

Paleoecological Significance of Holocene Insect Fossil Assemblages from the North Coast of Alaska

MANDY J. WILSON¹ and SCOTT A. ELIAS²

(Received 14 May 1985; accepted in revised form 24 September 1985)

ABSTRACT. Two peat sections containing insect fossil remains from the eastern coastal plain of the Alaskan North Slope were analyzed in comparison with pollen studies. The sections span a period from 10 400 B.P. to 1320 B.P., providing information on the post-glacial distributions of some of the beetles species that were a part of the Beringian refugium fauna. The fossil insect evidence suggests climatic conditions similar to modern parameters, especially in the early Holocene, in general agreement with paleobotanical and vertebrate fossil interpretations for the coastal plain and elsewhere in eastern Beringia.

Key words: Holocene, paleoenvironments, insect fossils, Alaska

RÉSUMÉ. Deux sections de tourbe contenant des restes d'insectes fossilisés de la plaine côtière est du nord de l'Alaska furent analysées de façon comparative avec des études polliniques. Les sections dataient d'entre 10 400 et 1320 avant notre ère et fournissaient des renseignements sur la distribution post-glaciaire de certaines espèces de coléoptères qui faisaient partie de la faune du refuge de Béringie. Les restes d'insectes fossilisés suggèrent des conditions climatiques semblables aux paramètres modernes, en particulier durant l'Holocène inférieur, et sont en général conformes aux interprétations des fossiles paléobotaniques et vertébrés pour la plaine côtière et d'autres régions dans l'est de la Béringie.

Mots clés: Holocène, paléoenvironnements, fossiles d'insectes, Alaska

Traduit pour le journal par Maurice Guibord.

INTRODUCTION

Studies of assemblages of insect fossils have great potential for the reconstruction of Late Quaternary environments, as demonstrated by many recent publications (Coope, 1977; Schwert *et al.*, 1985; Elias, 1985). In Alaska and the northern Yukon Territory, only three sites of Holocene age have been previously investigated (Matthews, 1975a; Nelson, 1982). To extend knowledge of Holocene climate and ecology in this region, we analyzed assemblages of insect fossils from two peat sections obtained from the northern coastal plain and compared our conclusions with those from pollen analyses from the same sites (Wilson, 1984) and with the conclusions of others.

THE STUDY SITES

The two analyzed peat sections come from Barter Island (70°8'N, 143°37'W) and Niguanak Uplands (69°53'N, 142°45'W) (unofficial name). Both sites are located on the eastern coastal plain of the North Slope of Alaska (Fig. 1).

The Barter Island section comes from the organic deposits that cap the actively eroding coastal bluffs along the north shore of the island to the west of the DEW Line Station. The exposure consists of a large convolution, about 5 m above present-day sea level, which at some time in the past was probably a horizontal deposit of interbedded sands and organic materials of detrital appearance. The lower part of the convolution was collected. The peat and sand layers were sampled separately. Permafrost, located a few centimeters in from the face of the exposure, limited the sample sizes, which ranged in volume from a few ml to 200 ml. A 90 cm section was obtained.

Three radiocarbon dates were obtained for the section (Table 1). The date at 0 cm (the top of the section, not the ground surface) of 7780 ± 240 years B.P. is older than the basal date of 6725 ± 240 years B.P. The convolution of the section may have

caused the deposit to be inverted or it may be that the section is reworked. Hence, the section has been treated as a bulk sample dating from 8000-7000 years B.P.

The Niguanak Uplands site is situated southeast of Barter Island. The site lies between the Niguanak and Sikrelurak rivers at an elevation of about 61 m. The area has some relief in the form of a series of east-west trending low ridges. Scattered thaw lakes have developed in the area, and the section was taken from sediments exposed by erosion of the east bank of a thaw lake. The vegetation at the top of the section is dominated by species of dwarf willow and included species of drier habitats.

The Niguanak Uplands exposure is composed of a series of peat and sand lenses of varying degrees of oxidation. Again, permafrost located a few centimeters in from the face limited the size of the samples. An 88 cm section was recovered.

The radiocarbon dates obtained for the section are shown in Table 2. The section spans a period from 10 400 ± 570 years B.P. to 1320 ± 160 years B.P. The date of 8725 ± 215 years B.P. is out of sequence with the other dates for the section and may be the result of reworking. For the purpose of the insect fossil analysis the date has been considered as anomalous and disregarded, although its effect on the validity of the section must be considered.

METHODS

Collection and Preparation of Specimens

The method used for extraction of insect fossils follows that of Coope (1968). Each sample was wet sieved through a 300 mesh. Samples that did not easily break down were soaked for 24 h in sodium hexa-meta-phosphate to disaggregate them before sieving. The standard kerosene flotation method for the concentration and extraction of insect fossils from organic detritus was employed. Sorting was carried out under a low-

¹18 Glamis Crescent, Rowlands Gill, Tyne and Wear, United Kingdom NE39 1AT

²Institute of Arctic and Alpine Research, Campus Box 450, University of Colorado, Boulder, Colorado 80309, U.S.A.

power stereo binocular microscope. The insect parts were mounted on modified micropaleontology slides with gum tragacanth. Caddisfly larval fossils were mounted in polyvinyl lactophenol medium on glass microscope slides.

