or steppe–tundra.

The middle deposit at this site are the Kutuyakh Beds, thought to be Late Pliocene in age (Sher et al., 1977b). The Kutuyakh Beds contain peaty silts and peat layers, disturbed by ice wedge casts. Most of the insect remains come from the upper part of the unit, from bedded sand and silt of possible alluvial origin.

The Kutuyakh Formation insect fauna contained only a few beetle taxa (Kiselyov, 1981). These represent a mixture of boreal and arctic taxa. The boreal element includes the weevil *Pissodes gyllenhali*. The arctic tundra element includes *Cryobius* species as well as the ground beetle *Blethisa catenaria*. The environmental reconstruction based on this fauna was of a larch forest–tundra landscape.

The insect assemblages from deposits (bedded sand and silt of possible alluvial origin) situated between the Kutuyakh beds and the overlying Olyorian deposits at the Krestovka site contain mostly tundra species. *Pterostichus* (*Cryobius*) species are abundant in these faunas, as well as the ground beetle *Amara alpina*, that prefers drier tundra habitats. These faunal assemblages also include some taiga species, such as the weevils *Hylobius piceus* and *Pissodes gyllenhali*. Notably, some steppe species were also found in these deposits, such as the leaf beetle cf. *Crosita*, the weevil *Coniocleonus ferrugineus*, and the pill beetle *Morychus viridis*. The paleoenvironmental reconstruction associated with this fauna is a larch forest–tundra landscape with patches of tundra–steppe. The species composition of the insect assemblages from Unit 3 of the Krestovka section provide the first indication of the tundra–steppe environment in Siberia.

The upper deposit comes from the Olyor Formation, thought to represent the Pliocene–Quaternary boundary. The origin of Olyor Formation is still unclear. These deposits probably represent alluvial-lacustrine deposition (e.g., deposition of organic matter in wetlands marginal to streams or in abandoned channels), with the possible addition of some other types of deposition, followed by gradual transformation into monotonous loess-like sediments by the action of permafrost.

The Olyor Formation beetle fauna contained 51 beetle taxa. Most of these species are found today in arctic tundra regions, although some taxa have steppe affinities today. The fauna is indicative of steppe–tundra landscape with patches of shrub tundra and single trees or small tree patches (probably birch and larch).

3.3. Chukochya River, Northeastern Siberia

The site on the Chukochya River, northwest of the Krestovka site (Fig. 1, No. 10), yielded an insect fauna associated with the Olyor Formation (Kiselyov, 1981). Today this site is situated in the tundra zone. This fauna comprised a somewhat richer assemblage, including 51 beetle taxa (Kiselyov, 1981). Most of these beetles are found today in arctic tundra regions of Siberia, but there are also some taxa that are found today in steppe regions, further south. According to pollen study, there was treeless open landscape here with steppe elements. Kiselyov (1981) described six stages of environmental change during Olyorian time. The fourth stage is characterized by the presence of some forest species, while all the other stages contain mixtures of tundra and steppe beetles in various proportions.

3.4. Alazea, Northeastern Siberia

The Alazea site is southwest of the Chukochya site (Fig. 1, No. 11). The insect fauna is associated with the

Olyor Formation, and contained 56 beetle species (Kuzmina, 1989). At the Alazea site, the upper part of Olyor Formation consists of coarse-grained sand and gravel beds, rich in lenses of organic detritus (including the insect remains). This deposit is evidently alluvial in origin. As in the Chukochya River fauna, most of these beetles are found today in arctic tundra regions, but some taxa have steppe affinities. There are two horizons with scattered wood remains in the lower part of the section, but only tundra and water beetles were found in these horizons. The proportion of steppe beetle species in the fossil assemblages increases from the lower to the upper parts of the section. The top of Olyor Formation (Early Pleistocene) contains an abundant and diverse steppe beetle fauna, together with tundra-dwelling species.

3.5. Sededema, Northeastern Siberia

The Sededema site is located in the Kolyma basin (Fig. 1, No. 12). It is the southernmost of the Siberian sites discussed here. This site also yielded a beetle fauna associated with the Olyor Formation. It contained 55 beetle species, indicative of the same environments described for the other Olyor Formation faunas (Kiselyov, 1981). The paleobotanical evidence shows an environmental change from forest-tundra in the lower part of the section to open tundra–steppe landscape in the upper part. The forest–tundra vegetation reconstruction is based on the presence of alder and shrub-birch pollen. The fossil beetle yielded a different reconstruction. According to the insect evidence, the landscape was mostly open tundra, with some steppe elements, but there was a noticeable increase in forest beetles above the middle part of the section, similar to the faunal trends in the Chukochya site. The importance of steppe species was a little less here, compared with the other Olyorian sites.

4. Research in Greenland

Fossil insect assemblages of Late Pliocene–Early Quaternary age in Greenland have only been found at one locality—Kap København in Pearly Land, northernmost Greenland (Fig. 1, No. 13). Although only one faunal assemblage is discussed here, this particular assemblage is truly outstanding in the quality and quantity of insect fossils preserved. Matthews and Telka (1997) described the Kap København fauna as ‘a reference against which all others from the arctic are compared.’

The fossil insect assemblages from this site have been described by Böcher (1995). The age of the deposits is estimated between 2.5 and 2 my, at approximately the boundary between the Pliocene and the Pleistocene. The insect fossils were extracted from lenses of organic material interpreted as fluvial detritus (Bennike and Böcher, 1990). The Kab København fossil beds may have been deposited soon after the first glaciation, marking the onset of Quaternary climates. Nevertheless, at that time, it is clear that northern high latitude climates were remarkably warm. The Kab København flora and insect fauna are indicative of northern treeline environments. This seems quite a remarkable finding for a site on one of the northernmost points of land in the Northern Hemisphere. The fauna contained 154 insect and arachnid taxa. MCR analysis of the beetle fauna yielded a TMAX value 8 °C warmer than modern, and a TMIN value about 10 °C warmer than modern. These levels of warming, while substantial, are not quite as high as those inferred from the Meighen Island and Stracona Fiord assemblages, which are thought to be 500,000–700,000 years older than the Kap København fauna. The Meighen Island fauna is also more diverse, and contains more warm-adapted species than the Kab København fauna (Matthews and Telka, 1997).

5. The Arctic beetle fauna of the Late Tertiary and Early Quaternary

For the most part, the beetle faunas discussed in this paper represent somewhat tentative identifications, based solely on morphological features of their major exoskeletal sclerites (head capsules, pronota, and elytra). In order to make definitive identifications for many of the species discussed here, the original investigators would have needed to see the associated fossil genitalia. However, these are only rarely preserved. We acknowledge that our discussion of the various beetle species is thus built on less-than-firm foundations. There is better evidence for beetle species through much if not all of the Quaternary (i.e., the last 2.6 my), based on greater numbers of species with fossil records including genitalia. By extending our discussions back into the Late Tertiary, we are pushing Quaternary entomological methods into uncharted territory. In order to make paleoenvironmental reconstructions, we have taken some fossil specimens that were only tentatively referred to modern species by previous workers as definitely belonging to those modern species.

