A PALEOENVIRONMENTAL ANALYSIS OF
THREE LATE PLEISTOCENE COLEOPTEROUS ASSEMBLAGES
FROM FAIRBANKS, ALASKA

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Fossils of beetles (Order Coleoptera) and other insects are abundant in Pleistocene silts and peats from interior Alaska. Three Wisconsin age silt samples from the Eva Creek exposure near Fairbanks, Alaska were examined for their content of fossil insects. A study of the coleopterous fauna -- and primarily the carabid (ground beetle) portion of the coleopterous fauna -- of each of these samples revealed that at the time of their deposition the environment of Fairbanks, Alaska was similar to alpine tundra at higher elevations or coastal tundra in other parts of the state. This conclusion concerning the paleoenvironment of lowland interior Alaska agrees with conclusions reached by the author and other workers after examination of fossil pollen spectra and fossil mammals from the Eva Creek mining cut and similar exposures near Fairbanks. Minor variations among the three coleopterous assemblages are provisionally related to local environmental differences rather than to changes of the macroclimate of interior Alaska during Wisconsin time.

Like the Quaternary peats and organic silts of Europe, the frozen colluvial silts exposed by placer gold mining in Alaska contain abundant fossils of insects -- predominately beetles (order Coleoptera). In Europe fossil insects have created interest for a long time (see Frey (1964) for a review of the early literature); however, only within the last ten years have such fossils become important for the study of paleoenvironments. Well preserved fossil insects occur in silts and peats in Alaska and Canada yet no paleoenvironmental studies such as those by G. R. Coope in England (Coope 1965) have thus far been published. This paper represents an initial attempt to interpret Pleistocene environments in Alaska using the evidence derived from insect fossils.

Previous Investigations

The success of Pleistocene insect studies in Europe is largely due to the efforts of G. R. Coope and his associates F. E. Shotton and P. J. Osborne at the University of Birmingham, England. This team has gained valuable insight to the glacial, interstadial, and interglacial climates of England since the mid-Pleistocene by comparing the former distributions of fossil Coleoptera with the distributions of their modern counterparts (Coope 1962; Coope 1965, general summary; Coope et al. 1961; Shotton and Osborne 1965). Similar studies have been carried out at Cambridge University by R. Pearson (1962, 1963).

Coope began his studies "blissfully unaware" of the doubts which many entomologists harbored concerning both the geologic longevity of insect species and the possibility of making specific identifications using only single skeletal parts or fragments thereof (Coope 1965). His work was to reveal the fallacy of this skepticism. Nearly all species of Coleoptera have a longevity which greatly exceeds the length of the late Pleistocene and specific identifications often are possible when the morphology of the fossil is compared in detail with modern museum speci - mens. These two facts form the base for all other studies of fossil insects including this one; however, before identifications of fossil Coleoptera can lead to paleoenvironmental conclusions, two other conditions must be satisfied: the classification of the more important insect groups (in this case certain families of Coleoptera) must be sound, and the ecology or at least the present distribution of the taxa represented by fossils must be known.

Some beetles are of more value than others as indicators of past environments. A fossil of a stenophagous, phytophagous species may be of value in indicating the presence of a certain plant; however, it will yield little direct information about the macro-environment in which the insect originally lived. The family Carabidae (ground beetles) provides the greatest amount of environmental information since its members are predators living in most instances on the surface of the ground and thus under the direct influence of the macro-climate. Some carabid beetles are even restricted to certain types of soils and sediments.