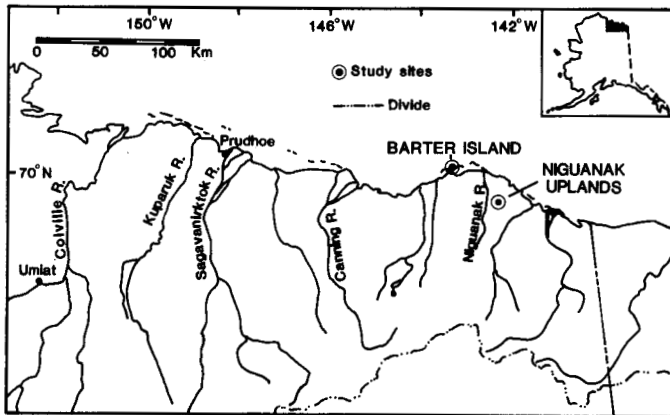


FIG. 1. Location of peat sections.

TABLE 1. Radiocarbon dates for the Barter Island section

Depth (cm)	Date (C-14 years B.P.)	Sediment	Geochron lab. no.
0-4	7780 ± 240	Moss detrital peat	GX-9392
26-27	7870 ± 310	Moss detrital peat	GX-9393
67-70	6725 ± 240	Sedge peat	GX-9306

TABLE 2. Radiocarbon dates for the Niguanak Uplands section

Depth (cm)	Date (C-14 years B.P.)	Sediment	Geochron lab. no.
4-5	1320 ± 160	Sandy peat	GX-9598
34-35	*8725 ± 215	Peat	GX-9599
47-48	3190 ± 175	Peat	GX-9832
49-50	4330 ± 225	Sandy peat	GX-9600
87-88	10,400 ± 570	Peat	GX-9394

*Anomalous date.

Identifications of some specimens were by Elias; some specimens were sent to specialists for identification. Taxonomic keys were used in some cases to help identify fossil specimens, but the absence of fragile exoskeletal parts, such as leg and antennal segments, disallows the use of such keys for most specific identifications. Specific determinations were made on the basis of comparisons between fossil parts and modern, identified specimens. When the only available fossil sclerites from a given taxon were lacking in sufficient diagnostic characters to allow specific identification, these fossils were determined to the generic or family level. Whenever possible, the fossils were compared with large series of modern specimens, in order to maximize the certainty of the fossil identifications. The level of intraspecific variation of beetle exoskeletal morphology appears to be greater in high latitude species than elsewhere; structural differences are especially common between northern and southern populations and across the east-west ranges of populations (Danks, 1981).

Interpretations of Data

The use of insect fossil evidence in the reconstruction of past

environments specifically for the Quaternary period has been facilitated during recent years by the realization that there has been no significant morphological evolution of the Coleoptera during the Quaternary. Prior to the fossil insect investigations of Lindroth (1948) and Coope (1959 onwards) and associates, many entomologists had been quick to describe beetle fossils as extinct species (e.g., Lomnicki, 1894; Mjöberg, 1916). Recent studies of these (Angus, 1973; Lindroth, 1948) and other assemblages supposed to contain extinct beetle species have proven otherwise, in that the specimens in question were shown to belong to extant species. This view of the stability of Coleoptera species during the Quaternary has been amply supported by the fossil evidence from scores of Quaternary insect assemblages examined recently. This evidence strongly suggests that there has been no appreciable morphological evolution in Coleoptera for at least the last million years. The most recent beetle fossils indicating variation of characters beyond the accepted range of variation for the modern species are found in late Tertiary deposits (Matthews, 1974, 1976). The constancy of beetle species has been more fully discussed by Coope (1978).

A necessary assumption that must be made if Quaternary insects are to be used as paleoenvironmental indicators is the stability of their ecological requirements during this period. This is an assumption common to all biological interpretations of past environments. Unlike external morphology, we have no way of directly observing any physiological changes in the fossil record. One may infer a great deal, however, from the constancy of associations of species, especially when the same suites of species associated in the past are found still living together in the modern environment. In European and North American fossil studies, suites of beetle species from numerous genera and families are repeatedly found associated together. Examinations of their modern ecological requirements and geographic ranges most often reveal a continuity of ecological and zoogeographic relationships and associations. One may argue that a given species has undergone physiological evolution between the time of fossil deposition and the present, and thus its ecological requirements have changed. But the probability is very small that a whole association of beetles found together in a fossil assemblage had undergone an exactly similar degree of physiological evolution such as would allow them to have collectively compatible, though different, ecological requirements in the past compared with the present (Elias and Wilkinson, 1983).

MODERN HABITATS AND DISTRIBUTION OF FOSSIL FAUNA

Barter Island

Table 3 presents a list of insect fossils recovered from the Barter Island site and their known ecological requirements. Only 102 insect and arachnid individuals (based on the minimum number of individuals) were recovered from the entire section. This low number reflects the small quantity of original sample and the low concentration of insect fossils in the samples. The 102 individuals represent 40 taxonomic groups (including specimens identified only to family level). Eleven of these taxa were identified to genus level; 15 species were identified. Of these individuals 85% were Coleoptera (beetles), 1% Hymenoptera (wasps), 6% Trichoptera (caddisflies) and 9% class Arachnida, order Acarina (mites). Numerous ephippia (egg cases) of the crustacean *Daphnia* were also found in the samples;

TABLE 3. Annotated list of insect species recovered from the Barter Island section, showing minimum number of individuals and habitat preferences