On the other hand, an inescapable fact is that the Late Tertiary beetle faunas are ecologically coherent assemblages. We consider this a strong argument, along with the constancy of their external morphology, for the longevity of many, if not most of the species discussed in this paper. Additional fossil research may eventually sort out these problems. From another perspective, some of the species considered by various paleoentomologists to represent extinct forms may eventually be discovered as extant species. New modern taxa are continually being described from the Arctic, including some of the same groups of taxa typically found in these Late Tertiary fossil assemblages (e.g., species of Carabidae, Staphylinidae, and Curculionidae). So some of the species listed as 'extinct' in Table 2 may eventually be matched with extant species that have yet to be described. The caveats discussed above definitely make this paper a 'work in progress,' rather than the last word on the subject.

The fossil insect faunas of Late Tertiary and Early Quaternary age from North America and Greenland comprise 437 taxa of insects and arachnids. Of these, 180 have been identified to the species level (Matthews and Telka, 1997). The beetle faunas of this age, along with ants (Hymenoptera: Formicidae) and true bugs (Heteroptera) have been published from northeastern Siberia by Kiselyov (1981) and Kuzmina (1989). These faunas include 156 beetle taxa, of which 127 species have been identified. Beetles are by far the most important order of insects in these fossil assemblages. Of the insect species identified from these assemblages, 251 species are beetles. The combined beetle species list is shown in Table 2. This list includes species in 22 beetle families, dominated by ground beetles (Carabidae) (109 species), weevils (Curculionidae) (46 species), leaf beetles (Chrysomelidae) (21 species), predaceous diving beetles (Dytiscidae) (12 species), and rove beetles (Staphylinidae) (11 species). Although predatory species dominate the faunal lists, plant-feeding beetles, such as weevils and leaf beetles, were found in all the assemblages, and their remains were sometimes preserved in considerable numbers. Other ecological groups represented in these faunal assemblages include detritivores, dung beetles, carrion beetles, and fungus-feeding beetles.

The faunal diversity of the assemblages is roughly equivalent for most regions, at about 50–60 species. However, the Siberian assemblages contained 120 species. The difference between the Siberian assemblages and those from the other study regions is that the Siberian assemblages contained large numbers of plant-feeding species (Chrysomelidae and Curculionidae). The assemblages from Alaska, Canada, and Greenland had far fewer species in these families.

Species diversity declined in Arctic beetle faunas, during and after the Tertiary–Quaternary transition from warmer to colder climates. Much of the Late Tertiary diversity was tied to the existence of coniferous forests or woodlands at high latitudes. As these biological communities gave way to Arctic tundra in the Quaternary, regional insect faunal diversity likewise diminished. This trend makes ecological sense, as few insects are adapted to life in extremely cold climates. Since insects are ectothermic, they are at a distinct disadvantage in extremely cold climates. The modern statistics clearly reveal this pattern. Danks (1981) listed just 1800 species of insects and other arthropods living today in Arctic North America. The number of insect species living today in North America as a whole exceeds 90,000 species (Borror and White, 1970). Thus, the Arctic insect fauna comprises only about 2% of the fauna of the North American continent, today.

5.1. Ecological affinities

Beetles associated with water, damp terrestrial habitats, and riparian habitats are important elements in most of the faunal assemblages (Table 2). Hygrophilous species are more-or-less equally represented in the faunas from the four study regions (Greenland, northeastern Siberia, the Canadian high arctic, and the combined regions of Alaska and the Yukon Territory that formed Eastern Beringia) (Fig. 2A). Water beetles are best represented from Kap København, and in the Siberian assemblages (Fig. 2B). The Canadian high arctic sites contained the greatest diversity of riparian beetles, but this group was reasonably well represented in all the study regions (Fig. 2C). All of the study sites represent water-lain deposits, such as peat bogs, ponds, or lakes, so it is not surprising that beetles living in or near water are well represented in such fossil assemblages. Their representation in the fossil assemblages did not change significantly through the time series of the fossil assemblages. In fact, the riparian group had the greatest faunal diversity of any of the ecological groups discussed here, with 58 identified species.

All of the fossil assemblages, taken in combination with plant macrofossils and pollen from the same horizons, are indicative of either coniferous forest or forest–tundra woodland. As discussed above, the Beaufort Formation fossil assemblages are probably more indicative of modern coniferous forests found in the Canadian Maritime region than of modern boreal forests of interior Canada and Alaska. More ecological details will certainly be brought to light with additional research, but for now we can say that coniferous forests of various kinds are indicated for the fossil assemblages from Alaska, the Yukon Territory, the Canadian high arctic, and northern Greenland. The latter is indicated for some of the northeast Siberian assemblages. Beetle species associated with coniferous forest environments were found in all the fossil sites, with the greatest diversity of species coming from the Siberian faunal assemblages (Fig. 2E). However, all of the forest species found in the Siberian assemblages are single individuals, so their ubiquity on the landscape remains uncertain. As discussed above, some of the high arctic site faunas were indicative of northern treeline environments. Needless to say, the position of northern treeline is far to the south of these sites, today. Only one bark beetle was identified from these assemblages, *Ips cembrae*. This species was found in the Olyor Formation fauna from the Krestova site in Siberia. This beetle mainly attacks larch today, although it has also been found on other conifers.

Table 2
Beetle species found in Late Tertiary and Early Quaternary fossil assemblages