Implied in the use of assemblages of fossil insects to interpret Pleistocene environments is the assumption that the habitat requirements of the species represented by fossils have remained stable. Some workers have considered this assumption to be unacceptable. Greenslade (1965) has cited evidence that certain species of carabid beetles do occupy entirely different habitats in different areas, and he doubts that the ecological requirements of some species can be considered as stable as have been assumed (Greenslade 1965, written communication). Several of the North American carabids, e. g. *Carabus chamissonis* Fisch. and *Nebria nivalis* Payk. possess ecologically disjunct distributions which might be interpreted as being evidence of a great variability in habitat requirements. In such cases, where for example a species common on the tundra is occasionally found in woodland areas, the explanation for the anomaly is best sought by looking for the possibility of accidental dispersal of individuals to areas which only locally fulfill the habitat requirements of the species. Lindroth has invoked this reasoning to explain the occurrence in the coniferous zone of Norway of a colony of the carabid *Amara alpina* Payk., normally an obligate tundra inhabitant (C. H. Lindroth 1965, written communication). Problems of this sort need not prohibit the use of insect fossils as long as the ecology of the species is interpreted in a broad sense and conclusions are based on groups of fossils rather than single specimens. Yet some fossil assemblages still possess anomalous characteristics. For example, studies in England reveal insect assemblages which contain a mixture of now disjunct species (Coope et al. 1961), but in all such cases the assemblages possess an internal consistency which makes the possibility that some species have changed their

ecologic requirements the least likely of several alternative explanations (Coope 1965).

Physical Environment and Biota of Interior Alaska

Fairbanks is located in interior Alaska at the south side of the Yukon-Tanana Upland and adjacent to the Tanana River (fig. 1). The climate is characterized by short, warm summers, cold winters and meager precipitation. The mean annual temperature is -3.28 C (26.1 F) and mean annual precipitation is 29.4 cm (11.6 inches) (Péwé and Paige 1963). Despite a mean annual temperature below 0 C, permafrost in the Fairbanks area has a discontinuous distribution, which has a strong effect on drainage and in turn on local plant communities (Péwé 1966a, Péwé et al. 1965). South facing, well drained slopes support stands of white spruce, birch, and quaking aspen while poorly drained north facing slopes and valley bottoms support more open communities of black spruce, willows, larch (on the poorest drained sites), and sedges (Péwé et al. 1965). Coniferous trees and other upright arboreal species are generally absent above an elevation of 1000 meters.

In Alaska, unlike central Canada, the division between tundra and closed woodland is a complex transition zone. Below the upper limit of conifers in Alaska is an open woodland, usually accompanied by a thick cover of mosses and lichens. This area, is often referred to as the Hudsonian Zone (after Merriam's lifezones) by entomologists (Mason 1956, 1965). Beyond this zone is the tundra, the lower parts of which in interior Alaska are quite shrubby. The tundra in northern Alaska, such as at Barrow (fig. 1), is characterized by a reduced number of plant taxa and a paucity of shrub-like arboreal species (Britton 1966). This type of tundra might be considered equivalent to the "true Arctic tundra" of the Canadian literature or "*regio alpina media*" in Scandinavia (Mason 1965).

A peculiar situation exists in the distribution of part of the Alaskan insect fauna. Whereas in eastern Canada the boundary between forest and tundra is as sharp with respect to insects as plants (Brown 1965), in Alaska members of the Hudsonian insect fauna extend well beyond coniferous treeline. For example, Brown (1965) has described the coleopterous fauna at Umiat (fig. 1) as "primarily Hudsonian", and Mason (1956) considers the insect fauna of all the treeless areas south of the north portion of the Seward Peninsula and including the Aleutian Islands to be Hudsonian in character. Lindroth (1961, 1963b, 1966) in his monographs on the carabid beetles of Canada and Alaska seldom uses Merriam's lifezones. Apparently he considers coniferous treeline to be an important ecologic boundary with the understanding that the distribution of some species seems to be more or less independent of it.

The Origin of the Frozen Silts in the Fairbanks Area

Although interior Alaska was only locally glaciated during the Pleistocene, heavy glaciation in the Alaska Range and the Brooks Range affected the interior indirectly by changing the fluvial regimes of its two major trunk streams, the Tanana and the Yukon Rivers. During periods of marked glacial advance and retreat in the Alaska Range, the Tanana

River at Fairbanks was an outwash stream with a wide, sparsely vege-
tated, silty flood-plain. Silt removed by wind from the flood-plain was
deposited on the hills near Fairbanks as loess, so that today silt partially
fills the valleys and mantles the slopes to depths of more than 100 feet
(Péwé 1955, 1966a). The loess of the valleys is different from that on
the slopes. The valley silt is bedded, perennially frozen, highly organic,
and fetid (which explains the miner's term for it -- "muck"). The upland
silt facies like the loess of the mid-continent of North America is mas-
sive, oxidized, buff brown in color, and compared to the valley bottom
facies, quite unfossiliferous. Péwé (1966a, et al. 1965) believes that
the "muck" facies is colluvium formed by redeposition of loess from the
slopes.

