

Climatic tolerances and zoogeography of the late Pleistocene beetle fauna of Beringia

La tolérance au climat et la zoogéographie de la faune des coléoptères de la Béringie, à la fin du Pléistocène

Klima-Toleranzen und Zoogeographie der Käfer-Fauna der Bering-Insel im späten Pleistozän

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Résumé de l'article

L'étude des coléoptères fossiles joue un rôle important dans la reconstitution des paléoenvironnements de la Béringie. À ce jour, plus de 25 sites fossilifères ont été étudiés pour leurs assemblages d'insectes. Plus de 300 espèces de coléoptères ont été identifiées, dont 147 espèces carnivores ou détritivores utiles aux reconstitutions paléoclimatiques. L'auteur a confectionné des enveloppes climatiques (les paramètres climatiques qui décrivent les sites où l'on trouve présentement les espèces de coléoptères) pour réaliser des études paléoclimatiques (aires climatiques mutuelles). Cet article décrit les exigences climatiques de plusieurs espèces de coléoptères et leur histoire zoogéographique depuis la période ayant précédé le dernier interglaciaire. Les assemblages fossiles incluent 14 espèces arctiques-alpines, 66 espèces boréales-arctiques et 68 espèces tempérées-boréales. Le plus grand pourcentage d'espèces ayant des exigences thermiques réduites se trouve dans le groupe des espèces arctiques-alpines. La majorité des autres espèces ont de grandes exigences thermiques. En comparant la répartition moderne des espèces à celles, plus anciennes, reconstituées grâce aux fossiles nord-américains, il semble que quelques espèces soient demeurées exclusivement en Béringie pendant la fin du Pléistocène. Ces espèces béringiennes représentent 64 % de toutes les espèces arctiques-alpines des assemblages fossiles, 34 % des espèces boréales-arctiques et seulement 1 % des espèces tempérées-boréales.

CLIMATIC TOLERANCES AND ZOOGEOGRAPHY OF THE LATE PLEISTOCENE BEETLE FAUNA OF BERINGIA

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ABSTRACT The study of fossil beetles has played an important role in the reconstruction of Beringian paleoenvironments. More than 25 fossil localities have yielded Late Pleistocene beetle assemblages, comprising more than 300 species, of which about 147 are predators and scavengers, groups which are suitable for paleoclimatic reconstruction. The author has developed climate envelopes (climatic parameters characterizing the modern localities in which species are found) for these species, in order to perform mutual climatic range paleotemperature studies. This paper describes the thermal requirements of these beetles, and their zoogeographic history since the interval just prior to the last interglacial period. The fossil assemblages include 14 arctic and alpine species, 66 boreo-arctic species, and 68 boreal and temperate species. The greatest percentage of species with restricted thermal requirements occurs in the arctic and alpine group. The majority of boreo-arctic and boreal and temperate species have very broad thermal requirements. Based on modern distribution and the North American fossil record, it appears that some species resided exclusively in Beringia during the Late Pleistocene. These Beringian species comprise 64 % of the arctic and alpine species found in the fossil assemblages, 34 % of the boreo-arctic species, and only 1 % of the boreal and temperate species.

RÉSUMÉ *La tolérance au climat et la zoogéographie de la faune des coléoptères de la Béringie, à la fin du Pléistocène.* L'étude des coléoptères fossiles joue un rôle important dans la reconstitution des paléoenvironnements de la Béringie. À ce jour, plus de 25 sites fossilifères ont été étudiés pour leurs assemblages d'insectes. Plus de 300 espèces de coléoptères ont été identifiées, dont 147 espèces carnivores ou détritivores utiles aux reconstitutions paléoclimatiques. L'auteur a confectionné des enveloppes climatiques (les paramètres climatiques qui décrivent les sites où l'on trouve présentement les espèces de coléoptères) pour réaliser des études paléoclimatiques (aires climatiques mutuelles). Cet article décrit les exigences climatiques de plusieurs espèces de coléoptères et leur histoire zoogéographique depuis la période ayant précédé le dernier interglaciaire. Les assemblages fossiles incluent 14 espèces arctiques-alpines, 66 espèces boréales-arctiques et 68 espèces tempérées-boréales. Le plus grand pourcentage d'espèces ayant des exigences thermiques réduites se trouve dans le groupe des espèces arctiques-alpines. La majorité des autres espèces ont de grandes exigences thermiques. En comparant la répartition moderne des espèces à celles, plus anciennes, reconstituées grâce aux fossiles nord-américains, il semble que quelques espèces soient demeurées exclusivement en Béringie pendant la fin du Pléistocène. Ces espèces béringiennes représentent 64 % de toutes les espèces arctiques-alpines des assemblages fossiles, 34 % des espèces boréales-arctiques et seulement 1 % des espèces tempérées-boréales.

ZUSAMMENFASSUNG *Klima-Toleranzen und Zoogeographie der Käfer-Fauna der Bering-Insel im späten Pleistozän.* Das Studium von Käfer-Fossilien hat bei der Rekonstruktion der Paläoumwelt der Bering-Insel eine wichtige Rolle gespielt. Über 25 Fossilfundstätten ergaben Käfer-Einheiten aus dem späten Pleistozän. Sie umfassten über 300 Arten, von denen etwa 147 den Fleisch- und Aasfressern angehören, den für die paläoklimatische Rekonstruktion brauchbaren Gruppen. Der Autor hat klimatische Hüllen (klimatische Parameter, welche die modernen Plätze charakterisieren, in denen die Arten zu finden sind) für diese Arten entwickelt, um paläoklimatische Studien durchzuführen (wechselseitige klimatische Reichweite). Dieser Artikel beschreibt die klimatischen Ansprüche dieser Käfer und ihre zoogeographische Geschichte seit dem direkt vor dem letzten Interglazial gelegenen Intervall. Die fossilen Einheiten umschließen 14 arktische und alpine Arten, 66 boreal-arktische Arten und 68 boreal-gemäßigte Arten. Der größte Anteil von Arten mit begrenzten klimatischen Ansprüchen ist in der arktischen und alpinen Gruppe zu finden. Die Mehrzahl der boreal-arktischen und boreal-gemäßigten Arten haben hohe klimatische Ansprüche. Stützt man sich auf die moderne Verteilung und den nordamerikanischen Fossil-Beleg, wird deutlich, dass einige Arten im späten Pleistozän ausschließlich in der Bering-Insel vorhanden waren. Diese Bering-Arten umfassen 64 % der in den Fossil-Einheiten gefundenen arktischen und alpinen Arten, 34 % der boreal-arktischen Arten und nur 1 % der boreal-gemäßigten Arten.

INTRODUCTION

The reconstruction of paleoenvironments is an essential element in the development of our understanding of the ancient region, Beringia. This was the only large, unglaciated landmass that existed in the northern high latitudes during Late Pleistocene glaciations. The ice-free regions of north-eastern Siberia, Alaska, the Yukon Territory, and the exposed continental shelf regions of the Bering and Chukchi seas served as a biological refuge for cold-adapted flora and fauna. Because of excellent fossil preservation in permanently frozen soils, Beringia has yielded an exceptionally detailed record of Pleistocene flora and fauna (*e.g.*, Guthrie, 1990). During the last 35 years, paleontologists including John Matthews, Richard Morlan, Robert Nelson, and myself have analyzed more than 25 sites containing fossil insect assemblages dating to the Late Pleistocene. These sites have yielded about 300 species of insects, mainly beetles (Coleoptera). These fossils have provided a wealth of proxy data that help us reconstruct Beringian environments. One of the chief kinds of paleoenvironmental data extracted from the fossil beetle assemblages is paleotemperature. Beetles, especially predators and scavengers, have been shown to be sensitive, reliable temperature indicators (Coope, 1977; Elias, 1994).