Taxon	Sites	Habitat/ecology	Modern range
Family Trachypachidae			
Trachypachus gibbsi LeC.	KpK	R	PNW
Trachypachus holmbergi Mnh.	A-M?, LC?, MI?	X,O	WNA
Trachypachus zetterstedti Gyll.	A-M, O-C, O-S	CL	NPA
Family Carabidae			
Carabus chamissonis Fisch.	Ng?	O, DT	N Am, B-Arc, Alp
Carabus maeander Fisch.	O-S	H, B	TA, B-Arc, Alp, Si
Carabus cf. *nemoralis* type A[a]	MI	?	?
Carabus cf. *nemoralis* type B[a]	LC	?	?
Carabus odoratus Motsch.	O-K, O-A, O-S	DT, X	Asia
Carabus taedatus Fab.	MI	X, O, TV	N Am, B-Arc, Alp
Carabus truncaticollis Esch.	O-K, O-C, CD	MT	AB
Carabus vietinghoffi Adams	MI?	O, MT, CF	NW N Am, NE As
Pelophila borealis Payk.	O-C	H, P	CP B-Arc
Pelophila rudis LeC.	MI?	R, P	B-Arc
Notiophilus aeneus Hbst.	LC?, MI?	M, DL	ENA
Notiophilus aquaticus L.	A-M, K-K, O-K, O-C, O-A, O-S, KpK?	O	CP, N
Notiophilus biguttatus Fab.	KpK?	CF, DF	Europe
Notiophilus directus Csy.	MI?	R, O	WNA
Notiophilus semistriatus Say	CD	O, TV	TA, B-Mon
Notiophilus sylvaticus Esch.	A-M	TA	WNA
Notiophilus sp. 2[a]	A-M	?	?
Opisthius richardsoni Kby.	MI?	R	WNA, B-Mon
Blethisa catenaria Brown.	K-K, O-K, O-C, O-S, MI?, SF?, KpK?	MT, P	Si, W Arc
Blethisa multipunctata L.	MI?	R, P	CP B-Mon
Diacheila arctica Gyll.	A-M?	MT	PA Arc
Diacheila matthewsi Böcher[a]	LC, Ng, MI, KpK	?	?
Diacheila polita Fald.	O-C, O-A, O-S, CD	MT, H	±CP Arc
Elaphrus angusticollis R.F. Sahlb.	O-S, KpK	R, DL	±CP
Elaphrus clairvillei Kby.	LC, MI?	H, DL	TA
Elaphrus lapponicus Gyll.	K-K, O-C, O-S, LC, BF?, MI?, KpK	H, R	CP B-Arc
Elaphrus lecontei Crotch	KpK	R, SW	±TA
Elaphrus olivaceus LeC.	KpK?	R, SW	E N Am
Elaphrus riparius L.	A-M?, O-C, O-A	R, SW, RW	NPA, NW N Am
Elaphrus sibiricus Motsch.	KpK?	R	Asia
Elaphrus tuberculatus Mäkl.	KpK	H, R	CP, B-Arc
Dyschirioides frigidus Mann.	CD	O, B	TA, N
Dyschirioides laevifasciatus Horn	MI?	R	WNA, B-Mon
Dyschiriodes nigricornis Motsch.	O-K, O-C, O-A, O-S, CD	R	CP N
Dyschiriodes varidens Fall	Ng?	R	WNA
Miscodera arctica Payk.	KpK	X, TV	CP B-Mon
Asaphidion alaskanum Wick.	SF, MI, KpK	R, TV	WNA, B-Arc
Asaphidion yukonense type A[a]	LC	?	?
Bembidion bimaculatum Kby.	MI?, KpK?	R, O, TV	WNA, B-Mon

Table 2 (*continued*)

Taxon	Sites	Habitat/ecology	Modern range
Family Carabidae			
Bembidion dyschirinum LeC.	MI, SF, KpK?	O, M, DL	WNA, Mon
Bembidion grapii Gyll.	SF, KpK	O, TV	CP, B-Arc, Alp
Bembidion hasti C.R. Sahlb.	MI?	R, MT	CP, B-Arc
Bembidion lapponicum Zett.	KpK?	R, O	±CP
Bembidion mckinleyi Fall	KpK?	R, O	WNA, B-Arc, Sc
Bembidion nigripes Kby.	MI?	R, O	TA, N
Bembidion nitidum Kby.	MI?	X, O, TV	TA, N
Bembidion planatum LeC.	MI, KpK?	R, O	WNA, ENA
Bembidion planiusculum Mann.	KpK?	R, O	WNA
Bembidion sordidum Kby.	KpK?	R, O	TA, B-Arc
Bembidion transparens Gebl.	KpK	H, P	CP, B-Arc
Bembidion umiatense Lth.	O-K?, O-C?, O-A?, O-S?, CD?	R, O	EB, Arc
Bembidion (*Peryphus*) sp. 1[a]	A-M	?	?
Bembidion (*Peryphus*) sp. 2[a]	A-M	?	?
Patrobus septentrionis Dej.	LCM?, LC?	R	CP, B-Arc, Alp
Patrobus stygicus Chaud.	KpK?	H, R	TA, B
Platidiolus vandykei Kurn.	MI?	R, O	WNA, M
Poecilus nearcticus Lth.	O-C, O-A, O-S	DT	EB
Poecilus samojedorum J. Sahlb.	K-K, O-K, O-C, O-S, KpK?	DT, X	Si
Pterostichus adstrictus Eschz.	KpK?	O	CP, B-Alp
Pterostichus agonus Horn.	O-C, O-A	MT, R	Si, W B-Arc
Pterostichus circulosus Lth.	MI?	H, B	EB
Pterostichus corvinus Dej.	LCM?	H	±TA
Pterostichus costatus Men.	A-M?, K-K, O-K, O-C, O-A, O-S, CD	H, P	CP, Arc
Pterostichus mannerheimi Dej.	O-S	CF	Asia
Pterostichus patruelis Dej.	LC	H, B	TA, N
Pterostichus punctatissimus Rand.	LC	CL, DL	TA, B-Mon
Pterostichus sublaevis Sahlb.	K-K, O-K, O-C, O-A, O-S, MI?	DT	Si, W Arc
Pterostichus tundrae Tschitsch.	O-C	DT	PA, Arc B
Pterostichus vermiculosus Men.	O-C, O-A, O-S, LCM?, NG?, MI, SF, KpK	DT or MT	CP, Arc
Pterostichus auriga Ball	CD	MT	EB, Arc
Pterostichus biocryus Ball	CD	MT	EB, Arc
Pterostichus brevicornis Kby	K-K?, O-K?, O-C?, O-A?, O-S?, CD, KpK?	MT, DL	CP, B-Arc, Alp
Pterostichus hudsonicus LeC.	MI?	DL, R	EB
Pterostichus kotzebuei Ball	CD, MI?	DL, P	EB
Pterostichus mandibularoides Ball	CD	DL, R	WNA, B-Arc
Pterostichus middendorfi J. Sahlb.	MI?	DT, R	PA, Arc
Pterostichus nivalis R. Sahlb.	CD	DT	AB
Pterostichus pinguedineus Eschz.	K-K?, O-K?, O-C?, O-A?, O-S?, CD	B, MT, CL	±CP, B-Arc, Alp
Pterostichus similis Mann.	CD	MT, DL	AB
Pterostichus tareumiut Ball	CD, MI?	MT, P	AB
Pterostichus tiliaceoradix Ball	CD	X, TV	EB, B-Arc, Alp
Pterostichus ventricosus Eschz.	K-K?, O-K?, O-C?, O-A?, O-S?, CD	MT, DL	CP, B-Arc
Pterostichus (*Cryobius*) sp. A[a]	K-K, O-K, O-C, O-A, O-S	?	?
Stereocerus haematopus (Dej.)	O-K, O-C, O-A, O-S, CD, Ng, MI?, KpK?	DT	CP, B-Arc
Amara alpina Payk.	K-K, O-K, O-C, O-A, O-S, CD, Ng, MI?	X, O, DT	CP, Arc, Alp
Amara bokori Csi.	MI?	DT?	AB, Arc
Amara carinata LeC.	MI?	O, Gr	Int N Am
Amara colvillensis Lth.	MI?	DT-MT	W Arc
Amara glacialis Mann.	MI?, KpK	R, O, X, TV	CP, B-Arc
Amara hyperborea Dej.	CD?, MI?	R, DL	CP, B-Arc
Amara interstitialis Dej.	K-K, O-K, O-C, O-A, O-S	O, X	TE, NW N A
Amara quenseli Schonh.	A-M	DT	H, B-Alp
Harpalus amputatus Say	MI?	O, X	Int N Am
Harpalus cordifer Not.	MI?	CL	WNA
Dicheirotrichus mannerheimi R. Sahlb.	O-K, O-C, O-A, O-S	DT, TV	CP
Dicheirotrichus cognatus Gyll.	A-M?	O, TV	CP, B-M