     Most exposures of frozen "muck" near Fairbanks have been created
by placer gold mining. The muck overlies early Pleistocene gravels
that contain gold; consequently, the overburden of silt must be hydraul-
ically removed before actual mining can begin. An operation of this sort
creates a mining "cut" with walls of frozen silt. One such mining cut is
at Eva Creek, ten miles west of Fairbanks (fig. 1). During the summer
of 1964 R. D. Guthrie (University of Alaska) and I made extensive fossil
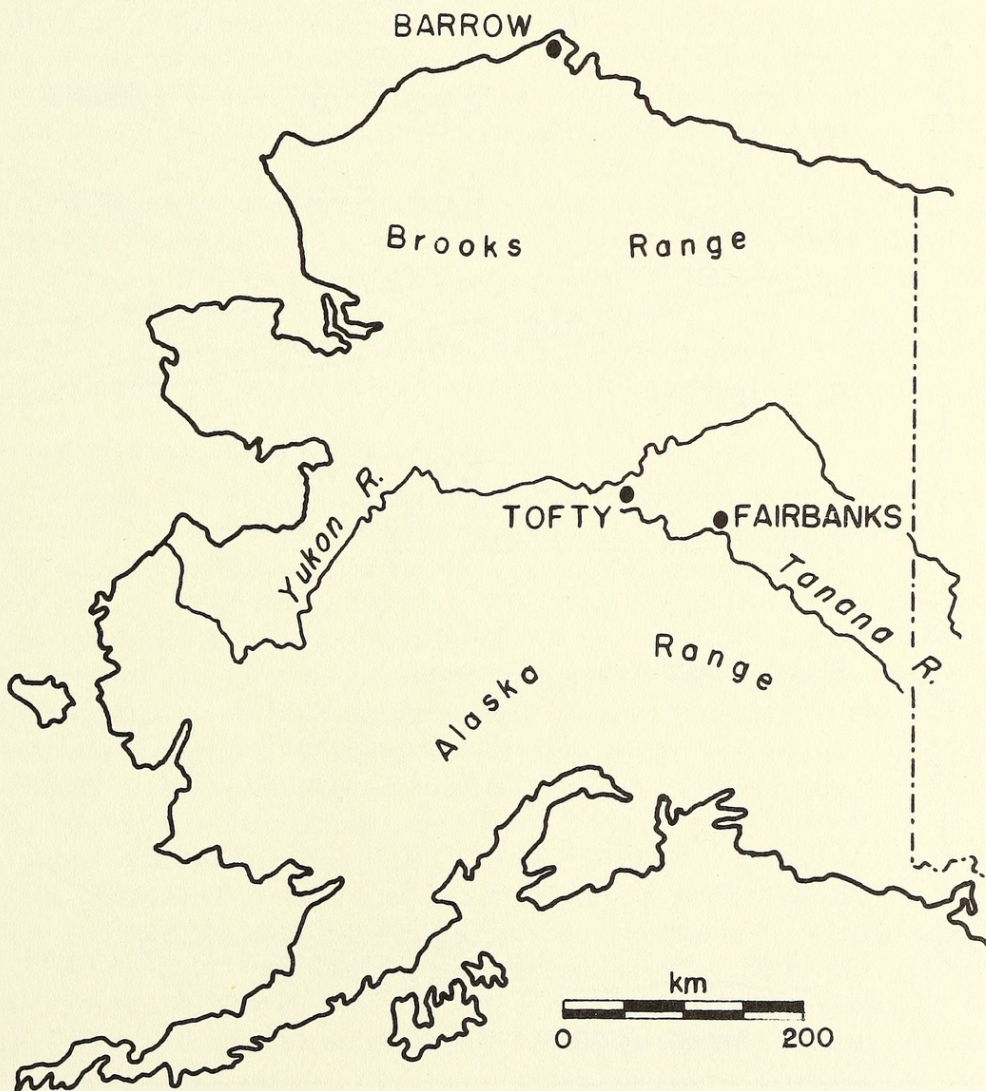collections at this site.