During the past few years, I have developed paleoclimatic reconstructions for Central Beringia (the Bering Land Bridge) and Eastern Beringia (Alaska and the Yukon Territory) (Elias *et al.*, 1996b; Elias *et al.*, 1997; Elias, 1999; Elias *et al.*, 1999a). This work has entailed the construction of "climate envelopes" for the predatory and scavenging beetle species found in the Beringian assemblages. The modern distributions of species found in fossil assemblages fall within certain climatic parameters. When these parameters are plotted for the modern collecting localities of a species, its geographic distribution translates into a climate envelope (Atkinson *et al.*, 1986). These climate envelopes vary from broad to narrow, depending on the range of thermal tolerances of the species. The two parameters developed thus far are the mean temperature of the warmest month of the year (TMAX), and the mean temperature of the coldest month of the year (TMIN). The primary use of these climate envelopes is to develop mutual climatic range (MCR) estimates of these parameters, based on the overlap of climate envelopes of species in fossil assemblages. However, the climate envelopes themselves reveal considerable information about the thermal requirements of the species concerned. In this paper, I discuss the climatic tolerances of species of predatory and scavenging beetles found in Beringian fossil assemblages. Surprisingly, the majority of species found in late Pleistocene Beringian fossil assemblages are not purely arctic tundra beetles. Many are adapted to both arctic and boreal climates, and others are adapted to boreal and temperate climates. An analysis of the thermal requirements of these various groups constitutes the first part of this paper.

Because Beringia was a refuge for cold-adapted beetles, the Pleistocene fossil record of that region is particularly interesting. Some of the beetle species found today in Alaska and the Yukon Territory are thought by taxonomists to

have evolved *in situ* in Beringia during late Tertiary to early Quaternary times (Ball, 1966). The fossil record sheds new light on this topic, documenting the species that lived in the various parts of Beringia during the glacial and interglacial periods. That is the second topic of this paper.

METHODS

The climate envelopes discussed here were developed by Kathy Anderson and me. We used a 25-km gridded North American climate database (Bartlein *et al.*, 1994) to pair climate parameters with the modern beetle collection sites, using the geographically nearest grid location to each collecting site. We then plotted the climatic parameters of each of these localities on diagrams of TMAX against the difference between the mean July and mean January temperature (TRANGE). We plotted climate envelopes for species of predators and scavengers found in Beringian fossil assemblages ranging in age from about 140 000 to 10 000 yr BP. The species belong to the families Carabidae (ground beetles), Dytiscidae (predaceous diving beetles), Hydrophilidae (water scavenger beetles), Staphylinidae (rove beetles), Scarabaeidae (dung beetles), and Silphidae (carrion beetles). The beetles in these families probably respond to climatic change by shifting their ranges more readily than do most plant-feeding beetles. The ranges of plant feeding insects are necessarily restricted to the ranges of their host plants, which may or may not respond rapidly to changing climates (Elias, 1994).

The species' climatic tolerance data are shown in Table I. I calculated the TMAX and TMIN ranges for each species, and listed the species in zoogeographic groups (each group is listed in taxonomic order). These groups are based on the modern distributions of the species. Arctic and alpine species are those that are found today only in tundra regions, either at high elevation, high latitude, or both. Boreo-arctic species are those with modern ranges that include both the arctic, alpine, and boreal (coniferous forest) zones of North America, including montane forests in mountain chains south of Canada. Boreal and temperate species are those with modern ranges either in the boreal zone, the temperate zone, or both.

To classify the thermal tolerances of the beetle species, I grouped them according to the range of their TMAX values. I considered as *stenothermic* the species with TMAX ranges less than or equal to 5 °C. These beetles have limited thermal tolerances. I considered as *mesothermic* the species with TMAX ranges between 5 and 10 °C. These beetles have only moderately restricted thermal tolerances. I considered as *eurythermic* the species with TMAX ranges greater than 10 °C. These beetles are adapted to a wide range of summer temperatures.

In an attempt to classify the long-term zoogeographic patterns of beetle species found in late Pleistocene Beringian assemblages, I searched the literature concerning late Pleistocene beetle assemblages from North American regions south of the Laurentide and Cordilleran ice sheets. These fossil assemblages have recently been analyzed for

TABLE I

Mutual Climatic Range estimates for beetle species found in late Pleistocene fossil assemblages from Alaska and the Yukon Territory

Species	TMAX (°C)	TMAX range	TMIN (°C)	TMIN range
Arctic & Alpine Species				
Carabidae				
<i>Blethisa catenaria</i> Brown	7-13.5	6.5	-38.5 to -21	17.5
<i>Bembidion dauricum</i> (Mots.)	7.5-13.5	6	-37.5 to -17	20.5
<i>Bembidion umiatense</i> Lth.*	7.5-10	2.5	-33 to -28	5
<i>Pterostichus agonus</i> Horn*	5-13	6	-39 to -15	24
<i>Pterostichus auriga</i> Ball*	2.5-14.5	12	-31.5 to -16.5	15
<i>Pterostichus costatus</i> (Mén.)*	5.25-10.25	5	-36.75 to -20.25	16.5
<i>Pterostichus sublaevis</i> (Sahlb.)*	6.5-14	7.5	-39 to -13.5	25.5
<i>Poecilus nearcticus</i> (Lth.)*	7-11	4	-36 to -27	9
<i>Amara alpina</i> (Payk.)	5-10.5	5.5	-39.5 to -5.5	34
<i>Amara bokori</i> Csiki*	7-16	9	-38 to -12.5	25.5
Hydrophilidae				
<i>Helophorus splendidus</i> Sahlb.	8.25-10.25	2	-34.25 to -27.25	7
Staphylinidae				
<i>Holoboreaphilus nordenskiöldi</i> Mäkl.	5.5-14.5	9	-37.75 to -14.5	23.25
<i>Micralymma brevilinque</i> Schiodt.*	3-12.5	9.5	-38.5 to -18	20.5
<i>Tachinus brevipennis</i> Sahlb.*	3.5-10.5	7	-36.5 to -17.5	19
Mean values	5.7-12.4	6.7	-36.8 to -18.1	18.7
Boreo-Arctic and Boreo-alpine species				
Carabidae				
<i>Carabus chamissonis</i> Fisch.	5.5-20	14.5	-39.5 to -7.5	32
<i>Carabus taedatus</i> Fabr.	10.5-17	6.5	-36 to 0	36
<i>Carabus truncatocollis</i> Eschz.	3.5-17.25	13.75	-42 to -9.25	32.75
<i>Pelophila borealis</i> (Payk.)	7.5-16.5	9	-37 to -3.5	33.5
<i>Nebria gebleri</i> Dej.	8.5-19.5	11	-30.5 to -6.75	23.75
<i>Nebria metallica</i> Fisch.	9-17	8	-23 to 0	23
<i>Nebria nivalis</i> (Payk.)	3-15.5	12.5	-42 to -10	32
<i>Notiophilus borealis</i> Harr.	4.5-20	15.5	-40.5 to -2	38.5
<i>Diacheila arctica</i> (Fald.)	11-12.5	1.5	-24.5 to -7.75	16.75
<i>Diacheila polita</i> (Fald.)	2.5-16	13.5	-41.75 to 0	41.75
<i>Elaphrus parviceps</i> VD*	8.75-16	7.25	-36.5 to -6	30.5
<i>Elaphrus tuberculatus</i> Mäkl.*	9-16	7	-36 to -14	22
<i>Dyschirius melancholicus</i> Putz..	7-16.5	9.5	-38 to -1	37
<i>Asaphidion alaskanum</i> Wickh.*	5-15	10	-39.75 to -13	26.75
<i>Bembidion arcticum</i> Lth.*	6-15	9	-38 to -9	29
<i>Bembidion grapii</i> Gyll.	8.5-20.5	12	-37.5 to -2.5	35
<i>Bembidion hastii</i> Sahlb.	6-16.75	10.75	-39.5 to -0.75	38.75
<i>Bembidion sordidum</i> (Kby.)	7-19.5	12.5	-37.5 to -2	35.5
<i>Bembidion transparens</i> (Geb.)	11-22	11	-34.5 to 0	34.5
<i>Stereocerus haematopus</i> (Dej.)	5-18.5	13.5	-40.5 to -6.5	34
<i>Pterostichus arcticola</i> (Chd.)	4-15	11	-42 to -15	27
<i>Pterostichus barryorum</i> Ball*	8-17.5	9.5	-39.5 to -19.5	20
<i>Pterostichus brevicornis</i> (Kby.)	4.5-15	10.5	-41.5 to -15	26.5
<i>Pterostichus bryanti</i> VD	7-16	9	-31 to -14.5	16.5
<i>Pterostichus caribou</i> Ball	5.5 to 14	8.5	-39.5 to -18.25	21.25
<i>Pterostichus circulosus</i> Lth.*	7.5-18	11.5	-35 to -21.5	13.5
<i>Pterostichus empetricola</i> (Dej.)	10.5-15.5	5	-34.5 to -4.5	30
<i>Pterostichus hudsonicus</i> LeC.*	7-16	9	-38 to -20	18
<i>Pterostichus kotzebuei</i> Ball*	2.5-17	14.5	-45 to -12.5	32.5