(continued on next page)

Table 2 (*continued*)

Taxon	Sites	Habitat/ecology	Modern range
Agonum albipes (Fab.)	KpK?	R, O	WPA
Family Carabidae			
Agonum exaratum Mann.	CD, LC, KpK?	MT, P	CP, Arc
Agonum bicolor Dej.	MI?	R	WNA
Agonum cincticolle Say	MI?	DF, CF, R	ENA
Agonum consimile Gyll.	MI?	H, R	CP, N
Agonum quinquepunctatum Motsch.	A-M	R	±CP Arc
Agonum (*Europhilus*) sp. 1[a]	A-M	?	
Agonum (*Europhilus*) sp. 2[a]	A-M	?	
Platynus decentis Say	LC	CF, H, R	TA
Platynus mannerheimi Dej.	LC	H, B	TA, N
Dromius piceus Dej.	MI?, KpK	CF, DF	TA
Cymindis arctica Kryzh. et Em.	O-C, O-A, O-S	St	Si
Cymindis vaporariorum L.	O-K	CF, O	PA
Family Dytiscidae			
Noterus crassicornis (Müll.)	KpK	SW, B	PA
Hydroporus acutangulus Thoms.	K-K?, O-K?, O-C?, O-A?, O-S?	SW	Arc
Hydroporus morio Aubé	KpK?	SW	H, N
Oreodytes sanmarki (Sahlb.)	KpK?	RW, SW	H, N
Agabus affinis (Payk.)	KpK?	B, SW	PA, B
Agabus anthracinus Mann.	KpK?	SW	TA
Agabus bifarius (Kby.)	MI, SF, KpK	SW	TA, B, EPA
Agabus moestus (Curt.)	K-K, O-K, O-C, O-A	SW	CP, Arc
Ilybius vittiger Gyll.	KpK?	SW, B	H, N
Colymbetes dolabratus (Payk.)	O-K, O-A	SW	CP, Arc
Colymbetes paykulli Er.	O-K	SW, B	H, B
Neoscutoperus hornii LeC.	CD?	SW	?
Family Gyrinidae			
Gyrinus pullatus Zaitz.	O-C	SW	PA
Gyrinus opacus C. Sahlb.	O-C	SW, B	CP, B-Arc
Family Hydrophilidae			
Hydrochus brevis Hbst.	O-C?	SW, B	PA, B
Helophorus frater Smet. (=*furius*)	KpK?	SW	TA, N
Helophorus niger J. Sahlb.	KpK?	SW	PA, Arc
Helophorus splendidus J. Sahlb.	O-K, O-C, O-A, O-S, CD	H, B, DL	CP, Arc
Helophorus sibiricus Motsch.	O-K, O-C	R, SW, Sn	H, B
Helophorus tuberculatus Gyll.	KpK?	B, R	H, B
Helophorus coopei Matth.[a]	LCM	?	?
Helophorus meighenensis Matth.[a]	MI		?
Hydrobius fuscipes F.	O-K, O-C, O-S, MI?	SW, P	CP, B-Arc, Alp
Coelostoma orbiculare F.	A-M	R	PA
Megasternum obscurum (Motsch.)	KpK?	Dung, Det	H
Family Leiodidae			
Cholevinus sibiricus (Jean.)	O-K, O-C, O-A, O-S	MT	PA, Arc
Agathidium marginatum Sturm.	O-K?, O-C?, O-A?, O-S?	DL	PA
Family Agyrtidae			
Pteroloma forsstoemi (Gyll.)	KpK?	R, B	NW Eur
Family Micropeplidae			
Kalissus nitidus LeC.	BF	R	NW N Am
Kalissus sp. A[a]	LCM, MI	?	
Micropeplus hoogendorni Matth.	LCM	?	WB
Micropeplus hopkinsi Matth.[a]	LCM	?	
Micropeplus nelsoni Mäkl.	SF	Fungi	NW N Am
Micropeplus sculptus LeC.	MI	B	B T
Micropeplus tesserula Curt.	LCM, SF	DL, B	CP, B-Alp
Family Silphidae			
Thanatophilus dispar Hbst.	O-K	R	N PA
Heterosilpha ramosa (Say)	MI?, KpK?	DW	W N Am
Aclypea opaca (L.)	O-K, O-C, O-S, MI?	FT	PA, NW N Am

Table 2 (*continued*)

Taxon	Sites	Habitat/ecology	Modern range
Family Silphidae			
Phosphuga atrata L.	O-C	FT	NPA
Family Staphylinidae			
Pycnoglytpa lurida (Gyll.)	MI	H, B, DL	CP, B-Arc
Micralymma brevilingue Schiødt.	CD, LC, SF	MT, DT	W Arc
Coryphium hyperboreum (Mäkl.)	Ng	R	PA, Arc, EB
Olophrum boreale (Payk.)	SF	B, DL, H, MT	CP, B-Arc
Olophrum consimile (Gyll.)	SF?, KpK?	B, DL, P, R	CP, B-Arc
Olophrum rotundicolle (C.R. Sahlb.)	KpK?	B, DL, H, P	CP, B-Arc
Eucnecosum brachypterum (Grav.)	KpK?	H, DL	CP, B-Arc
Tachinus jacuticus Popp.	MI?	DW	TA, Arc Alp, WB
Tachinus arcticus Motsch.	O-K, O-C, O-A, O-S	MT, DT	WB
Tachinus brevipennis J. Sahlb.	CD, Ng	MT, DT	AB
Tachyporus nimbicola Camp.	KpK?	DL, MT, O	TA, B-Arc, Alp
Family Scarabaeidae			
Aegialia sabuleti (Panz.)	KpK?	O, Det	NW Eur
Aphodius sp. A[a]	O-K, O-C, O-A	?	?
Family Byrrhidae			
Curimopsis cyclolepidia Muenst.	O-K, O-C, O-S	MT	NPA
Byrrhus fasciatus Forst.	O-C, O-S	O, X	PA
Simplocaria arctica Popp	O-K, O-C	MT	NPA
Simplocaria basalis Sahlb.	A-M?	MT	PA, B
Simplocaria elongata Sahlb.	CD	H	CP, N
Morychus aeneus F.	A-M?	X	PA, B-Arc
Morychus viridis Kuzm. et Kor.	K-K, O-K, O-C, O-A, O-S	SS	Si
Cytilus alternatus (Say)	Ng	CL, DL	TA
Family Elateridae			
Denticollis varians Germ.	O-K, O-C, O-A	CF	Asia, ENA
Hypolithus cf. *sandborni* (Horn)	MI	R	TA
Hypnoidus hyperboreus Gyll.	O-C, O-S	FT-ME	NPA
Family Cantharidae			
Podabrus alpinus (Payk.)	SF	CF, DF	PA
Family Anobiidae			
Hadrobregmus pertinax (L.)	KpK?	CF, DF, B	Eur
Family Melyridae			
Troglocollops arcticus Medv.	O-C, O-A	MS	Arc
Family Tenebrionidae			
Upis ceramboides L.	O-A	DF	CP B
Family Anthicidae			
Anthicus ater Panz.	O-A	R, Det	PA
Family Chrysomelidae			
Chrysolina aurichalcea Mann.	K-K, O-K, O-C	MS	PA
Chrysolina basilaris (Say)	CD		NW N Am
Chrysolina brunnicornis Medv.	O-A	ST	Si
Chrysolina perforata Gebl.	O-C	ST	Si
Chrysolina subsulcata Mannh.	K-K, O-C, O-A, O-S	MT, DT	CP, Arc
Chrysolina septentrionalis Men	O-C, O-S	MT	CP
Chrysolina tolli Jac. (=*cavigera*)	O-K, O-C, O-S, CD	MT, DT	CP, Arc
Calophellus alpinus Payk.	O-K, O-C	ME	PA
Phaedon cyanescens Stål.	CD		TA
Phaedon concinnus Steph.	O-S	ME	PA
Gastrolina peltoidea Gebl.	O-C	FT-SH	Asia
Hydrothassa hannoverana F.	O-K, O-C, O-A	R	PA
Chrysomela taimyrensis Medv.	O-C	FT-SH	Si, Arc
Gonioctena affinis Gyll.	O-C	FT-SH	PA
Sternoplatys fausti Weise	O-K, O-C	MS	Asia
Phratora polaris Schn.	O-C	FT-SH	Asia
Galeruca daurica Jeann.	O-S	ST	Asia