Fig. 1. Alaska. Localities mentioned in text.

The Eva Creek cut is of particular significance because it exposes all of the silt units which Péwé has described for the Fairbanks area (Péwé et al. 1965 and unpublished MS); however, since this report involves only samples from Wisconsin age sediments, details of the other stratigraphic units will not be discussed.

The thickness of the entire silt exposure at Eva Creek is approximately 35 m of which 11 m are of Wisconsin age. The Wisconsin silt is overlain by a Holocene silt unit containing, at some localities, buried forest beds (fig. 2). It rests unconformably on silt thought to be of Illinoian age (Péwé 1965, personal communication) (fig. 2). This unconformity is related to a long period of thaw and erosion (Péwé 1966a) probably representing the Sangamon interglacial.
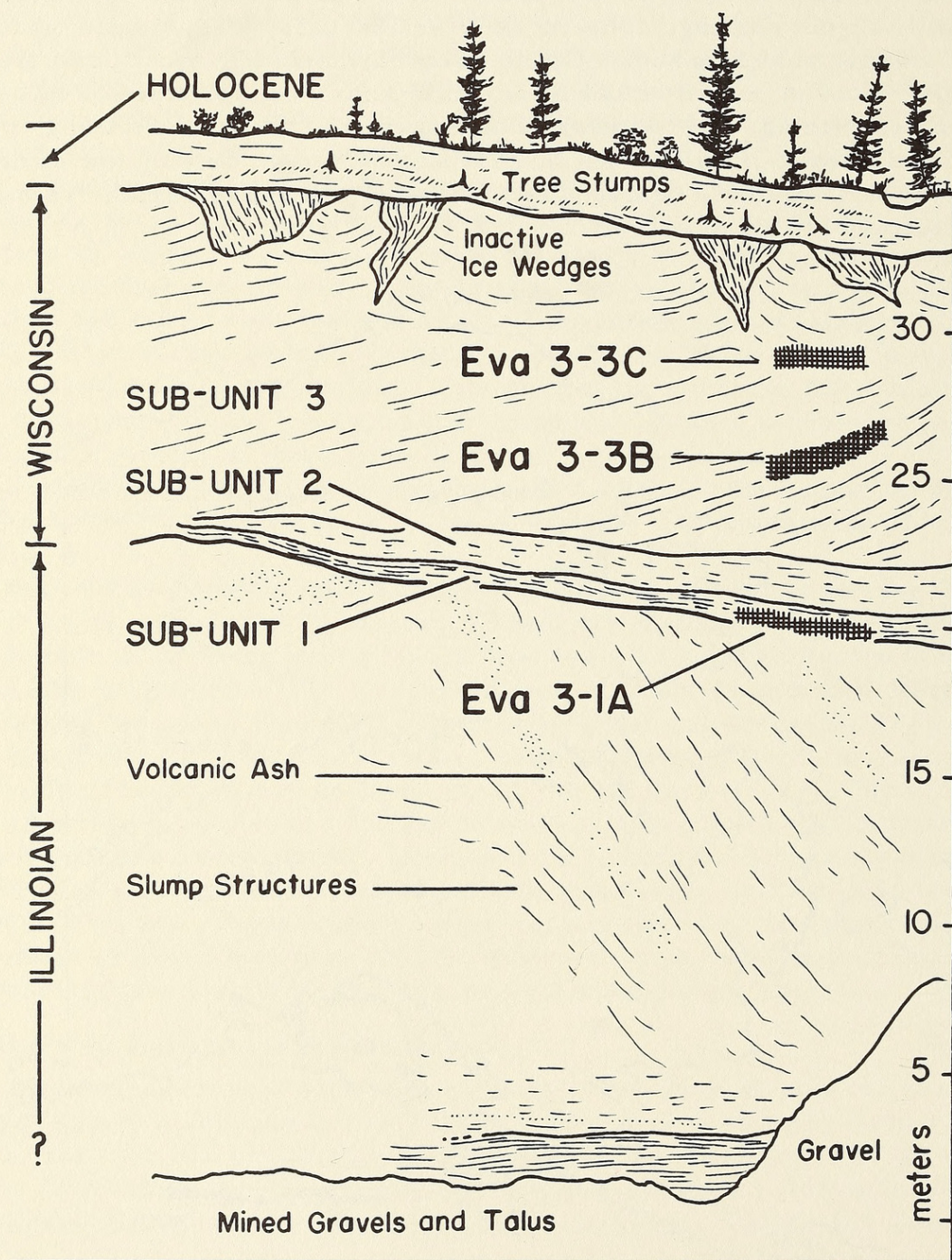

Fig. 2. Eva Creek Exposure, 1965.