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Species	TMAX (°C)	TMAX range	TMIN (°C)	TMIN range
<i>Pterostichus mandibularoides</i> Ball*	7.5-16	8.7	-37.5 to -11.5	26
<i>Pterostichus nivalis</i> (Sahlb.)*	2.5-15.5	13	-22 to -7	15
<i>Pterostichus parasimilis</i> Ball*	5.5-16.5	11	-40 to -11.5	28.5
<i>Pterostichus pinguedineus</i> (Eschz.)*	7-15.5	8.5	-38 to -15.5	22.5
<i>Pterostichus similis</i> Mann.	5.5-15.5	10	-37.5 to -6.5	31
<i>Pterostichus soperi</i> Ball*	7.5-17	9.5	-40 to -15	25
<i>Pterostichus tareumiut</i> Ball*	2.5 to 17.5	15	-40 to -6.5	33.5
<i>Pterostichus ventricosus</i> (Eschz.)*	6-15.5	9.5	-39 to -1.5	37.5
<i>Pterostichus vermiculosus</i> Mén.*	7-14	7	-38 to -17	21
<i>Agonum consimile</i> (Gyll.)	4-16	12	-41 to +1	42
<i>Agonum exaratum</i> (Mannh.)*	8-18	10	-37 to -17	20
<i>Agonum quinquepunctatum</i> Mots.	9.5-16.5	7	-39 to -1.5	37.5
<i>Amara browni</i> Lth.*	11.5-15	3.5	-33 to -26	7
<i>Amara erratica</i> (Duft.)*	9.5-18	8.5	-35 to +0.5	35.5
<i>Amara glacialis</i> (Mannh.)	5-16	11	-39.5 to +2	41.5
<i>Amara hyperborea</i> Dej.	7-17.5	10.5	-38 to -6	32
<i>Trichocellus mannerheimii</i> (Sahlb.)	6-15.5	9.5	-39.5 to -17.5	22
<i>Cymindis unicolor</i> Kby.	5-23	17	-41 to +4.5	45.5
Dytiscidae				
<i>Colymbetes dolobratius</i> (Payk.)	4.5-15	10.5	-41 to -9.5	31.5
<i>Hydroporus lapponum</i> Gyll.	4-15.5	11.5	-42 to -5	37
<i>Hydroporus morio</i> Aube	5.5-18	12.5	-41.5 to -3	38.5
<i>Hydroporus notabilis</i> LeC.	8-20.5	12.5	-35.5 to 0	35.5
<i>Hydroporus polaris</i> Fall	4-16	12	-41.5 to -14	27.5
<i>Agabus arcticus</i> Payk.	7-17.5	10.5	-37.5 to +0.5	38
<i>Agabus inscriptus</i> Crotch	6.5-20.5	14	-37.5 to +1.5	39
<i>Agabus moestus</i> Curtis	5-17.5	12.5	-41 to -9.5	31.5
<i>Ilybius angustior</i> Gyll	7-22.5	15.5	-37.5 to +2.5	40
Staphylinidae				
<i>Arpedium brachypterum</i> (Grav.)	7-16	9	-35 to +3	38
<i>Acidota quadrata</i> (Zett.)	7-20.5	13.5	-37 to +0.5	37.5
<i>Olophrum boreale</i> (Payk.)	9-20.5	11.5	-36 to -1.5	37.5
<i>Olophrum latum</i> Mäkl.	8.5-16.5	8	-36 to -0.5	36.5
<i>Tachinus instabilis</i> Mäkl.*	8-14.5	6.5	-33 to -6	27
<i>Mycetoporus nigrans</i> Mäkl	6.5-21	14.5	-38 to +4.5	42.5
Silphidae				
<i>Thanatophilus coloradensis</i> Wickh.	10.5-15	4.5	-34 to -10	24
<i>Silpha trituberculata</i> Kby.*	8-20	12	-37.5 to -11	26.5
Scarabaeidae				
<i>Aphodius congregatus</i> Mannh.	6.5-18	11.5	-25 to +2.5	27.5
Mean values	6.8-18.9	12.1	-37.3 to -6.8	30.5
Boreal, montane, and temperate species				
Carabidae				
<i>Carabus maeander</i> Fisch.	9-22.5	13.5	-36 to +4.75	31.25
<i>Pelophila rudis</i> (LeC.)	11.5-16.5	5	-33 to -8.5	24.5
<i>Opisthius richardsoni</i> Kby.	10-20.75	10.75	-35.5 to +3	38.5
<i>Notiophilus intermedius</i> Lth.	12.5-19.5	7	-29 to -5.25	23.75
<i>Notiophilus semistriatus</i> Say	9.5-27	17.5	-36.5 to +8	44.5
<i>Notiophilus sylvaticus</i> Eschz.	9.5-19	9.5	-20.5 to +5.25	25.75
<i>Blethisa multipunctata</i> Fisch.	10.5-20.5	10	-35 to -2	33