Taxon	Minimum number of individuals	Habitat preference
Class: INSECTA		
Order: COLEOPTERA		
Family: Carabidae		
<i>Notiophilus borealis</i> Harris	1	X,O,B-Arc
<i>Bembidion</i> sp.	2	M
<i>Pterostichus (Cryobius)</i> cf. <i>nivalis</i> F. Sahlb.	1	X,T
<i>Pterostichus</i> sp.	1	M
<i>Cymindis</i> cf. <i>unicolor</i> Kby.	1	X,(T)
Genus indet.	7	
Family: Dytiscidae		
<i>Hydroporus</i> cf. <i>fuscipennis</i> Schaum	1	A,C
<i>Hydroporus morio</i> Aube.	2	A,SP,B
<i>Hydroporus</i> cf. <i>notabilis</i> Leconte	1	A,B,Arc
<i>Hydroporus</i> cf. <i>notabilis</i> Leconte or <i>arcticus</i> Thoms. complex	1	A
<i>Agabus</i> cf. <i>inscriptus</i> Crotch	1	A,SP
<i>Agabus</i> sp.	3	A
<i>Ilybius angustior</i> Gyll.	1	A,EmV
Genus indet.	3	A
Family Gyrinidae		
Genus indet.	1	A
Family Hydrophilidae		
<i>Helophorus</i> cf. <i>parasplendidus</i> Ang.	1	A,EmV,Arc
<i>Enochrus</i> sp.	1	A
Genus indet.	1	A
Family Hydraenidae		
Genus indet.	1	A
Family Staphylinidae		
<i>Eucnecosum</i> sp.	3	M,L
<i>Olophrum</i> sp.	3	M
<i>Holoboreaphilus nordenskiöldi</i> (Makl.)	7	M,Arc,L
Omalinae indet.	10	
<i>Micralymma brevilingue</i> Schiödt	1	X,Arc
<i>Stenus hyperboreus</i> J. Sahlb.	3	M,B-Arc,C,EmV
<i>Stenus kamschaticus</i> Mots.	1	M,Arc,C,EmV
<i>Stenus sibiricus</i> J. Sahlb.	1	M,T,L
<i>Stenus</i> sp.	6	M
<i>Lathrobium</i> sp.	2	
<i>Quedius</i> sp.	1	M
Aleocharinae indet.		
Genus indet.	5	
Family: Leiodidae		
Genus indet.	1	A
Family: Elateridae		
Genus indet.	1	M
Family: Chrysomelidae		
<i>Pyrrhalta</i> sp.	2	A
Family: Curculionidae		
cf. <i>Dorytomus</i> sp.	4	M,S
Genus indet.	3	
Order: HYMENOPTERA		
Family: Belytidae		
<i>Belyta</i> sp.	1	
Order: TRICHOPTERA		
Family: Limnephilidae		
Genus indet. (Larvae)	6	A
Class: ARACHNIDA		
Order: ACARI		
Family: Oribatidae		
Genus indet.	9	M
Class: CRUSTACEA		
Order: CLADOCERA		
<i>Daphnia</i> sp.	Abundant	A

Key

A	Aquatic environment	EmV	Emergent vegetation at edge	S	Associated with <i>Salix</i>
Arc	Arctic		of standing water	SP	Small vegetation ringed pools
B	Boreal forest region	L	Leaf litter	T	Only on tundra
B-Arc	Boreal-Arctic distribution	M	Mesic environment	(T)	Predominantly on tundra but not obligatory
C	<i>Carex</i> marshes, shallow water	O	Open ground	X	Xeric environment

these have been excluded from the calculation of the minimum number of individuals.

Figure 2A illustrates the percentage of individuals known to prefer aquatic, mesic and xeric habitats respectively. Twenty-eight percent of the individuals are associated with aquatic habitats, 39% with mesic habitats and 4% with xeric habitats. Twenty-nine percent of the individuals could not be classified into one of the three substrate moisture preference categories because of lack of specific identifications.

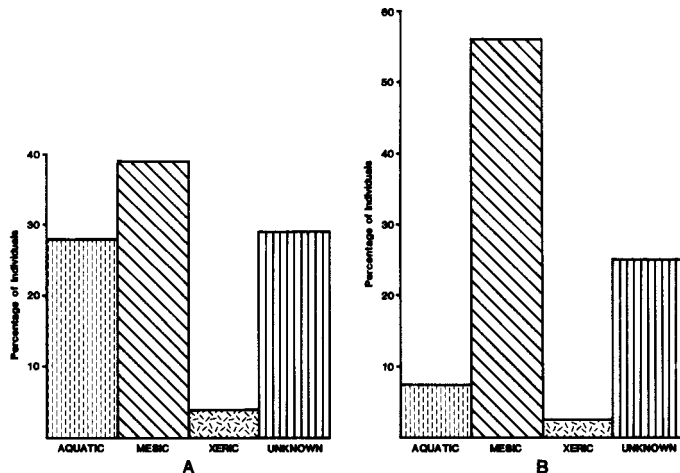


FIG. 2. Habitat moisture preferences of fossil insects recovered from (A) the Barter Island section and (B) the Niguanak Uplands section.

All the genera identified are characteristic of northern tundra environments today. Most species of *Bembidion* are commonly associated with stream or lake margins; *Pterostichus* (*Cryobius*) species are for the most part associated with mesic tundra habitats where the vegetation is moderately continuous, consisting, at least in part, of graminoid species but often including low shrub species such as *Betula nana* and *Ledum palustre* (Nelson, 1982). Matthews (pers. comm. 1983) notes that one of the *Cryobius* fossil *pronota* (Fig. 3B) is a good match for *P. (Cryobius) nivalis*, a species characteristic of well-drained sandy substrates with a discontinuous vegetation cover (Ball, 1966; Lindroth, 1966). *Pterostichus nivalis* has a modern distribution corresponding to the Beringian regions of eastern Siberia and Alaska (Fig. 4A). *Eucnecosum*, *Olophrum*, *Stenus* and *Quedius* are other examples of genera that prefer damp or riparian areas. *Stenus hyperboreus* (Fig. 3H) and *Stenus kamschaticus* (Fig. 3I) are both common at high latitudes in North America today, living mainly near ponds in *Carex* swamps and humid meadows or in *Sphagnum*. Both species have a holarctic distribution, although *S. kamschaticus* is more restricted (Fig. 4D), recorded in Alaska only from Unalakleet, Mile 1249 of the Alaska Highway (Deadman Lake), and at Bonanza Creek (150°40'W, 66°40'N) on the Dalton Highway (Puthz, pers. comm. 1983). *Stenus sibiricus* (Fig. 3J) also has a wide holarctic range and is found on the open tundra, in *Vaccinium*, lichen, moss and *Populus* litter. Puthz (pers. comm. 1983) notes that two different forms of the species exist. He identifies the Barter Island fossil as belonging to *S. sibiricus* A, as he designates it. *Holoboreaphilus nordenskiöldi* (Fig. 3G) is known from northern Siberia and arctic localities in North America. It appears to be associated with damp habitats. Campbell (1978) notes that adults have been collected by sifting arctic willow litter near streams, by sifting moss and grass near a