Sample Localities within the Wisconsin Unit (Eva Creek)

The Wisconsin portion of the Eva Creek exposure may be divided into three sub-units (fig. 2) which are differentiated by color, ice content, and organic content. Some of these sub-units are probably only of local extent.

Sample Eva 3-1A comes from the basal two feet of Wisconsin silts. It is part of sub-unit 1 which is characterized by an extremely high content of wood (including a few stumps of small trees) and other plant fragments, most of which seem to be from mosses. This unit thickens toward the axis of the north-south trending valley and dips in a down valley direction. M.A. Geyh of Niedersächsisches Landesamt Für Bodenforschung, Hanover, has attempted C-14 analysis of a spruce stump (Hv. 1328) from several feet above the sample interval, but still within sub-unit 1. A final date is not yet available, but Geyh states (1967, written communication) that the first tests indicate an age greater than 56,900 years B.P. This date may not, however, indicate the time of deposition of the sediments in sub-unit 1 since the tree stumps in that unit could have been derived from older sedimentary units (Sangamon forest bed?).

A second sub-unit -- not sampled -- lies immediately above sub-unit 1. It consists of greenish, inorganic silt with a high content of seam ice (Taber ice, sirloin ice).

Sub-unit 3, from which samples 3-3B and 3-3C were taken is the thickest of the three sub-units and most like the dark brown Wisconsin "muck" at other frozen silt exposures in the Fairbanks area. Sample 3-3B was taken from a level 5.5 m above the base of the Wisconsin unit; sample 3-3C was collected 3.7 m above 3-3B. The only criteria used for selection of the two samples from sub-unit 3 was that they come from different levels in the sub-unit. A radiocarbon date of 24,400 ± 650 years B.P. (I-2116) was obtained on wood from the site of sample 3-3C. No radiocarbon date is available for 3-3B, but its position with respect to 3-3C and 3-1A indicates an age greater than 24,400 years B. P. and less than the age of the early Wisconsin sediments of sub-unit 1.

Sampling Procedure and Processing Notes

The insect fossils reported on in this paper were collected in conjunction with a search for small mammal fossils. The procedure followed for each sample was to take several thousand pounds of silt from a two foot interval at the exposure. This was then screened through 40 mesh per inch screens. A portion of the organic extract that remained on the screens was then processed for fossil insects. Since insect fossils are very abundant often only a small portion of the total residue from a sample was required in order to obtain a large number of specimens. This portion of the residue was washed through 80 mesh per inch screens in order to remove any remaining silt.

A process developed by G.R. Coope (1961) was used to concentrate the insect fossils in order that they might be more readily extracted from the organic residue. In this process, the residue remaining in the 80 mesh screens is immersed in light weight oil. When the oil soaked mass of residue is placed in hot water many insect fragments rise to the surface. The concentration of insect fossils obtained in this manner is

stored in alcohol and later examined with a binocular microscope. In-
sect fossils are mounted on slides similar to those used in the study of
Foraminifera. This facilitates storage of the fossils, prevents their
warping when they have dried, and allows detailed examination under
high magnifications.

Identification Notes

The most striking feature of the faunal list (table 1) is the imbalance
in the level of identifications. With few exceptions specific determinations
were possible only among the carabid fossils. Generic determinations
must suffice for the other families because of my unfamiliarity with many
of these families and the real scarcity of knowledge concerning the col-
eopterous fauna of Alaska. Generic determinations of beetles often have
little paleoenvironmental value inasmuch as few genera are restricted
to specific habitats. Tabulation of the identified genera within each fam-
ily and especially a recognition of the number of specimen types (species?)
within each genus nevertheless permits an estimate of the total number
of taxa present in each fauna. For the same reason, fossils which could
not be identified to the familial or generic level are listed in table 1.