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<i>Elaphrus lapponicus</i> Gyll.	10.5-16.25	5.75	-35 to -1.75	33.25
<i>Loricera pilicornis</i> (Fab.)	11-26	15	-35.5 to +2	37.5
<i>Dyschirius aeneolus</i> Lec.	11.5-20.5	9	-33 to -2.75	30.25
<i>Dyschirius integer</i> LeC.	11-27	16	-35 to +5	40
<i>Dyschirius laevifasciatus</i> Horn	8.5-19.5	11	-28 to -7	21
<i>Dyschirius subarcticus</i> Lth.	11-16.5	5.5	-34 to -1.5	32.5
<i>Patrobis foveocollis</i> (Eschz.)	8.25-20.5	12.25	-35.75 to -6.5	29.25
<i>Patrobis septentrionis</i> Dej.	8-19	11	-37 to -6	31
<i>Patrobis stygicus</i> Chd.	7-20.75	13.75	-39.75 to -1.25	38.5
<i>Trechus apicalis</i> Mots.	7.5-22.5	15	-37 to +2.5	39.5
<i>Trechus chalybeus</i> Dej.	8.75-27.75	19	-29.75 to +14.25	44
<i>Bembidion breve</i> Mots.	7-20.5	13.5	-31.25 to +0.5	31.75
<i>Bembidion concolor</i> (Kby.)	11-20.75	9.75	-33.75 to +1.75	35.5
<i>Bembidion concretum</i> Csy.	12-23	11	-34 to +1	35
<i>Bembidion convexulum</i> Hayw.	7-19	12	-37 to +5	42
<i>Bembidion fortetrium</i> (Mots.)	11.5-22	10.5	-34 to +3.5	37.5
<i>Bembidion gratiosum</i> Csy.	7.5-17.5	10	-35.5 to -0.5	35
<i>Bembidion intermedium</i> (Kby.)	12-20.5	8.5	-29.5 to -2.5	27
<i>Bembidion morulum</i> LeC.	8.75-15.5	6.75	-36.75 to -8	28.75
<i>Bembidion quadrimaculatum</i> (LeC.)	10.5-27.5	17	-33.5 to +9.5	43
<i>Pterostichus adstrictus</i> Eschz.	7-25.5	18	-38 to +7	45
<i>Pterostichus chipewyan</i> Ball	11-18	7	-37 to -18	19
<i>Pterostichus gerstlensis</i> Ball*	13-17	4	-33 to -22	11
<i>Pterostichus punctatissimus</i> (Rand.)	10-19	9	-33.75 to -5	28.75
<i>Agonum gratiosum</i> (Mannh.)	12-26	14	-34 to -5.5	28.5
<i>Agonum picicornoides</i> Lth.	12-20.25	8.25	-28 to -3.25	24.75
<i>Agonum thoreyi</i> Dej.	10.5-26.5	16	-35.5 to +6.5	42
<i>Amara discors</i> Kby.	8.5-27.5	19	-35.5 to +5.5	41
<i>Amara laevipennis</i> Kby.	9-21	12	-35 to +0.5	35.5
<i>Amara quenseli</i> (Schönh.)	7-22	15	-37.75 to +6	43.75
<i>Amara sinuosa</i> (Csy.)	9-20	11	-36 to +3	39
<i>Harpalus amputatus</i> Say	9.5-24.5	15	-35.5 to +2.25	37.75
<i>Harpalus nigratarsus</i> Sahlb.	6.25-23.75	17.5	-38.75 to +6.5	45.25
<i>Bradycellus lecontei</i> Csiki	7.5-21.75	14.25	-37.25 to +0.25	37.5
<i>Chlaenius niger</i> Rand.	11.5-26	14.5	-31.75 to +7.25	39
Dytiscidae				
<i>Agabus colymbus</i> Leech	10.5-13.5	3	-37 to -29	8
<i>Hydroporus griseostriatus</i> (DeG.)	9-24	15	-34 to +14	48
<i>Ilybius discidens</i> Sharp	7-23	16	-39 to +4	43
Hydrophilidae				
<i>Cercyon herceus</i> Smet.	11.75-28.5	16.75	-26.75 to +3.5	30.25
<i>Cercyon marinus</i> Ths.	9.5-23	13.5	-35 to +3.5	38.5
<i>Helophorus oblongus</i> LeC.	7-24.5	17.5	-37.25 to +4	41.25
<i>Ochthebius kaszabi</i> Janss.	10-21	11	-34 to -0.5	33.5
<i>Ochthebius marinus</i> (Payk.)	9.75-32	22.25	-29.75 to +7	36.75
<i>Hydraena angulicollis</i> Notm.	13.5-24	10.5	-29.25 to -2	27.25
Staphylinidae				
<i>Pycnoglypta lurida</i> (Gyll.)	9.5-24	14.5	-34.5 to +4.75	39.25
<i>Acidota crenata</i> (Fab.)	9-24	15	-31.5 to +4	35.5
<i>Boreaphilus henningianus</i> Sahlb.	7-23.5	16.5	-36.5 to -1.5	35

TABLE I

Mutual Climatic Range estimates for beetle species found in late Pleistocene fossil assemblages from Alaska and the Yukon Territory

Species	TMAX (°C)	TMAX range	TMIN (°C)	TMIN range
<i>Quedius fellmani</i> (Zett.)	9-19.5	10.5	-35 to +1	36
<i>Quedius fulvicollis</i> (Steph.)	8.5-23	14.5	-31.5 to +5	36.5
<i>Quedius pediculus</i> (Nordm.)	8-19	11	-22 to +2	24
<i>Tachinus frigidus</i> Er.	8-19.5	11.5	-36.5 to +9	45.5
<i>Tachyporus borealis</i> Campbl.	8.5-22.5	14	-35.5 to +5.5	41
<i>Tachyporus canadensis</i> Campbl.	10-23.75	13.75	-34 to +6.25	40.25
<i>Tachyporus nimbicola</i> Campbl.	8-22	14	-35 to +2.5	37.5
<i>Tachyporus rulomus</i> Blackwldr.	6.25-20	13.75	-40.25 to +1	41.25
<i>Gymnusa atra</i> Csy	11.5-23	11.5	-31.5 to +5	36.5
Micropeplidae				
<i>Micropeplus tesserula</i> Curtis	11.5-23	11.5	-28.5 to +11.5	40
<i>Micropeplus sculptus</i> LeC.	15.5-29	13.5	-19 to +9	28
<i>Micropeplus laticollis</i> Mäkl.	9.25-19.5	10.25	-25.75 to -1.5	24.25
Scarabaeidae				
<i>Aegialia lacustris</i> LeC.	9.5-22	12.5	-25.5 to +5	30.5
<i>Aphodius distinctus</i> (Mull.)	9.5-27	17.5	-33 to +8.5	41.5
Mean values	9.7-21.5	11.8	-33.6 to +0.6	34.2

* Species with Beringian distribution pattern

paleoclimatic reconstructions, using the MCR method, and the original faunal descriptions can be found in the literature cited in Elias (1996) and Elias *et al.* (1996a).

While it is tempting to speculate on endemism of beetle species in the Beringian fauna, previous fossil studies have shown that modern or even late Pleistocene ranges of species may not necessarily reflect the total history of a species' movements. In the strictest meaning of the word, a species is considered endemic to a given region only if it has existed exclusively in that region since its evolution. Many if not most of the beetle species found in Pleistocene assemblages from Beringia have existed for hundreds of thousands or even millions of years (Matthews, 1977). Some of these species might appear to be endemic to some part of Beringia, based on their modern range, but the fossil record belies this idea. For instance, the rove beetle, *Micropeplus hoogendorni*, is known today only from specimens in northeastern Siberia, but it has been found as a fossil in middle Pleistocene deposits from Europe and from Pliocene deposits in Alaska (Elias, 1994). The fossil record can provide evidence about the past ranges of species, but only within limits. It usually provides only 'snapshots' of a given species' range during brief segments of its history.

STUDY SITES

For this study, I selected 25 fossil sites in Alaska, the Yukon Territory, and the formerly-exposed continental shelf regions of the Bering and Chukchi seas (Figure 1; Tables II and III). These sites contain fossil assemblages spanning the interval from just prior to the last interglacial period to the end of the last glaciation (ca. 10 000 ¹⁴C yr BP). Beyond that

time, Beringia ceased to exist because the Bering Land Bridge was inundated by sea water. There are older Pleistocene deposits in Alaska and the Yukon that have yielded insect fossil assemblages, but the dating of these older assemblages is problematic at best. The oldest samples discussed here are stratigraphically linked to the deposition of the Old Crow tephra, an ash layer deposited in many regions of Alaska and the Yukon approximately 140 000 years ago (Preece *et al.*, 1999). Most of the sites discussed here yielded fossil assemblages from only one brief interval of time. Some sites, such as localities at Hungry Creek, the Nushagak Lowland, the Old Crow River, and the Noatak River, yielded a series of discrete organic units representing two or more time intervals. None of the sites yielded fossils representing continuous organic deposition through long periods of time (*i.e.*, tens of thousands or hundreds of thousands of years). The original descriptions of the fossil assemblages are referenced in Table III.

Many of the study sites are cutbank exposures of large rivers, such as the Porcupine and Old Crow rivers in the Yukon, and the Noatak, Foraker, Toklat, and Kuskokwim rivers in Alaska. Other sites, such as the Nushagak Lowland sites, are coastal bluff exposures. Most of the organic deposits from which the fossil insects were extracted accumulated in ponds, lakes, or slack-water fluvial environments. The taphonomy of the fossil assemblages exerts considerable influence on insect faunal composition (Morlan and Matthews, 1983). In spite of the fact that all of the fossil assemblages represent water-lain deposits, the majority of specimens in most assemblages represent terrestrial species, and very few assemblages are dominated by aquatic taxa.