small wet area and by treading grass clumps growing in shallow water; it occurs in both tundra and in the forest-tundra ecotone.

Where it is possible to assign specific ecological requirements, most of the aquatic beetles are found in standing or slow flowing water. Most species of *Agabus* live in shallow water along the margins of small pools where the emergent vegetation or detritus is very dense (Larson, 1975). Larson has tentatively identified one of the *Agabus* fossils as *A. inscriptus*, a species characteristic of small, vegetation-ringed pools.

Hydroporus fuscipennis is holarctic in distribution and has been recorded from the Northwest Territories and the Yukon Territory (Larson, 1975). Larson records it from shallow water and *Carex* marshes in Alberta. *Hydroporus morio* (Fig. 3F) has a circumpolar distribution and has been found in small, cold woodland pools usually in or near coniferous forests, again in Alberta (Larson, 1975). *Hydroporus notabilis* is a species of more southern distribution. However, Larson (1975) notes that Fall (1923) and other subsequent authors have suggested that the species *H. arcticus* includes small northern adults of *H. notabilis*. It is likely that the specimen recorded in the Barter

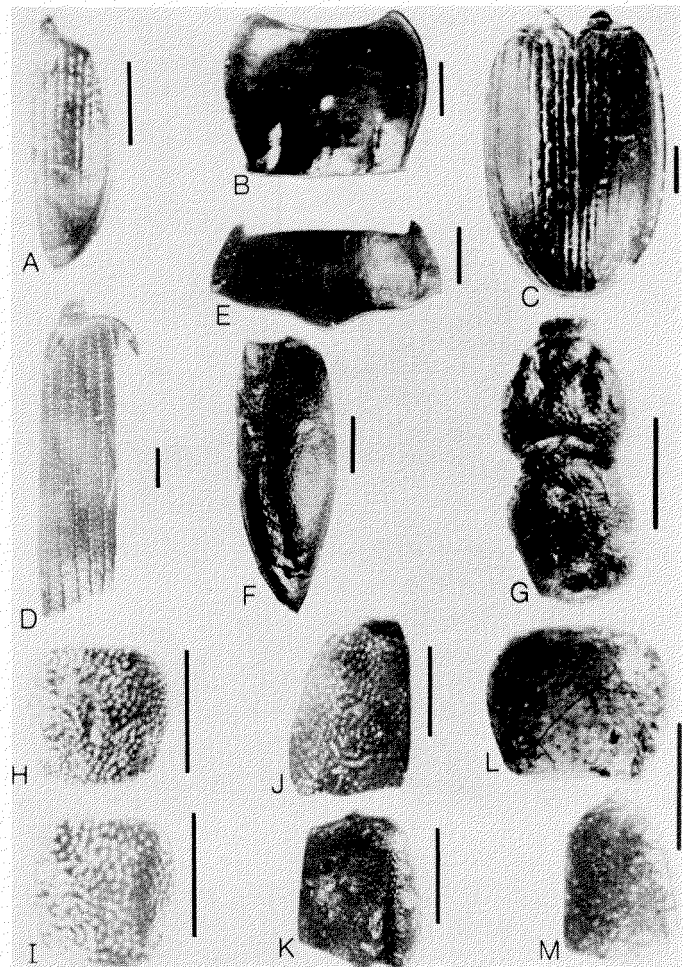


FIG. 3. Fossil beetles recovered from the two sites. A. Right elytron of *Dyschirius* sp. B. Pronotum of *Pterostichus (Cryobius) nivalis*. C. Fused elytra of *Pterostichus (Cryobius)* sp. D. Right elytron of *Cymindis unicolor*. E. Pronotum of *Hydroporus (notabilis-arcticus complex)* sp. F. Left elytron of *Hydroporus morio*. G. Head and pronotum of *Holoboreaphilus nordenskiöldi*. H. Pronotum of *Stenus hyperboreus*. I. Right elytron of *Gymnusa* sp. L. Pronotum of *Micralymma brevilingue*. M. Right elytron of *Micralymma brevilingue*. Scale bar equals 0.5 mm.

Island section (Fig. 3E) belongs to this complex, which has a range extending to the arctic and boreal regions of the holarctic.

The fossil specimen of *Ilybius* has been tentatively identified as *I. angustior*, a holarctic species found among emergent vegetation at the edge of standing water. The species of *Helophorus* is most likely *H. parasplendidus* (Smetana, pers. comm. 1983), which has been recorded from a number of arctic localities in North America (Angus, 1970).