(continued on next page)

Table 2 (*continued*)

Taxon	Sites	Habitat/ecology	Modern range
Family Chrysomelidae			
Chaetocnema costulata Motsch.	K-K	ST	Asia
Cassida berolinensis Suffr.	O-K	MS, ST	PA
Cassida flaveola Thunb.	CD	DW, ST, R	PA
Cassida nebulosa L.	O-C	ME	PA
Family Apionidae			
Pseudoprotapion astragali Payk.	O-A?	MS	PA
Hemitrichapion tschernovi T.-M.	O-A	DT	Si Arc
Eutrichapion rectirostre Schilsky	O-K?, O-C?	R	PA, B
Betulapion simile Kby.	O-C, O-S	DF	PA, B
Family Curculionidae			
Sitona borealis Kor.	O-K, O-C, O-A, O-S	DT, MS	NE As
Sitona lineellus Bonsd.	O-S	FT-ME	CP, B
Phyllobius virideaeris Laich.	O-K, O-A, O-S	ME	PA
Phyllobius kolymensis Kor. et Egorov	O-K, O-C, O-A, O-S	MS	NE As
Lepidophorus lineaticollis Kby.	A-M, LC	X, ST	±AB
Lepidophorus pumilis Buch.	LC?	X, O	NW N Am
Vitavitus thulius Kiss.	K-K, O-K, O-C, O-A, O-S, CD, LC	X, ST	EB
Hypera diversipunctata Schrank.	O-K, O-C, O-A, O-S	DT, MS	Asia
Hypera nigrirostris F.	A-M?	ME	PA
Hypera ornata Cap.	O-K, O-C, O-A, O-S	DT, MS	PA
Coniocleonus astragali T.-M.et Kor.	O-K, O-C, O-A	MS	Asia
Coniocleonus cinerascens Hochh.	O-C, O-A	MS, ST	Asia
Coniocleonus ferrugineus Fahr.	K-K, O-K, O-C, O-S	MS, ST	Asia Alp
Coniocleonus vinokurovi T.-M.et Kor.	O-A	MS, ST	Asia Alp
Coniocleonus zherichini T.-M.et Kor.	O-C	DT, O	CP
Stephanocleonus deportatus Chevr.	O-A	ST	Asia
Stephanocleonus eruditus Faust	O-K, O-C, O-A, O-S	ST	Asia Alp
Stephanocleonus fossulatus F-W.	O-K, O-A	ST	Asia Alp
Stephanocleonus incertus T-M.	O-K, O-C, O-A, O-S	ST	Asia Alp
Stephanocleonus paradoxus Fahr.	O-A	ST	Asia
Stephanocleonus tricarinatus F.-W.	O-A	ST	Asia
Lepyrus canadensis Casey	O-C, O-S	FT-SH	AB
Lepyrus gemellus Kby.	O-C, O-S	FT-SH	AB
Lepyrus nordenskioeldi Faust	K-K, O-K, O-C, O-A, O-S	FT-SH	±CP, B-Arc
Lepyrus volgensis Faust	K-K	FT-SH	PA
Hylobius piceus DeG.	K-K, O-C	CF	PA
Pissodes gyllenhali Gyll.	K-K, O-C	CF	PA
Pissodes insignatus Boh.	O-C	CF	Asia
Pissodes irroratus Reitt.	K-K, O-C, O-S	CF	PA
Pissodes piniphilus Hbst.	O-C	CF	PA
Dorytomus rufulus Tourn.	O-A	FT-SH	Asia
Grypus equiseti F.	O-C, O-S, Ng, MI?, KpK?	R	H, N
Grypus mannerheimi Faust	O-C, O-S	R	NE As
Dactylotus globosus Gebl.	O-A	MT, ME	Asia Alp
Notaris aethiops F.	O-C, O-S, BF	R, H, B	H, B-M
Notaris bimaculatus F.	A-M?, K-K, O-K, O-C, O-A, O-S, LC, MI	R, H, B	H, N
Notaris eversmanni Faust	K-K	R, H, B	Asia
Notaris flavipilosus Chitt.	CD	R, H	EB
Tychius tectus LeC.	O-A	ME, MS	H
Isochnus arcticus Kor.	O-A	SH, DT	NE As Arc
Isochnus flagellum Erics.	O-A	SH, DT	AB Arc
Ceutorhynchus subpubescens LeC.	CD	ST	W Na
Rhinoncus jakovlevi Faust	O-K	R	PA, B
Rhinoncus castor Hbst.	O-C, O-S	R	PA, B
Pelonomus velaris Gyll	K-K, O-C, O-A, O-S	R	PA, Alp
Dryophthorus americanus Bedl.	LC	CF	ENA
Family Scolytidae			
Ips cembrae Heer	O-K	CF	PA

Steppe-inhabiting beetles were found in the fossil assemblages from all the Arctic regions except Greenland (Fig. 2D). By far the greatest number of steppic species was found in the faunal assemblages from northeastern Siberia. Here, both leaf beetles and weevils associated with steppe vegetation are represented in all of the fossil assemblages of Late Pliocene age or younger.

The origins of the Siberian steppe fauna can be traced back to the Olyorian Formation faunas, dating to the transition from Pliocene to Quaternary. These deposits are very widespread in northeastern Siberia. The only significant difference between the Olyorian Formation beetle faunas and regional faunal assemblages from the Middle and Late Pleistocene is that the steppe component of Olyorian Suite assemblages is less important than in most Middle and Late Pleistocene insect assemblages. The typical Olyorian insect fauna consists mostly of tundra species, with dry tundra species relatively more abundant, and wet tundra species less so. About one-third of the fossil beetle specimens in these deposits represent the xerophylic pill beetle *M. viridis*. The steppe weevils in the genus *Stephanocleonus* are also well represented. There are few shrub-feeding species, dominated by the willow-feeding weevil *Lepyrus nordenskioeldi* that is very widespread in the modern shrub tundra.