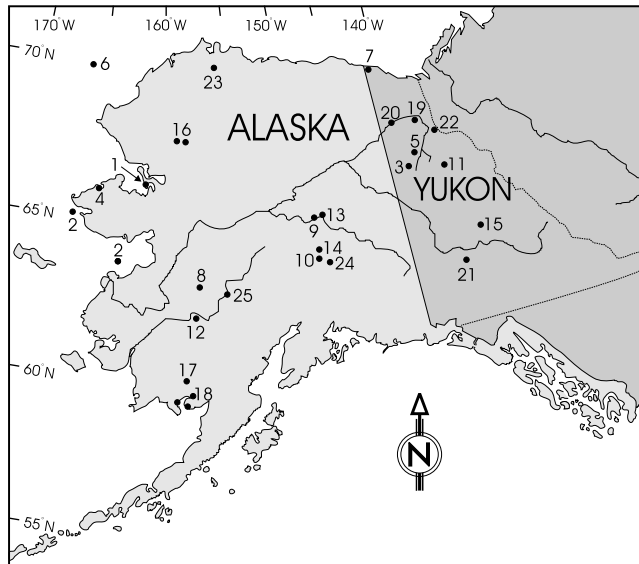


FIGURE 1. Map of Alaska and the Yukon Territory, showing location of fossil sites discussed in text. Site numbers correspond to those shown in Table III. Numbers 2, 16, and 18 have multiple localities, as discussed in text.

Carte de l'Alaska et du Territoire du Yukon montrant la localisation des sites fossiles dont on parle dans le texte. Les numéros de sites correspondent à ceux du tableau III. Les numéros 2, 16 et 18 correspondent à de multiples localités, tel qu'indiqué dans le texte.

RESULTS

The Late Pleistocene assemblages from the study region yielded 147 species of predators and scavengers (Table I). These beetle species fall into three zoogeographic categories, based on their modern distributions: arctic and alpine, boreo-arctic or boreo-alpine, and boreal to temperate. The arctic and alpine species comprise the smallest component (14 species, or 10 %) of the fossil assemblages, even though these beetles dominate many fossil assemblages from glacial periods. The boreo-arctic and boreo-alpine species comprise 65 species, or 44 % of the total number of predatory and scavenging species found in the fossil assemblages. Some of these species were found in glacial as well as interglacial and interstadial fossil assemblages, presumably because of their tolerance of cold climates. The third group, those with modern distributions in the boreal forest, montane forest, or temperate regions, comprise 68 species, or 46 % of the total.

THERMAL REQUIREMENTS OF THE BERINGIAN BEETLE FAUNA

Not surprisingly, the arctic and alpine group is the most cold-adapted of the three. The mean TMAX values for the arctic and alpine group fall within 5.7-12.4 °C, a range of 6.7 °C. The overall range of TMAX represented by the climate envelopes of the arctic and alpine species is somewhat greater, from 3 to 16 °C (Fig. 2). The mean TMIN values for this group fall within -36.8 to -18.1 °C, a range of 18.7 °C. The overall range of TMIN values for this group is -39.5 to -5.5 °C. Of the arctic and alpine species, four (29 %) are stenothermic,

ten (71 %) are mesothermic, and none are eurythermic. The small number of arctic and alpine species and their great degree of climatic specificity make sense ecologically. The survival of insects in cold climates requires unusual physiological and behavioral adaptations (Danks, 1981a). There are relatively few species of beetles adapted to life in arctic and alpine habitats. A few cosmopolitan species (species adapted to a wide range of temperatures) are found in arctic and alpine regions, but for the most part these regions are inhabited by taxa adapted to cold climates. Danks (1981b) discussed the distribution patterns of arctic arthropods, and reported that there are several species with cosmopolitan ranges, but that these include chiefly soil-dwelling taxa, such as Collembola (springtails). Of the 78 species of arctic ground beetles listed in Danks (1981b), none is cosmopolitan. None of the 66 species of predators and scavengers in other beetle families listed in Danks (1981b) (Halipilidae, Dytiscidae, Hydrophilidae, Silphidae, Staphylinidae, and Coccinellidae) has a cosmopolitan range.

The fossil assemblages yielded 65 species of boreo-arctic beetles. As expected, most of these species are adapted to a broader range of summer temperatures than the arctic and alpine group. The mean TMAX values for this group fall within 6.8-18.9 °C, a range of 12.1 °C. The overall range of TMAX values for this group is substantially greater, from 2.5 to 22.5 °C. The mean TMIN values for this group fall within -37.3 to -6.8 °C, a range of 30.5 °C. The overall range of TMIN values for this group is from -45 to 4.5 °C. Winter temperatures in the boreal region are often extremely cold, and not much different than those found in the Arctic. However, summer temperatures are generally much warmer in the boreal region. Of the boreo-arctic species in the fossil assemblages, four (6 %) are stenothermic, 23 (35 %) are mesothermic, and 39 (57 %) are eurythermic.

There were 68 species of beetles whose modern populations have either boreal or temperate distributions. Among these species, only two (3 %) are stenothermic, 18 (23 %) are mesothermic, and 57 (74 %) are eurythermic. The mean TMAX values for this group fall within 9.7-21.5 °C, a range of 11.8 °C. The overall range of TMAX values for this group is from 6.25 to 29 °C (Fig. 2). The mean TMIN values for this group fall within -33.6 to 0.6 °C, a range of 34.2 °C. The overall range of TMIN values for this group is from -40.25 to 14.25 °C. Thus there is a differentiation in the climatic tolerances between the arctic and alpine group and the other two groups of beetles. The arctic and alpine species tend to have narrower climatic tolerances, whereas boreo-arctic and temperate species tend to have much broader climatic tolerances.

A plot of the range of TMAX and TMIN temperatures associated with the three distributional groups (Fig. 2) shows that there is considerable overlap between groups, although each of the three groups has a mean value distinct from the other two. The separation of mean values between groups is clearer for TMAX values than for TMIN. This observation is in keeping with the life histories of the beetles in the arctic, boreal, and temperate life zones. Most of these beetles are inactive during the winter months, or pass the winter as eggs,

TABLE II

Quaternary fossil beetle species identified from Beringian sites

Taxon	Sites ¹
CARABIDAE	
<i>Carabus chamissonis</i> Fisch.	EC,HC,PR,RR
<i>Carabus maeander</i> Fisch.	NL
<i>Carabus taedatus</i> Fabr.	NL
<i>Carabus truncaticollis</i> Eschz.	BB,CD,EC,HC,NL,RR
<i>Pelophila borealis</i> (Payk.)	CB,CD,MV
<i>Pelophila rudis</i> (LeC.)	HC
<i>Nebria gebleri</i> Dej.	NL
<i>Nebria metallica</i> Fisch.	NL,NY
<i>Nebria nivalis</i> (Payk.)	NL
<i>Opisthius richardsoni</i> Kby.	OC
<i>Notiophilus borealis</i> Harr.	CD,EC,NL
<i>Notiophilus intermedius</i> Lth.	NL
<i>Notiophilus semistriatus</i> Say	CD,EC,FR,TO
<i>Notiophilus sylvaticus</i> Eschz.	HC
<i>Diacheila arctica</i> Gyll.	HL,NY,UKL
<i>Diacheila polita</i> (Fald.)	BS,CB,CD,EC,HC,HL,NL, NR,NY,OC,RR,UKL
<i>Blethisa catenaria</i> Brown	CB,HL
<i>Blethisa multipunctata</i> Fisch.	CB
<i>Elaphrus lapponicus</i> Gyll.	CB,CD,NL,PR
<i>Elaphrus parviceps</i> VD.	HL,MV
<i>Elaphrus tuberculatus</i> Mäkl.	HL
<i>Loricera pilicornis</i> (Fab.)	NL
<i>Dyschirius aeneolus</i> (<i>frigidus</i>) LeC.	CD,NL
<i>Dyschirius integer</i> LeC.	NL
<i>Dyschirius laevifasciatus</i> Horn	CB
<i>Dyschirius melancholicus</i> (<i>nigricornis</i>) Putz.	BS,CD,EC,FR,NL,NR,NY,OC,UKL
<i>Dyschirius subarcticus</i> Lth.	OC
<i>Patrobus foveocollis</i> (Eschz.)	NL
<i>Patrobus septentrionis</i> Dej.	CB,HL,NL,OC
<i>Patrobus stygicus</i> Chd.	NL
<i>Trechus apicalis</i> Mots.	HC,HL,NL,NY
<i>Trechus chalybeus</i> Dej.	NL
<i>Asaphidion alaskanum</i> Wickh.	PR,RR,UKL
<i>Bembidion arcticum</i> Lth.	EC
<i>Bembidion concolor</i> Kby.	CB
<i>Bembidion concretum</i> Csy.	CB,NL,NY
<i>Bembidion convexulum</i> Hayw.	CB
<i>Bembidion dauricum</i> (Mots.)	CB,EC,PR
<i>Bembidion forttestriatum</i> (Mots.)	NL,NY
<i>Bembidion grapii</i> Gyll.	BS,CB,CS,EC,HC,NL,NY
<i>Bembidion gratiosum</i> Csy.	NL
<i>Bembidion hastii</i> Sahlb.	MV