Including the tentatively identified *Pterostichus (Cryobius) nivalis* previously mentioned, only four specimens, representing four species, can be classified as preferring xeric-type environments. The carabid beetle, *Notiophilus borealis*, is a northern species characteristic of xeric areas with sparse vegetation. It is distributed today throughout much of northern Alaska and Canada (Lindroth, 1969). *Cymindis unicolor* is a North American species found in areas of dry tundra (Fig. 4B; Lindroth, 1969). The elytral specimen recovered from the sediments possesses an incomplete basal margin (Fig. 3D), which according to Lindroth (1969) makes it *C. vaporariorum*, a palearctic species. However, Matthews (pers. comm. 1983) suspects that the character is more variable in *C. unicolor* than

Lindroth (1969) indicates. Matthews (pers. comm. 1983) has collected a teneral specimen of another (undescribed) species of *Cymindis* similar to both *C. vaporariorum* and *C. unicolor*. The fossil may represent this undescribed species. The staphylinid, *Micralymma brevilingue* (Fig. 3L, M), was considered to have primarily a coastal distribution in Alaska (Matthews, 1975a). However, Nelson (1982) has collected *M. brevilingue* on damp flanks of high-centered polygons in the vicinity of Barrow. Nelson has also recovered specimens of this species from the 9700-year-old sediments at a site on the Ikpikpuk River, which is well inland. The occurrence of this species is consistent with well-drained, sandy sites (Nelson, 1982).

One of the fossil weevil specimens has been assigned to the genus *Dorytomus*. The other weevil fossils are similar to both *Dorytomus* and other genera (Matthews, pers. comm. 1983). The genus *Dorytomus* is known to feed on willow.

Niguanak Uplands

The species recovered from the Niguanak Uplands site are presented in Table 4, as well as information on the habitat requirements of the taxa.

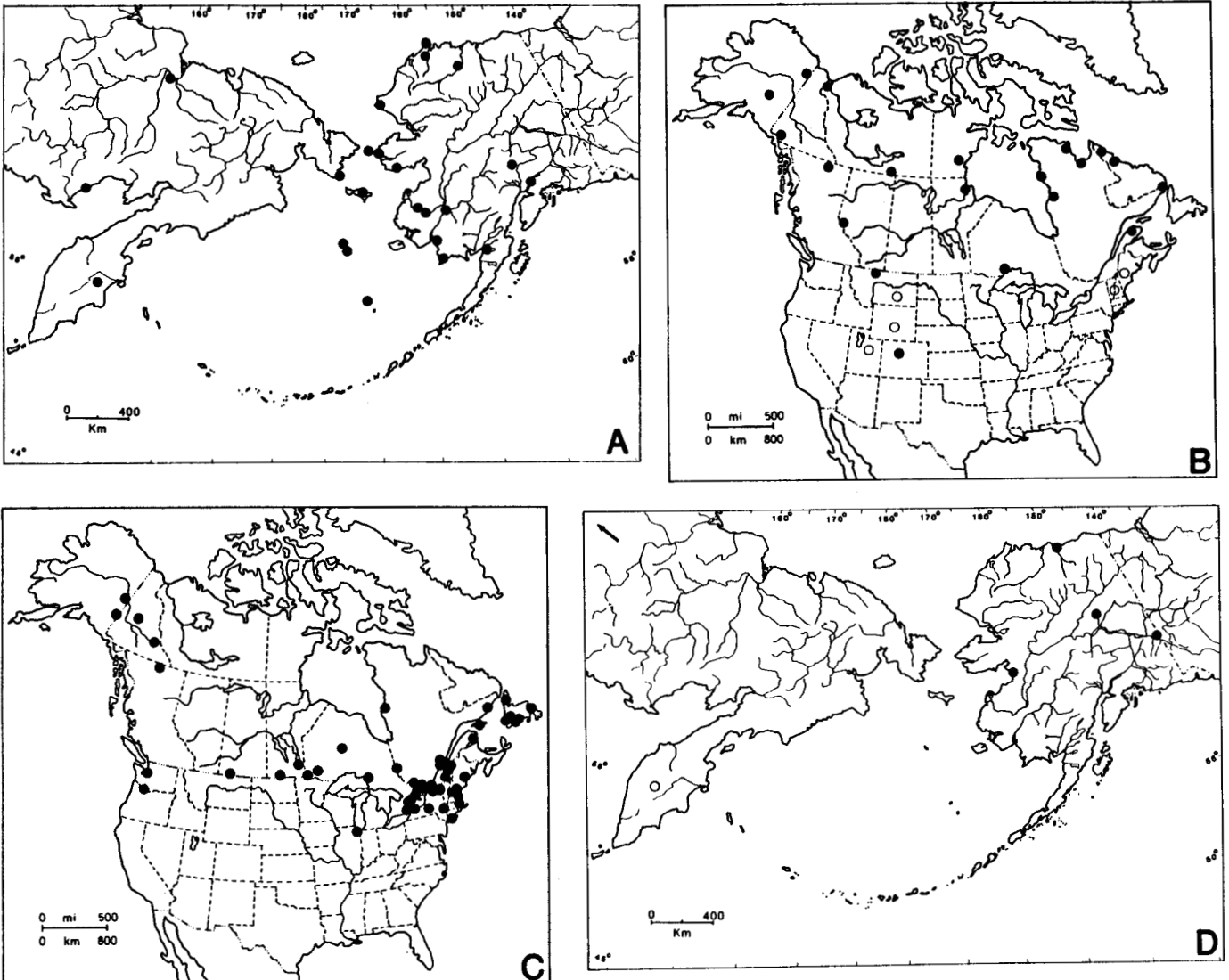


FIG. 4. Distribution maps of A. *Pterostichus (Cryobius) nivalis* (from Lindroth, 1966), B. *Cymindis unicolor* (from Lindroth, 1969), C. *Tachyporus canadensis* (from Campbell, 1979), and D. *Stenus kamtschaticus* (from Puthz, pers. comm. 1983).