In Alaska, evidence of open grasslands that may have been the precursors of Pleistocene steppe habitats comes from such species as the grassland ground beetle, *T. holmbergi*, and the weevils, *L. lineaticollis*, *Vitavitus thulius*, and *Ceuthorhynchus subpubescens*. These beetles were present in Late Tertiary and Early Quaternary faunal assemblages. Interestingly, *L. lineaticollis* was present in northeastern Siberia in the Miocene (at the Ary-Mas site), but was not recorded in any younger faunal assemblages, even in the Pleistocene. In High Arctic Canada, the open grassland beetles found in Late Tertiary faunas include the ground beetles *Carabus taedatus*, *Bembidion nitidum*, and *Harpalus amputatus*. The ecological interpretation of these species is not straightforward, however. For instance, although *C. taedatus* is a typical semi-arid short-grass steppe species on the Great Plains of North America, it is also common today on many kinds of open ground habitats in Alaska, including quite moist environments on the Alaskan Peninsula and Kodiak Island. *V. thulius* has been collected by Matthews (personal communication, 3/06), along with specimens of the pill beetle *Morychus*, in an area of discontinuous tundra near Old Crow, Yukon. Its abundance in fossil assemblages may mean no more than that open areas were more prevalent, not that an area was steppe.

Each of these three regions, therefore, had different open grassland beetle faunas. The fact that there was not a homogeneous steppe fauna that was circumpolar in the Arctic during the Late Tertiary and Early Quaternary suggests that both the areal extent and ecological attributes of steppic habitats in the three regions were somewhat different. Based on the abundance and diversity of plant-feeding steppe beetles, northeastern Siberia appears to have supported a rich, diverse steppe vegetation that covered large regions. The ground beetles discussed above from northern Canada are not directly tied to steppe vegetation today. Rather, they live in open, dry environments with thin cover of herbaceous vegetation. Such vegetation may have borne little resemblance to any modern steppe plant communities. The faunal evidence from Late Tertiary and Early Quaternary sites in Alaska falls somewhere between

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Notes to Table 2:

A-M: Ary-Mas site, age: Miocene; K-K: Kutuyakh beds, Krestovka site, lower Kolyma basin, NE Siberia; age: Late Pliocene; O-K: Olyorian Formation, Krestova site, Kolyma basin, NE Siberia; age: Early Quaternary; O-C: Olyorian Formation, Chukochya River site, NE Siberia; age: Early Quaternary; O-A: Olyorian Formation, Alazea site, Indigirka basin, NE Siberia; age: Early Quaternary; O-S: Olyorian Formation, Sededema site, upper Kolyma basin, NE Siberia; age: Early Quaternary; LCM: Lava Camp Mine, Alaska; age: Late Miocene; CD: Cape Deceit Formation, Cape Deceit, Alaska; age: ca. 1.8 million years; LC: Lost Chicken site, Alaska; age: 3 million years (Late Pliocene); Ng: Nigauanak exposure, Alaska: age: Early Pliocene?; BF: Bluefish exposure, Old Crow region, Yukon Territory; age: Pliocene?; MI: Meighen Island, Northwest Territories; age: ca. 3 million years (Late Pliocene); SF: Beaver pond deposit, Strathcona Fiord, Ellesmere Island, Northwest Territories; age: Pliocene?; KK: Kap København site, Greenland; age: 2.5–2 million years (Latest Pliocene or Early Quaternary).

Ecological and habitat abbreviations: B, Bogs; Bur, Mammal burrows; CF, Coniferous forest; CL, Coniferous leaf litter; Det: Detritus; DF: Deciduous forest; DL, Deciduous leaf litter; DT, Dry tundra; DW: Deciduous woodland; FT: Forest tundra; Gr: Grasslands; H, Hygrophilous; ME: Meadow; MS: Meadow-steppe; MT, Mesic tundra; O, Open ground; P, Peaty soil; Pr, Prairie; R, Riparian; RW: Running water; SH: Shrubs; Sn, Snowfield margins; ST: Steppe; SW, Standing water; TA, Taiga; TV, Thin vegetation; X, Xeric habitats.

Modern range abbreviations: AB, Amphiberingian; B, Boreal; B-M, Boreo-montane; Arc, Arctic; Alp, Alpine; CP, Circumpolar; ±CP, nearly circumpolar; EB, Eastern Beringian; ENA: Eastern North America; EPA: Eastern Palearctic; H, Holarctic region; Int N Amer: Interior regions of North America; Mon, Montane; N: Northern; NE As: Northeast Asia; NPA: Northern Palearctic region; NW Eur, Northwest Europe; NW N Am, Northwestern North America; PA, Palearctic region; Sc: Scandinavia; Si, Siberian; T, Temperate North America; TA, Trans-American; TE, Trans-Eurasian; W NA, Western North America; WB, Western Beringia; WPA, Western Palearctic.

[a] Denotes species thought to be extinct.

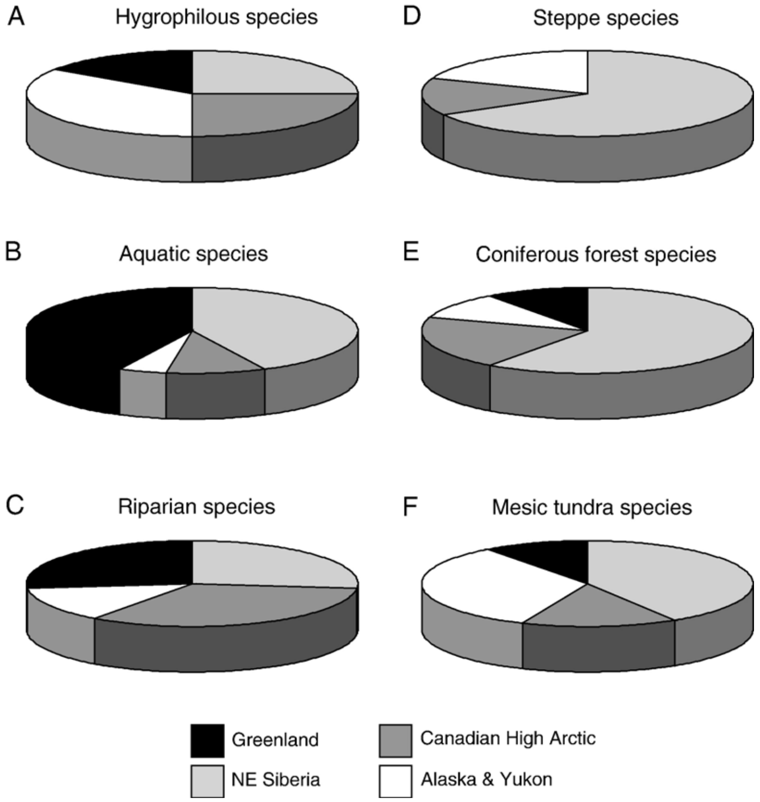

Fig. 2. Major habitat groups represented in the fossil beetle assemblages from the study sites. (A) Hygrophilous species; (B) aquatic species; (C) riparian species; (D) steppe species; (E) coniferous forest species; (F) mesic tundra species.

these two extremes. There is some indication of steppic communities, and some of dry, open ground with thin vegetation. An alternate explanation is that the habitat that supported the steppe species was highly discontinuous. Matthews (written communication, 3/06) believes that the presence of fossils tentatively referred to *H. amputatus* on Meighen Island may mean no more than that there were some open areas within the forest that could support that species or a close relative.