TABLE II

Quaternary fossil beetle species identified from Beringian sites

Taxon	Sites ¹
<i>Bembidion breve</i> (<i>incertum</i>) (Mots.)	NL
<i>Bembidion intermedium</i> (Kby.)	CB
<i>Bembidion morulum</i> LeC.	HC,OC,RR
<i>Bembidion quadrimaculatum</i> (LeC.)	CB
<i>Bembidion sordidum</i> (Kby.)	HC,MV
<i>Bembidion transparens</i> (Geb.)	CB,IB
<i>Bembidion umiatense</i> Lth.	CD,HC,MV,OC,RR
<i>Stereocerus</i> (<i>Pterostichus</i>) <i>haematopus</i> Dej.	CB,CD,EC,HC,MV,NL,OC,PR
<i>Pterostichus adstrictus</i> Eschz.	CB,NL
<i>Pterostichus agonus</i> Horn	BS,CD,HL,NL,NY
<i>Pterostichus arcticola</i> (Chd.)	HL,NL,UKL
<i>Pterostichus auriga</i> Ball	CD,EC
<i>Pterostichus bryanti</i> VD	CD,HL
<i>Pterostichus brevicornis</i> (Kby.)	BS,CB,CD,EC,FR,HC,HL,MV,NL,N R,NY,OC,PR,RC,TO,UKL
<i>Pterostichus caribou</i> Ball	BS,CC,EC,HC,MV,NL,OC,PR,UKL
<i>Pterostichus chipewyan</i> Ball	EC
<i>Pterostichus circulosus</i> Lth.	NL,NY
<i>Pterostichus costatus</i> (Mén.)	CB,CD,PR
<i>Pterostichus empetricola</i> (Dej.)	HL,NL,NR
<i>Pterostichus gerstlensis</i> Ball	CB,EC
<i>Pterostichus hudsonicus</i> LeC.	CD,HC,OC?,RC
<i>Pterostichus kotzebuei</i> Ball	CB,CD,EC,HL,NL,NY,OC,PR
<i>Pterostichus mandibularoides</i> Ball	CD,EC,MC,NR,PR
<i>Pterostichus nearcticus</i> (Lth.)	BB,CD,HC,OC?,PR
<i>Pterostichus nivalis</i> (Sahlb.)	BS,CB,CD,EC,HL,HB,MV,NL,NR,P R,RC,UKL
<i>Pterostichus parasimilis</i> Ball	CB,CD,EC,HL,NL,PR
<i>Pterostichus pinguedineus</i> (Eschz.)	BB,CB,CD,EC,HC,HL,MV,NL,NY,O C,PR
<i>Pterostichus punctatissimus</i> (Rand.)	HC
<i>Pterostichus similis</i> Mann.	CD,EC,HC,HL,NL
<i>Pterostichus soperi</i> Ball	CB,CD,EC,PR
<i>Pterostichus sublaevis</i> (Sahlb.)	BB,BS,CD,HC,HL,OC,PR
<i>Pterostichus tareumiut</i> Ball	CB,CD,EC,HL,NL,NY,OC,PR,UKL
<i>Pterostichus ventricosus</i> (Eschz.)	BB,CB,CD,EC,HC,OC,PR,RR
<i>Pterostichus vermiculosus</i> Mén.	CD,HC,OC,PR,RR
<i>Agonum consimile</i> (Gyll.)	CB
<i>Agonum exaratum</i> (Mannh.)	CD

TABLE II

Quaternary fossil beetle species identified from Beringian sites

Taxon	Sites ¹
<i>Agonum gratiosum</i> (Mannh.)	IB,HL,NL,NY,TO
<i>Agonum picicornoides</i> Lth.	NL
<i>Agonum quinquepunctatum</i> Mots.	CB,EC,HC,HL,MC
<i>Agonum thoreyi</i> Dej.	NL?
<i>Amara alpina</i> (Payk.)	BB,CB,CD,EC,HC,HL,NL,OC,PR,R
<i>Amara bokeri</i> Csiki	CB,CD,HC,OC,PR
<i>Amara browni</i> Lth.	CD
<i>Amara discors</i> Kby.	TO
<i>Amara glacialis</i> (Mannh.)	BB,HC,MV,PR
<i>Amara hyperborea</i> Dej.	CD
<i>Amara laevipennis</i> Kby.	TO
<i>Amara quelseli</i> (Schönrh.)	HC
<i>Amara sinuosa</i> (Csy.)	NL,NY
<i>Harpalus amputatus</i> Say	CD,HC,MV,OC,PR
<i>Harpalus nigratarsus</i> Sahlb.	CD
<i>Trichocellus mannerheimi</i> (Sahlb.)	CB,CD,HC,MV,NL,OC,PR,RR
<i>Bradycellus lecontei</i> Csiki	CB
<i>Chlaenius niger</i> Rand.	HC
<i>Cymindis unicolor</i> Kby.	NU
DYTISCIDAE	
<i>Agabus arcticus</i> Payk.	HL,NR
<i>Agabus colymbus</i> Leech	HL,NY
<i>Agabus moestus</i> Curtis	BS
<i>Ilybius discidens</i> Sharp	HL,NY
<i>Colymbetes dolobratius</i> (Payk.)	BS
<i>Hydroporus griseostriatus</i> (DeG.)	HL
<i>Hydroporus polaris</i> Fall	CS,HL
HYDROPHILIDAE	
<i>Cercyon herceus</i> Smet.	HC
<i>Cercyon marinus</i> Ths.	CB,CL
<i>Helophorus oblongus</i> LeC.	CB
<i>Helophorus splendidus</i> Sahlb.	BB,BP,CD,CS,OC,PR,RR
HYDRAENIDAE	
<i>Hydraena angulicollis</i> Notm.	HL,NY
<i>Ochthebius marinus</i> (Payk.)	CB
<i>Ochthebius kaszabi</i> Janss.	CB
STAPHYLINIDAE	
<i>Megarthus sinuaticollis</i> Boisd.	CD
<i>Arpedium brachypterum</i> (Grav.)	BS,CD,CS,NR
<i>Eucnecus brunnescens</i> Sahlb.	TR
<i>Olophrum boreale</i> (Payk.)	CB,FR,HC,HL,TO,UKL
<i>Olophrum consimile</i> Gyll.	CB,FR,HL,NY,RR,TO,TR