TABLE 4. Number of individuals recorded from the Niguanak Uplands section, showing habitat preferences

Taxon	Minimum number of individuals	Habitat preference
Class: INSECTA		
Order: COLEOPTERA		
Family: Carabidae		
<i>Dyschirius</i> sp.	10	M,Sa
<i>Pterostichus (Cryobius)</i> sp.	4	M
<i>Cymindis unicolor</i> Kby.	1	X,(T)
Genus indet.	5	
Family: Dytiscidae		
<i>Hydronorus</i> sp.	1	A
<i>Agabus</i> sp.	1	A
Genus indet.	2	A
Family: Hydrophilidae		
<i>Helophorus</i> sp.	1	A
Family: Staphylinidae		
<i>Olophrum</i> sp.	1	M
<i>Holoboreaphilus nordenskiöldi</i> (Mäkl.)	4	M,Arc, L
Omaliinae indet.	2	
<i>Micralymma brevilingue</i> Schiödt.	1	X,Arc
<i>Stenus</i> sp.	7	M
<i>Lathrobium</i> sp.	4	
<i>Lordithon</i> sp.	1	M
<i>Tachinus</i> sp.	1	
<i>Tachyporus canadensis</i> Campbl.	1	M,L
<i>Tachyporus</i> sp.	1	
<i>Gymnusa</i> sp.	1	M
Genus indet.	6	
Family: Elateridae		
Genus indet.	1	M
Family: Curculionidae		
Genus indet.	4	
Order: DIPTERA		
Genus indet.	1	
Order: TRICHOPTERA		
Family: Limnephilidae		
Genus indet.	1	A
Order: HEMIPTERA		
Genus indet.	1	
Class: ARACHNIDA		
Order: ACARINA		
Family: Oribatidae		
Genus indet.	16	

Key			
A	Aquatic environment	M	Mesic environment
Arc	Arctic	SA	Sandy streamsides
EmV	Emergent vegetation at edge of standing water	(T)	Predominantly on tundra but not obligatory
L	Leaf litter	X	Xeric environment

Again, the small sample sizes and low concentration of beetles has resulted in the recovery of only 79 insect and arachnid fossils from the entire section. The 79 individuals comprise 26 taxa (including specimens only identified to family level). Twelve of these taxa were identified only to genus level and only four species were identified. Of the 79 individuals 76% belong to the order Coleoptera, 20% are Oribatidae (class Arachnida), and the other 4% are from the orders Diptera, Trichoptera and Hemiptera.

The percentages of individuals from the whole section associated with aquatic, mesic and xeric habitats are illustrated in Figure 2B. Fifty-six percent of the individuals present are taxa characteristic of mesic habitats. Those taxa that are riparian, including *Dyschirius* (Fig. 3A) and *Gymnusa* (Fig. 3K), are also included in this group. Only 7.5% of the species are characteristic of aquatic habitats and 2.5% are characteristic of xeric habitats. Twenty-five percent of the individuals could not be classified into a substrate moisture preference category.

The carabid genus *Dyschirius* is often found on sandy banks of streams, rivers and ponds. It feeds almost exclusively on the

staphylinid beetle *Bledius*, which burrows into moist sand or mud along shores of oceans, lakes, rivers, streams or in salt flats or temporarily moist soil. *Bledius* feed on algae and diatoms (White, 1983). Other taxa found in mesic environments include *Pterostichus (Cryobius)* sp. (Fig. 3C), *Olophrum*, *Holoboreaphilus nordenskiöldi*, *Stenus*, *Lordithon*, *Tachinus*, *Tachyporus canadensis* and *Gymnusa*. *Gymnusa* is a genus characteristic of boggy environments near open water. The adults and larvae of species of *Lordithon* are often associated with mushrooms, although adults are occasionally found in leaf litter or moss where mushrooms are absent. Adults of *Lordithon* are active predators of Diptera larvae (Campbell, 1982). *Tachyporus canadensis* is usually found in litter of vegetation in mesic habitats or in the nests of small mammals. Modern specimens have not as yet been found in northern Alaska (Fig. 4C; Campbell, 1979). *Holoboreaphilus nordenskiöldi*, *Olophrum* and *Stenus* are all characteristic of moist or riparian northern tundra environments.

The aquatic insect species recovered from the sediments are, in general, found in slow-flowing or standing water.

Micralymma brevilingue and *Cymindis* cf. *unicolor* are the only species represented characteristic of xeric environments. The *C.* cf. *unicolor* possibly belongs to the "undescribed" species mentioned previously.

All the species recovered from the Niguanak Uplands site are characteristic of tundra environments today.

PALEOENVIRONMENTAL INTERPRETATIONS

The predominance of aquatic beetles in the fossil beetle assemblage from the 8000-7000 B.P. sediments at Barter Island site, the laminated appearance of the deposit and the detrital nature of the organic sediment suggest that the sediments were deposited in a shallow lake or thaw lake environment. The habitat requirements of the mesic adapted beetles suggests that the vegetation surrounding the lake was probably damp sedge marsh, similar to that of thaw lake edges in the region today. The occurrence of *Dorytomus* fossils implies the presence of willow in the vegetation.

Undoubtedly, the local beetle fauna of the shallow lake is overrepresented. A few xeric beetles and the occurrence of sand layers in the deposit imply that some xeric situations were probably in the vicinity, although the number of beetles preferring xeric environments is very low.

The paleoenvironmental data from the Niguanak Uplands site from 10 400 B.P. until 1320 B.P. suggest that the section may have been associated with a mesic vegetation growing along a sandy stream bank during that interval.