The dominance of steppe and steppe–tundra communities in the Western Beringian region persisted throughout the Pleistocene. During the Late Pleistocene, fossil beetle assemblages indicative of steppe–tundra come mainly from the interior regions of Eastern Beringia, whereas these assemblages dominate nearly all Late Pleistocene fossil sites in Western Beringia. Late Pleistocene faunas from Eastern Beringian contained a much larger proportion of mesic to hygrophilous species and very few dry-adapted species (Elias and Berman, 2000).

What is clear from the fossil beetle evidence is that steppe communities were in place in the far north well before the onset of Pleistocene glaciations. Certainly in Western Beringia, steppe species did not arrive in the north during the Pleistocene, when they formed a major constituent of the steppe–tundra biome that covered much of Beringia during that interval. Assuming that there was such a northward movement of steppe communities in Asia, it must have predated the Late Pliocene.

The origins of Arctic tundra insect communities are also suggested by some of the beetle faunas of Late Tertiary and Early Quaternary age. During the Pliocene, cold-adapted beetles were widespread on the Kolyma Lowland region of Siberia. The fossil evidence indicates that many of modern tundra species have lived there since the Early Pliocene, and some of them, such as *D. arctica*, have lived there since the Miocene. They formed part of an azonal association within the taiga ecosystem. During the Pliocene, there was a natural selection process favoring cold-resistant species; this process continued through the late Pleistocene. Among these beetle species were representatives from the three main biological communities: tundra, forest and steppe. During the Pliocene on the Kolyma lowland, boggy tundra–forest landscapes were widespread at first, eventually giving way to the peculiar "forest–tundra–steppe" landscape of the later Pliocene. This reconstruction is corroborated by paleobotanical studies.

All four study regions yielded beetle species associated with mesic tundra habitats, such as are found in northern Alaska and northeastern Siberia today (Fig. 2F). Both Alaska and northeastern Siberia had considerable numbers of tundra-dwelling species, but they were also found in the Canadian high arctic and in Greenland. The majority of these are ground beetles, but rove beetles, pill beetles, leaf beetles and weevils are also represented in this group. Matthews and Telka (1997) considered the beetle fauna of the Cape Deceit formation (1.8 my) to have the first clear indications of tundra beetle communities. However, some of the same species, such as *Pterostichus agonus*, *P. brevicornis*, *P. pinguedineus*, and *P. ventricosus* were present in northeastern Siberia during the Late Pliocene.

5.2. Biogeographic patterns

If the taxa shown in Table 2 all represent the listed species, then the beetle species found in Late Tertiary and Early Quaternary Arctic beetle faunas comprise 237 species. Of these, 82 species are found today only in the Palearctic regions. Most of these species are widely distributed across the Palearctic regions today. Considerable numbers of species are found today in northern parts of Eurasia, as might be expected for beetles that previously lived in the Arctic. Many of these Palearctic species are either steppe-associated leaf beetles (12 species) or weevils (19 species). Steppe–tundra dominated northeastern Siberia throughout the Pleistocene, and since these beetles rely on steppic host plants for food, many of them were apparently forced to shift their distributions to other steppe regions following the last glaciation (Fig. 3A). Only four species out of the 237 have modern distributions that are restricted to Western

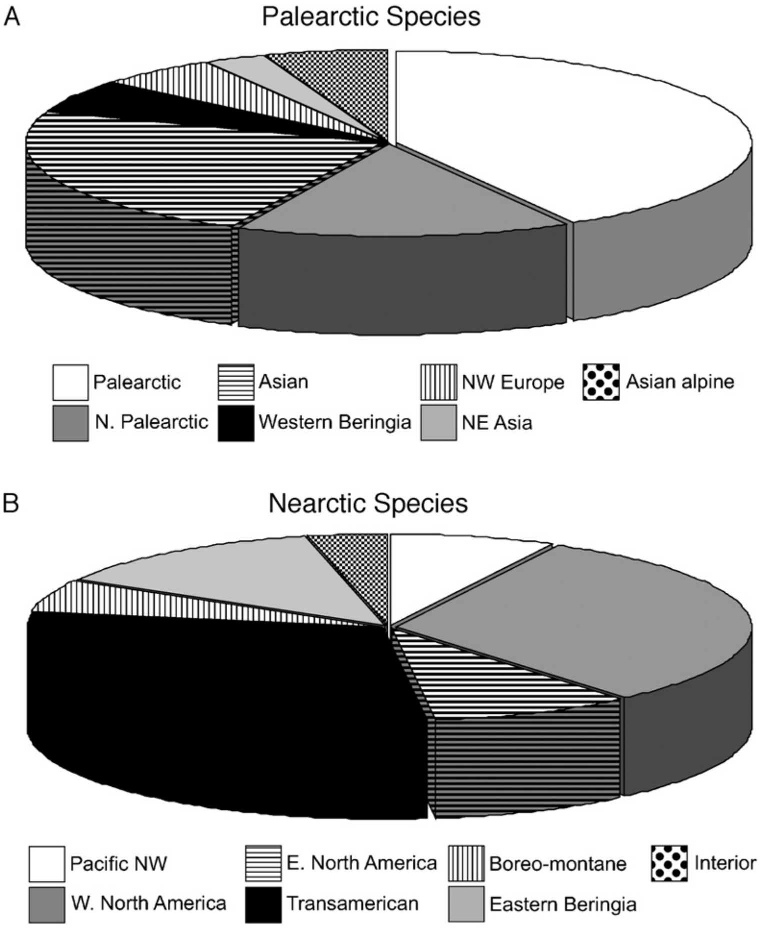

Fig. 3. Modern distribution patterns of species found in the fossil beetle assemblages from the study sites. (A) Distribution patterns of species found today only in the Palearctic region; (B) distribution patterns of species found today only in the Nearctic region.

Beringia (Fig. 3A). These are the rove beetles *Micropeplus hoogendorni* and *Tachinus arcticus*, the soft-winged flower beetle *Troglocollops arcticus*, and the weevil *Hemitrichapion tschernovi*. *T. arcticus* is found in mesic to dry tundra habitats. *M. hoogendorni* has quite a fascinating history during the last 6 my. It was identified by Matthews (1970) from the Lava Camp Mine site. He thought that it might be extinct, because he could not find a match for it in the modern fauna. Coope (1987) found specimens of *M. hoogendorni* in British fossil assemblages from the last interglaciation, and the Russian entomologist, Rjabukhin, described a Siberian species, *M. dokuchaevi*, that appears to be synonymous with *M. hoogendorni* (Elias, 1994). The fossil evidence thus shows that this species was not restricted to Beringia during the Pleistocene. *T. arcticus* is found today on Wrangel Island, in relict steppe habitat.