TABLE II

Quaternary fossil beetle species identified from Beringian sites

Taxon	Sites ¹
<i>Olophrum latum</i> Mäkl.	CB,CL,HC,HL,NR,NY,PR,RC,RR,T R,UKL
<i>Olophrum rotundicollis</i> Sahlb.	CB,FR,HC,HL,NY
<i>Pycnoglypta lurida</i> (Gyll.)	BS,CS,TR
<i>Acidota crenata</i> (Fab.)	HL,NY
<i>Acidota quadrata</i> (Zett.)	HL,NY
<i>Boreaphilus henningianus</i> Sahlb.	CB,CD,HL,NY,PR
<i>Holoboreaphilus nordenskiöldi</i> Mäkl.	BS,CC,CS,HL,NL,NY,TR
<i>Micralymma brevilingue</i> Schiodt.	BB,CB,CD,EC,HL,NL,NR,PR,RR,T R
<i>Quedius fellmani</i> (Zett.)	HL
<i>Quedius fulvicollis</i> (Steph.)	HL
<i>Quedius pediculus</i> (Nordm.)	HL
<i>Tachinus brevipennis</i> Sahlb.	BB,BP,BS,CB,CD,CS,EC,FR,HC,H L,NR,NY,OC,PR,TR
<i>Tachinus frigidus</i> Er.	HL
<i>Tachinus instabilis</i> Mäkl.	MV
<i>Mycetoporus</i> cf. <i>nigrans</i> Mäkl.	BS
<i>Tachyporus borealis</i> Campbl.	HL
<i>Tachyporus canadensis</i> Campbl.	HL,NL
<i>Tachyporus nimbicola</i> Campbl.	HL
<i>Tachyporus rulomus</i> Blkwldr	BS,HL
<i>Gymnusa atra</i> Csy.	BS
MICROPEPLIDAE	
<i>Micropeplus laticollis</i> Mäkl.	HC
<i>Micropeplus sculptus</i> LeC.	CB
<i>Micropeplus tesseraula</i> Curtis	CB
SILPHIDAE	
<i>Thanatophilus lapponicus</i> (L.)	TR
<i>Thanatophilus coloradensis</i> Wickh.	CB,CC,PR
<i>Silpha trituberculata</i> Kby.	EC,HL
SCARABAEIDAE	
<i>Aegialia lacustris</i> LeC.	HL,NY
<i>Aphodius congregatus</i> Mannh.	CC
<i>Aphodius distinctus</i> (Mull.)	CD

¹ Site Names: BB - Bluefish Basin; BP - Baldwin Peninsula, Alaska; BS - Bering Sea Shelf, Alaska; CB - Chi'jee's Bluff, Yukon Territory; CC - Colorado Creek, Alaska; CD - Cape Deceit, Alaska; CL - Clarence Lagoon, Yukon Territory; CS - Chukchi Sea Shelf, Alaska; EC - Eva Creek, Alaska; FR - Foraker River, Alaska; HC - Hungry Creek, Yukon Territory; HL - Holitna Lowland, Alaska; IB - Isabella Basin, Alaska; LB - Landslide Bluff, Alaska; MV - Mayo Village, Yukon Territory; NL - Nushagak Lowland, Alaska; NR - Noatak River, Alaska; NY - Nuyakuk, Alaska; OC - Old Crow, Yukon Territory; PR - Porcupine River, Yukon Territory; RC - Revenue Creek, Yukon Territory; RR - Rock River, Yukon Territory; TO - Toklat River, Alaska; TR - Titaluk River, Alaska; UKL - Upper Kuskokwim Lowland, Alaska.

TABLE III
List of fossil insect sites and assemblage age ranges, Central and Eastern Beringia

Site	Age Range ¹	Reference
1. Baldwin Peninsula, Alaska	MW	Hopkins <i>et al.</i> , 1976
2. Bering Sea Shelf, Alaska	LW	Elias <i>et al.</i> , 1996b
3. Bluefish Basin, Yukon	LW	Matthews and Telka, 1997
4. Cape Deceit, Alaska	LI, EW	Matthews, 1974a
5. Chi'jee's Bluff, Yukon	LI	Matthews <i>et al.</i> , 1990a
6. Chukchi Sea Shelf, Alaska	LW	Elias <i>et al.</i> , 1996b
7. Clarence Lagoon, Yukon	LW	Matthews, 1975a
8. Colorado Creek, Alaska	LGM	Elias, 1992a
9. Eva Creek, Alaska	LI, MW	Matthews, 1968
10. Foraker River, Alaska	MW	Elias <i>et al.</i> , 1996c
11. Hungry Creek, Yukon	LI,EW, MW	Hughes <i>et al.</i> , 1981
12. Holitna Lowland, Alaska	LI,MW,LGM,LW	Elias, 1992b
13. Isabella Basin, Alaska	MW,LW	Matthews, 1974b
14. Landslide Bluff, Alaska	LI	Waythomas <i>et al.</i> , 1989
15. Mayo Village, Yukon	MW	Matthews <i>et al.</i> , 1990b
16. Noatak River, Alaska	PLI,LI	Elias <i>et al.</i> , 1999b
17. Nushagak Lowland, Alaska	EW,MW,LGM,LW	Elias, 1992b
18. Nuyakuk, Alaska	LI	Elias and Short, 1992
19. Old Crow, Yukon	PLI,LI,EW,MW,LW	Matthews, 1975b; Morlan and Matthews, 1983
20. Porcupine River, Yukon	MW	Matthews, 1975b
21. Revenue Creek, Yukon	LI	Matthews and Telka, 1997
22. Rock River, Yukon	LGM	Matthews and Telka, 1997
23. Titaluk River, Alaska	MW	Nelson and Carter, 1987
24. Toklat River, Alaska	MW	Elias <i>et al.</i> , 1996b
25. Upper Kuskokwim Lowland, Alaska	MW	Elias, 1992b

¹ Age range categories: PLI - Pre-Last Interglacial; LI - Last Interglacial; EW - Early Wisconsin; MW - Mid- Wisconsin; LGM - Last Glacial Maximum; LW - Late Wisconsin.

larvae, or pupae that are buried in the soil, beneath stones or logs, or in the mud at the bottom of streams, lakes, or ponds. This is particularly true of arctic and alpine and boreo-arctic species. Winter air temperatures in the arctic and boreal regions often fall to levels that are lethal for most beetle species. In order to avoid exposure to such temperatures, the beetle fauna of these regions spend the winter months in thermally buffered habitats, beneath leaf litter, stones, pond mud, or soil. These species are therefore adapted to the winter temperatures experienced in these sheltered habitats, not to the much colder air temperatures. As such these beetles are not very sensitive indicators of winter air temperatures. The same could be said of most other invertebrates and most plants, which are likewise more-or-less dormant during winter. Nevertheless, as shown by a study of predicted vs. observed TMIN from sites throughout North America (Elias *et al.*, 1996a), beetle data provides at least a crude estimate of mean winter temperatures.

ZOOGEOGRAPHY OF THE BERINGIAN FAUNA

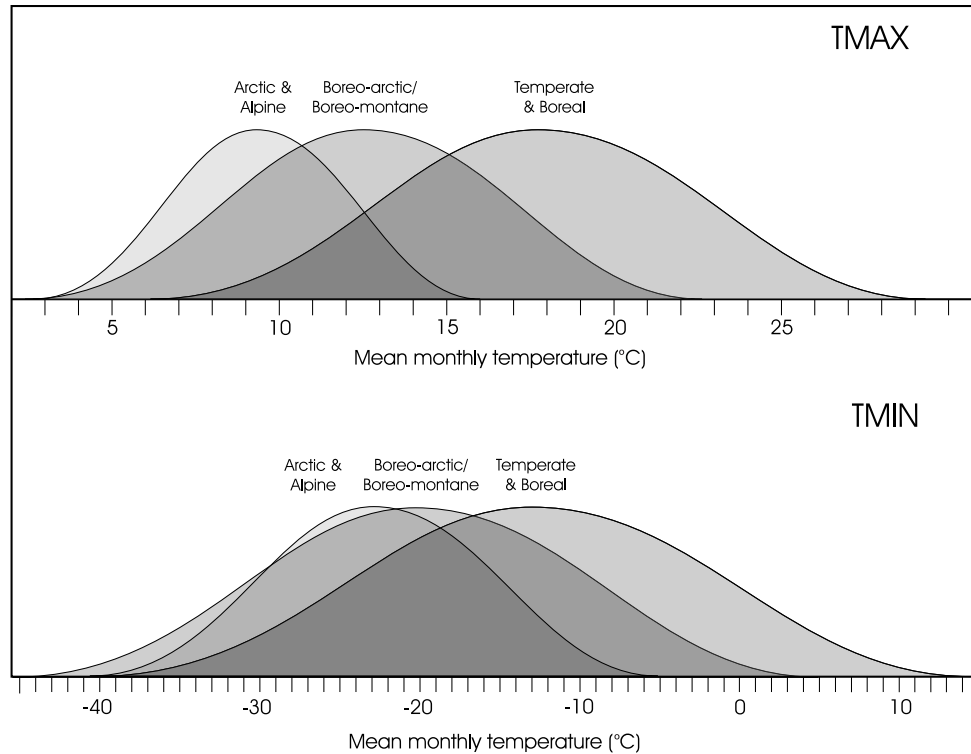
Among the arctic and alpine beetles found in the fossil assemblages, the majority (64 %) have Beringian distributions today. Their modern ranges are centered in Alaska and the Yukon Territory, although many species have spread