With the exception of the fossil *Tachyporus canadensis* from 6000 B.P. sediments at the Niguanak Uplands site, the fossil insects recovered from both of the sections are characteristic of the northern Alaskan tundra today. The presence of *Tachyporus canadensis* beyond its present limit may suggest a warmer climate than today. However, the recovery of a single specimen is not convincing evidence, and as yet little other evidence from either beetle, pollen or macrofossil records support a warm climatic episode for this time interval. The thermophilous beetle assemblages recorded by Nelson (1982) from the 9700 B.P. sediments at Ikpikpuk River and by Matthews (1975a) from 10 900 B.P. deposits at Clarence Lagoon suggest a climatic amelioration at these times. However, the fossil beetle assemblages recovered from samples of similar age from these sections do not provide any evidence for a climate significantly different from that of today. Few fossils have been recovered thus far and the regional significance of the paleoenvironmental information from the assemblages is unknown.

Wilson (1984) suggests an increase of mean July temperatures of 2-3°C, corresponding to a *Betula* (birch) pollen peak between 10 400 and 800 B.P. The spread of birch is documented in many regions of Alaska during this period. Ager (1982) correlates *Betula* pollen zone assemblages with a shift to less continental climate in western Alaska between about 14 000 and 6000-7000 B.P. Guthrie (1982) proposes a link between the large-scale extinctions of Beringian megafauna and changes in climate during this interval. He stresses changes in the seasonal distribution of moisture, winds and temperature between 14 000 and 10 000 B.P. as having resulted in increased zonation of vegetation, wet swampy ground and deep winter snows, resulting in a marked decrease of food for ungulates.

ZOOGEOGRAPHIC IMPLICATIONS

Danks (1981) notes that the Beringian insect fauna "emerged" from refugia following the final retreat of Wisconsin glacial ice. On the arctic coastal plain, rapid climatic amelioration commenced before 13 500 B.P., the time of first establishment of balsam poplar in this region (Hopkins *et al.*, 1981). Of the beetle species represented in the Barter Island and Niguanak fossil assemblages, several have been found in late Pleistocene age deposits from eastern Beringia. The ground beetles *Notiophilus borealis* and *Pterostichus nivalis* have been found in Wisconsin and Pre-Wisconsin age sediments at Cape Deceit (Matthews, 1974) and Eva Creek, Alaska (Matthews, 1968). *Pterostichus nivalis* has also been found in Mid-Wisconsin age deposits at Igushik, southwestern Alaska (Elias, unpubl. data) and in similar age deposits from the Porcupine River, Yukon Territory (Matthews, 1975b). The staphylinid beetles *Holoboreaphilus nordenskioldi* and *Stenus kamtschaticus* have also been identified from Mid-Wisconsin age deposits along the Nuyukuk River, southwestern Alaska (Elias, unpubl. data). Morgan *et al.* (1984) have discussed possible refugia and post-glacial migration routes for *Holoboreaphilus nordenskioldi*. It appears likely that most if not all of the Barter Island and Niguanak fossil insect taxa were a part of the Beringian insect fauna of the last glacial interval, and yet over half of the identified species from these assemblages currently have holarctic distributions. Only two of the species from the fossil lists are presently restricted to Alaska, the eastern Yukon Territory and eastern Siberia (amphiberingian distribution pattern, as described by Danks, 1981). These are *Pterostichus nivalis* (Fig. 4A) and *Stenus kamtschaticus* (Fig. 4D). While the Quaternary insect fossil record of central and eastern Canada is poorly known at best, it would appear likely that many of the species preserved in the Niguanak and Barter Island deposits survived at least the Wisconsin glaciation in Beringia and spread to the east following deglaciation.

FUTURE INVESTIGATIONS

There is an obvious need for additional investigations of late Pleistocene and Holocene fossil materials on the arctic coastal plain, as well as elsewhere in arctic North America, in order to delineate patterns of climatic and biotic change. Data on past and present insect distribution are meager, due to the patchy distribution of modern collecting and the paucity of studied fossil sites. Whenever possible, interdisciplinary studies should be performed, combining information from pollen, plant macrofossils, insects, other arthropod and vertebrate fossils. Logistical problems in the Arctic make it necessary that the broadest variety of modern and fossil sampling be done at every opportunity.

ACKNOWLEDGEMENTS

Funding for this research has been provided by the Arctic Institute of North America, the Explorers Club, the American Alpine Club, Sigma Xi and the Geological Society of America. Support for the final preparation of the manuscript was provided by a grant to Elias from the National Science Foundation, DPP 8314957. The authors would like to thank Drs. D.J. Larson, J.V. Matthews, Jr., V. Puthz, and A. Smetana for their help in identification of the insect fossils.