Were it not for the fact that the ecology and taxonomy of the carabid
beetles of Alaska are now reasonably well documented, a paleoenviron-
mental analysis such as the one presented here would be impossible.
Except for fossils of curculionid beetles (weevils) the carabids are the
most abundant group within each of the fossil assemblages. Fortunately,
the anatomical parts which are of particular value in carabid identifi-
cation -- the pronotum, head, and elytra -- are often well preserved
in organic silts and peats.

Most of the carabid fossils can be identified using C. H. Lindroth's
detailed descriptions (Lindroth 1961, 1963b, 1966) and comparative mu-
seum specimens. Determinations within one group, however, the sub-
genus *Cryobius* of the genus *Pterostichus*, are very difficult. Specific iden-
tification of members of *Cryobius* is critical in this study because of the
importance of *Cryobius* species in present arctic and subarctic habitats.
A recent revision of *Cryobius* by G. E. Ball (1966) has placed the classifi-
cation of the group on a firm basis, but the similarity among members
of certain species pairs causes specific determinations of some fossils
to be very uncertain. Indeed, to identify many living specimens to the
specific level requires an examination of the median lobe of the male
genitalia which is rarely encountered as a fossil in Pleistocene silts.

I have hesitated to assign specific names to many of the *Cryobius* fos-
sils, this being especially the case where the fossils (pronota) were
broken or otherwise damaged. Ball (1966) has divided the species of the
subgenus *Cryobius* into species groups; therefore, in those cases in which
I have not been able to make a specific determination, I have, neverthe-
less, carried the identification as far as the species group level. Cer-
tain of the species groups are restricted to specific habitats, and thus
yield definite paleoenvironmental information. For example, the mem-
bers of the *similis* subgroup are largely tundra inhabitants. A determin-
ation to the *ochoticus* subgroup level has certain special implications. One
of the species of this group, *P. gerstlensis* Ball, may be eliminated from

consideration because it is quite distinct and readily identified. Thus, an *ochoticus* subgroup determination implies that *P. gerstlensis* Ball, a woodland inhabitant, has been ruled out as a possibility. All the remaining members of the group are tundra residents (Ball 1966). This is not the place to consider in detail the pitfalls of identification of fossil *Cryobius* specimens, but because the *Cryobius* identifications are so important for the conclusions reached in this paper and because my confidence in the specific identifications varies, I have indicated in table 1 with a question mark (?) those determinations which are suspect.

TABLE 1. Coleopterous fauna of Eva Creek samples 3-1A, 3-3B, 3-3C.

Taxa	Number of individuals			Ecology*
	3-1A	3-3B	3-3C	
Carabidae				
Carabus truncaticollis Eschz.	1		1	A
Carabus chamissonis Fisch.	2		1	Be
Notiophilus sp.	3			
Notiophilus semistriatus Say	2		3	BeF
Notiophilus borealis Harr.	2			BeF
Diacheila polita Fald.	6			BeF
Elaphrus riparius L. or *pallipes* Horn	1			
Dyschirius sp.	1			
Dyschirius nigricornis Mtsch.	1			BeF
Bembidion sp.			4	
Bembidion (Plataphodes) sp.		1		
B. (Plataphodes) arcticum Lth.	1			A
B. (Peryphus) sp.	2	2	5	
B. (Peryphus) grapei Gyll.			1	BeF
B. (Peryphus) dauricum Mtsch.	1	9	9	A
Pterostichus (Cryobius) sp.	18	2	19	
P. (Cryobius) pinguedineus grp.	5	3	2	
P. (Cryobius) ochoticus subgrp.		6	9	
P. (Cryobius) soperi Ball	5	4	4	Bx
P. (Cryobius) kotzebuei Ball	2	6	27	Bx
P. (Cryobius) tareumiut Ball	9	2		Bx
P. (Cryobius) gerstlensis Ball		2		CF
P. (Cryobius) chipewyan Ball	1?			
P. (Cryobius) similis subgrp.	3		3	
P. (Cryobius) similis Mann.	4			Ba
P. (Cryobius) parasimilis Ball	3	1		A
P. (Cryobius) pinguedineus Eschz.	2	1	2	BaF
P. (Cryobius) auriga Ball	1?		1?	