eastward across the Northwest Territories during the Holocene (Scudder, 1979). Their dispersal farther east was blocked by Hudson Bay and late-lying ice in central and northern Québec. Typical of this group are several species in the *Cryobius* group of the ground beetle genus, *Pterostichus*. Many of the species in this group have both their fossil record and modern range entirely within Alaska and the Yukon Territory. Others in this group include the arctic rove beetles, *Micralymma brevilingue* and *Tachinus brevipennis*. It appears that these species may have never ranged outside of the Beringian region, although the absence of fossil evidence outside this region cannot be taken as evidence of their absence.

The arctic and alpine species not considered to have a Beringian distribution are an interesting group in their own right. The fossil record documents the fact that the ground beetles, *Amara alpina*, *Blethisa catenaria*, and *Bembidion dauricum*, had populations in Beringia during the late Pleistocene, but they also had populations in regions of the United States that were south of the continental ice sheets. *Amara alpina* has been found in Wisconsinan-age assemblages from Montana, Iowa, and southern Québec. These assemblages span an interval from greater than 50 000 to 11 000 yr BP. *Blethisa catenaria* has been found in Middle

FIGURE 2. TMAX and TMIN ranges for arctic and alpine, boreo-arctic, and temperate and boreal species groups, based on data presented in Table I.

Étendue des valeurs de TMAX et TMIN pour les groupes d'espèces arctiques-alpines, boréales-arctiques et tempérées-boréales, selon les données présentées au tableau I.



Wisconsinan assemblages from Pennsylvania, and *Bembidion dauricum* has been found in mid- and late-Wisconsin assemblages in Ontario and Iowa, respectively. As has been pointed out by Schwert and Ashworth (1988), arctic and alpine beetles living in the central and eastern United States and southern Canada at the end of the last glaciation were unable to disperse north as climate warmed, because glacial ice blocked their path. Some cold-adapted beetles living in or near the Appalachians or Rocky Mountains, such as *Amara alpina*, were able to disperse upslope and become established in the alpine tundra zone following deglaciation (Elias, 1991). Other species, like the water scavenger beetle, *Helophorus splendidus*, lived in the Colorado Rocky Mountains as late as 13 000 years ago, but failed to become established in the alpine tundra habitats that formed in the Rockies following deglaciation. Likewise the rove beetle, *Holoboreaphilus nordenskiöldi* lived in the Rocky Mountains of Montana during the late glacial period, but no Rocky Mountain populations of this species are known to have survived through the Holocene.

The fossil record of such species is very instructive. Were we to base the zoogeographic history of such species as *H. splendidus* or *H. nordenskiöldi* strictly on their modern ranges, these beetles would be classified as "Beringian," because their modern ranges match those of the Beringian fauna. However, the fossil record shows that Pleistocene populations existed far south of Beringia, probably in a narrow band of arctic tundra habitats that bordered the continental ice sheets. These habitats probably persisted for tens of thousands of years, shifting south and north with the wax-

ing and waning of ice sheet margins. The Quaternary insect fossil record for North America is relatively poorly known, so it seems likely that other species typically considered "Beringian" may eventually prove to have existed in regions south of continental ice sheets during Pleistocene glaciations.

Nearly half of the species found in the Beringian fossil assemblages have boreo-arctic distributions today. In a sense, these species are the best-adapted to the series of climatic conditions presented in the late Pleistocene of Beringia. They succeeded well during interglacial, glacial, and interstadial periods, because of their ability to live in both arctic- and boreal-style climatic regimes. About one-third of these boreo-arctic beetles are considered Beringian species. Two-thirds of them have been wider-ranging in North America, both in the late Pleistocene and presently.

The climatic classification employed here shows that nearly half of the species diversity in the Beringian fossil assemblages comes from boreal and temperate species. This is an interesting observation, because many of those species only lived in Beringia during the relatively brief interglacial and/or interstadial warm periods. Only one species of this group is considered a Beringian species. *Pterostichus gerstlensis* is a ground beetle known today only in the boreal regions of Alaska. Of the temperate and boreal species from the late Pleistocene Beringian assemblages, 54 % (37 species) were found only in deposits dating to the last interglacial period. This was an interval of warmer-than-modern climate, based on fossil beetle evidence (Elias *et al.*, 1999b). Boreal forest expanded throughout much of Eastern Beringia, and with it came boreal and temperate beetles.

However, as the TMAX data in Table I shows, many of these boreal and temperate species have broad climate envelopes. The minimum TMAX values for these species are not greater than 15.5 °C, a level of summer warmth below that of many interior regions of Alaska and the Yukon today.

Roughly one-third of the boreal and temperate beetle species were found in Beringian fossil assemblages dating to interstadial or glacial intervals. Many of these fossil finds have been ascribed to the Early Wisconsin interval, based on stratigraphic evidence. In many cases it remains unclear whether these assemblages represent full glacial or interstadial conditions. We have better chronological control over assemblages dating to the last glacial maximum (LGM), because this interval falls within the range of radiocarbon dating. Of the boreal and temperate beetles associated with the Beringian fossil assemblages discussed here, only two species have been identified from LGM deposits: *Bembidion morulum* and *Harpalus amputatus*. *Bembidion morulum* has a modern TMAX of 8.75-15.5 °C. Although I have classified it as a boreal species, it is found today at sites near northern treeline (Churchill, Manitoba) and on coastal tundra in Labrador (Lindroth, 1963). Therefore its modern range is on the cusp between boreal and boreo-arctic. *Harpalus amputatus* has an unusually broad TMAX range, from 9.5 to 24.5 °C. This corresponds to a geographic range from the northern edge of the boreal forest south to prairie regions of Colorado and New Mexico. This species was found in Middle Wisconsin interstadial, the LGM, and late glacial deposits in both Alaska and the Yukon.

The late Pleistocene beetle fauna of Beringia was comprised of mixtures of widespread and regional endemic species. It also contained mixtures of species with narrow and broad thermal tolerances. No simple patterns emerge from the fossil data. As with the ancient vegetation of Beringia, the ancient beetle communities were ecological mosaics. Species distribution patterns shifted considerably through the last 140 000 years. During the lengthy cold stages, a relatively small number of cold-adapted species dominated most fossil assemblages. The warm episodes, including interstadials and especially the last interglacial period, ushered in large numbers of warm-adapted species. Some of these species were able to persist in Beringia during the glacial intervals, because of their relatively broad thermal tolerances. The changing climatic regimes of the late Pleistocene brought expansion of the ranges of one group of species at the expense of another. At least small populations of many species persisted, even when regional climatic conditions were marginal. Today the arctic and alpine species are the group that are relatively restricted in range, while the boreal species flourish across broad regions of Alaska and the Yukon. When another glaciation occurs, these roles will be reversed. There are still many gaps in our understanding of these processes, and whole regions of the former Beringia await paleoentomological investigation. When making paleoclimatological reconstructions from fossil beetle assemblages, it is tempting to take the fossil data at face value, but we must maintain an ecological and zoogeographic perspective on the data if our interpretations are to be meaningful.

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