REFERENCES

- AGER, T.A. 1982. Vegetational history of western Alaska during the Wisconsin glacial interval and the Holocene. In: Hopkins, D.M., Matthews, J.V., Schweger, C.E., and Young, S.B., eds. *Paleoecology of Beringia*. New York: Academic Press. 75-94.
- ANGUS, R.B. 1970. Revision studies of east palearctic and some nearctic species of *Helophorus* F. (Coleoptera; Hydrophilidae). *Acta Zoologica Academiae Scientiarum Hungaricae* 16:249-290.
- _____. 1973. Pleistocene *Helophorus* (Coleoptera: Hydrophilidae) from Borislav and Starunialin in the western Ukraine, with a reinterpretation of M. Lomnicki's species and a comparison with British Weichselian faunas. *Philosophical Transactions of the Royal Society of London, Series B*, 265:299-326.
- BALL, G.E. 1966. A revision of the North American species of the subgenus *Cryobius* Chaudoir (*Pterostichus*, Carabidae, Coleoptera). *Opuscula Entomologica Supplementum* 28. 166 p.
- CAMPBELL, J.M. 1978. A revision of the North American Omaliinae (Coleoptera: Staphylinidae). 1. The General *Haida* Keen, *Pseudohaida* Hatch, and *Eudectoides* New Genus. 2. The Tribe Coryphiini. *Memoirs of the Entomological Society of Canada*, No. 106. 87 p.
- _____. 1979. A revision of the genus *Tachyporus* Gravenhorst (Coleoptera: Staphylinidae) of North and Central America. *Memoirs of the Entomological Society of Canada*, No. 109. 95 p.
- _____. 1982. A revision of the genus *Lordithon* Thompson of North and Central America (Coleoptera: Staphylinidae). *Memoirs of the Entomological Society of Canada*, No. 119. 116 p.
- COOPE, G.R. 1959. A Late Pleistocene insect fauna from Chelford, Cheshire. *Proceedings of the Royal Society*, B151:70-86.
- _____. 1968. An insect fauna from Mid-Weichselian deposits at Brandon, Warwickshire. *Philosophical Transactions of the Royal Society of London, Series B*, 254:425-456.
- _____. 1977. Fossil coleopteran assemblages as sensitive indicators of climatic changes during the Devensian (Last) cold stage. *Philosophical Transactions of the Royal Society of London, Series B*, 280:313-340.
- _____. 1978. Constancy of insect species versus inconstancy of Quaternary environments. In: Mound, L.A., and Waloff, N., eds. *Diversity of Insect Faunas*. Royal Entomological Society of London Symposium 9:176-187.
- DANKS, H.V., ed. 1981. *Arctic Arthropods. A review of systematics and ecology with particular reference to the North American fauna*. Ottawa: Entomological Society of Canada. 608 p.
- ELIAS, S.A. 1985. Paleoenvironmental interpretations of Holocene insect fossil assemblages from four high-altitude sites in the Front Range, Colorado, U.S.A. *Arctic and Alpine Research* 17:31-48.
- _____. and WILKINSON, B. 1983. Lateglacial insect fossil assemblages from Logsigensee (Swiss Plateau). *Studies in the Late Quaternary of Lobsigensee* 3. *Revue de Paléobiologie* 2:189-204.
- FALL, H.C. 1923. A revision of the North American species of *Hydroporus* and *Agaporus*. Privately printed. 129 p.
- GUTHRIE, R.D. 1982. Mammals of the Mammoth Steppe as paleoenvironmental indicators. In: Hopkins, D.M., Matthews, J.V., Schweger, C.E., and Young, S.B., eds. *Paleoecology of Beringia*. New York: Academic Press. 307-328.
- HOPKINS, D.M., SMITH, P.A., and MATTHEWS, J.V. 1981. Dated wood from Alaska and the Yukon: implications for forest refugia in Beringia. *Quaternary Research* 15:217-249.
- LARSON, D.J. 1975. The predaceous water beetles (Coleoptera: Dytiscidae) of Alberta: systematics, natural history and distribution. *Questiones Entomologicae* 11:245-498.
- LINDROTH, C.H. 1948. Interglacial insect remains from Sweden. *Sveriges Geologiska Undersökning Serie C*, 492 (Årsbok 42).
- _____. 1966. The ground-beetles of Canada and Alaska, Part 4. *Opuscula Entomologica, Supplementum* 29:409-648.
- _____. 1969. The Ground-Beetles of Canada and Alaska, part 6. *Opuscula Entomologica Supplementum* 34:945-1192.
- LOMNICKI, A.M. 1894. Pleistocene owdady z Boryslawia (Fauna Pleistocena Insectorum Boryslavenium). *Wydaw Muzy Dzieduszyck* 4:3-116.
- MATTHEWS, J.V. 1968. A paleoenvironmental analysis of three Late Pleistocene coleopterous assemblages from Fairbanks, Alaska. *Questiones Entomologicae* 4:202-224.
- _____. 1974. Quaternary environments at Cape Deceit (Seward Peninsula, Alaska): evolution of a tundra ecosystem. *Geological Society of America Bulletin* 85:1353-1384.
- _____. 1975a. Incongruence of macrofossil and pollen evidence: A case from the Late Pleistocene of the northern Yukon Coast. *Geological Survey of Canada Paper* 75-1, Part B:139-146.
- _____. 1975b. Insects and plant macrofossils from two Quaternary exposures in the Old Crow-Porcupine region, Yukon Territory, Canada. *Arctic and Alpine Research* 7:249-260.
- _____. 1976. Evolution of the subgenus *Cyphelophorus* (Genus *Helophorus*, Hydrophilidae): description of two new fossil species and discussion of *Helophorus tuberculatus*. *Canadian Journal of Zoology* 54:653-673.
- MJÖBERG, E. 1916. Über die Insektenreste der sog. "Harnogytija" im nordlichen Schweden. *Sveriges Geologiska Undersökning Serie C*, 268 (Årsbok 9).
- MORGAN, A.V., MORGAN, A., and MILLER, R.F. 1984. Range extension and fossil occurrences of *Holoboreaphilus nordenskiöldi* (Mäklin) (Coleoptera: Staphylinidae) in North America. *Canadian Journal of Zoology* 62:463-467.
- NELSON, R.E. 1982. Late Quaternary environments of the western Arctic Slope, Alaska. Ph.D. thesis, Multidisciplinary Quaternary Paleocology, University of Washington. 90 p.
- SCHWERT, D.P., ANDERSON, T.W., MORGAN, A., MORGAN, A.V., and KARROW, P.F. 1985. Changes in Late Quaternary vegetation and insect communities in southwestern Ontario. *Quaternary Research* 23:205-226.
- WHITE, R.E. 1983. *A Field Guide to the Beetles of North America*. Boston: Houghton Mifflin Company. 368 p.
- WILSON, M.J. 1984. Modern and Holocene environments of the North Slope of Alaska. M.A. thesis, Institute of Arctic and Alpine Research, University of Colorado, Boulder. 253 p.