Among the beetle species found in the fossil assemblages discussed in this paper, 54 are found only in the Nearctic regions today. Several of the Nearctic group (seven species) are restricted today to Alaska and the Yukon Territory—the region that formed Eastern Beringia during much of the Quaternary. These species are mostly ground beetles in the *Cryobius* group of the genus *Pterostichus*. Most of these species appear to have arisen in the Eastern Beringian region and to have remained there. However, during the Tertiary–Quaternary transition, such species as the weevil *V. thulius* were apparently more widespread, ranging at least as far west as northeastern Siberia. Its range has subsequently retracted to Eastern Beringia during the Late Pleistocene or the Holocene. One biogeographic curiosity concerns species that were living in the Arctic during the Late Tertiary and Early Quaternary, and are now found only in temperate regions of eastern North America. This group includes the ground beetles *Notiophilus aeneus*, *Elaphrus olivaceus*, and *Agonum cincticolle*, as well as the weevil *Dryophthorus americanus*. It would be tempting to explain this unusual faunal connection between modern-day eastern North America with the ancient Arctic by invoking the very warm Arctic temperatures of the Late Tertiary as the common denominator. However, Elias (unpublished data) has also found beetles with modern eastern North American affinities in Late Pleistocene interglacial faunas from Alaska, so the answer to this zoogeographic puzzle remains to be solved.

6. Longevity of insect species

Elias and Matthews (2002) were able to reconstruct mean July and mean January temperatures for the Late Tertiary and Early Quaternary fossil beetle assemblages from Alaska, Canada, and Greenland. The climatic tolerances of the species in the assemblages, expressed as ‘climate envelopes’ (Atkinson et al., 1986), overlapped in each case, yielding mutual climatic range (MCR) estimates that were internally consistent, as well as regionally consistent. The fact that this MCR exercise succeeded indicates that the species in question have not evolved new sets of climatic tolerances since the Late Tertiary. Dozens of species were used in the MCR reconstructions. If this kind of physiological evolution had taken place, then it would be extremely unlikely that the climate envelopes based on the modern distribution of these beetles would overlap to produce a sensible MCR.

Given the fact that the modern representatives of the species in the fossil assemblages remain climatically compatible with each other, then there has either been no evolution of their thermal tolerances since the Late Tertiary, or whole suites of species have evolved new tolerances in concert with each other.

However, as Matthews and Telka (1997) discussed, the Late Tertiary beetle faunas from the Alaska and Canada contain ‘clear examples of extinct species’. It appears likely that most of these were relatively warm-adapted species that failed to become established in more southerly regions during the climatic cooling that signaled the beginning of glaciations in the Quaternary. Of the 251 beetle species in Table 2, only 13 are known to have become extinct. This number represents 5% of the species. Other species that were tentatively identified as extant may in fact be extinct, but on the other hand, some of the species thought to be extinct may eventually be discovered living in some other region of the modern world, albeit under a different name (e.g. *M. hoogendorni*). This problem arises when modern insect taxonomists are unaware of the fossil record, or do not have access to comparative specimens from other continents.

6.1. Evidence of evolution

The issue of extinction vs. survival is not cut and dried, however. Some Late Tertiary species apparently were precursors to modern species that evolved during the Quaternary. Matthews and Telka (1997) discussed the possible evolutionary history of a fossil ground beetle, *Asaphidion*, that represents an extinct species closely related to the contemporary subarctic carabid *Asaphidion yukonense*. A fossil elytron from the Lost Chicken site in Alaska clearly shows bare (impunctate) patches that characterize the modern species, but the patches are less well developed and elytral microsculpture is better developed than in the extant species. Fossils similar to *A. yukonense* have been found in other Late Tertiary assemblages from the Arctic (Matthews and Telka, 1997), but some of those have even more primitive elytral sculpture than the Lost Chicken specimens. These fossils could represent various stages in the evolution of the modern species. Matthews (1976) also described Late Tertiary fossil specimens of the water scavenger beetle *Helophorus* that appear to be precursors to the modern species *H. tuberculatus*. The fossils, from Lava Camp Mine and Meighen Island, exhibit a more primitive form of elytral sculpture. Matthews traced the possible evolution of these fossil types to the extant species. Matthews also (1977) postulated a gradual reduction in wing size in the now-flightless rove beetle *Tachinus apterus*, using a chronological sequence of Alaskan fossils, spanning the Quaternary.

A similar trend towards loss of flight wings may have occurred in pill beetles of the genus *Morychus*. Sergey Kiselyov, who was quite familiar with the common Western Beringian tundra–steppe pill beetle *M. viridis*, recognized a difference in the elytral shoulder in fossil *Morychus* specimens from the Late Tertiary Ary-Mas assemblages. He compared this fossil with the fully winged *M. aeneus* F., because other species with rounded shoulders (such as *M. jamalus* Thern.) had not yet been described at the time when he was analyzing the beetle fauna from this site (the 1980s). The Late Tertiary–Early Quaternary series of pill beetle fossils may be showing an evolutionary succession, as follows: (1) full-wing forms with a well-developed shoulder, such as *M. aeneus* F. or *M. aeneolus* LeC.; (2) semi-winged forms with moderately developed shoulders, such as *M. jamalus* Thern., the Ary-Mas fossil *Morychus* and the Western Beringian fossil *Morychus*; (3) the brachypterous, rounded-shoulder species *M. viridis* Kuzm. et Kor. The third form is the most evolutionarily progressive, so the Tertiary Ary-Mas fossil *Morychus* belongs to the primitive form, along with all Western Beringian fossil *Morychus*. The presence of *Morychus* fossils in the Ary-Mas assemblage is a possible first indicator of tundra–steppe environment in Arctic Siberia.

7. Conclusions

The fossil insect history of the Arctic give us fascinating glimpses into a world that ceased to exist about 2 my—a world in which a substantially warmer Arctic was home to coniferous forests, even at 80°N, near the northernmost point of land in the Northern Hemisphere. The ecosystems of this warm Arctic zone collapsed as Quaternary glaciation began. However, most of the insect fauna managed to persist for at least several hundred thousand years, probably by shifting south during glacial intervals, then recolonizing the far north during lengthy interglacial periods. This phenomenon is demonstrated by the remarkable Kap København fauna in northernmost Greenland.

Eventually, the warm adapted fauna that had inhabited the northern high latitudes in the Tertiary was forced to abandon this region. The various species went their separate ways, some into eastern North America, some to unglaciated regions of Beringia, others to other parts of Asia or Europe. In one extreme case, a nearly blind, flightless weevil (*Otibazo*) that lived in Alaska during the Late Tertiary has managed to become established today in Japan (Matthews et al., 2003). Each species has its own unique history, its own remarkable story of survival in the face of shifting climates. Before the fossil data were published, few biologists would have guessed that perhaps 95% of the Arctic fauna of the Pliocene has remained extant to the present day. Thus, the trend of beetles shifting their ranges in response to climate change, first noted for Pleistocene fossil assemblages (Coope, 1978), began far earlier than we might have expected.

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