TABLE 1 (cont.).

Taxa	Number of individuals			Ecol- ogy*
	3-1A	3-3B	3-3C	
P. (Cryobius) ventricosus grp.	2			
P. (Cryobius) ventricosus Eschz.	8	1	4	Be
P. (Cryobius) caribou Ball		1		A
P. (Cryobius) brevicornis grp.	15	7	12	
P. (Cryobius) brevicornis Kby.	11	6	11	BaF
P. (Cryobius) mandibularoides Ball	2?	2?	2?	
P. (Cryobius) nivalis Sahlb.	34	6	5	A
P. (Stereocerus) haematopus Dej.	2	4	1	Ba
Agonum quinquepunctatum Mtsch.	1			CF
Amara alpina Payk.	3	5	5	A
Cymindis sp.			1	
Trichocellus porsildi Brown	2		6	Bx
Genus sp.	1	1		
Dytiscidae				
Colymbetes sp.			1	
Staphylinidae				
Staphylininae				
Acylophorus sp.	1		1	
Paederinae				
Lathrobium sp.	9			
Omaliinae				
Olophrum sp.	30		4	
Micralymma sp.	4	36		
Tachyporinae				
Tachinus sp. A	7	2	1	
Tachinus sp. B	2	5		
Genus sp.			1	
Steninae				
Stenus sp. (A and B)			6	
Stenus sp. A	2			
Stenus sp. B	2			
Dianous sp.		7		
Aleocharinae				
Genus sp.			8	

TABLE 1 (cont.).

Taxa	Number of individuals			Ecol- ogy*
	3-1A	3-3B	3-3C	
Silphidae				
Silpha trituberculata Kby. or sagax Mann.			1	
Scydmaenidae				
Veraphis sp.			2	
Scarabaeidae				
Aphodius sp. A	1			
Aphodius sp. B	1	1	35	
Byrrhidae				
Curimopsis sp.	1	17	2	
Caenocara sp.			1	
Simplocaria sp.	6			
Morychus sp. A	1	1	2	
Morychus sp. B		1		
Elateridae				
Genus sp. A	1		2	
Genus sp. B	1		2	
Genus sp. C		1		
Cryptophagidae				
Cryptophagus sp. A			2	
Cryptophagus sp. B			1	
Chrysomelidae				
Chrysolina sp. A	1	1	2	
Chrysolina sp. B		1		
Curculionidae				
Lepyrus gemellus Kby.	1	4	1	
Genus spp.	68	165	240	
	2 spp.	5 spp.	5 spp.	
Family and Genus unknown				
Genus sp. A	1			
Genus sp. B	2	13	1	
Genus sp. C	3			
Genus sp. D	2		1	
Genus sp. E	1			

TABLE 1 (cont.).

Taxa	Number of individuals			Ecology*
	3-1A	3-3B	3-3C	
Genus sp. F	1			
Genus sp. G	1			
Genus sp. H	1			
Genus sp. I	1			
Genus sp. J	2	2	5	
Genus sp. K	1	1	3	
Genus sp. L			16	
Genus sp. M			2	
Genus sp. N			4	
Genus sp. O			1	
Genus sp. P			1	
Genus sp. Q			1	
Total individuals	312	330	488	

Ecologic class symbols are explained in the text.

Notwithstanding the proven longevity of many coleopteran species, the similarity of some of the species of the subgenus *Cryobius* seems to indicate relatively late divergence; in fact, Ball (1963a) in his first zoogeographical paper on the group suggested that speciation may have occurred as late as Wisconsin time. Now (Ball 1966) he feels that the last episode of taxonomic splitting occurred earlier than 90, 000 years ago, but he emphasizes that this must be supported by fossil evidence of which there was little available when he published the revision. Fossil evidence substantiating Ball's statements on speciation within *Cryobius* would add strength to the assumption that all of the *Cryobius* fossils in the three Eva Creek samples represent extant species. Such fossil evidence does exist, but not from Eva Creek.

A peat sample from the McGee cut (fig. 1) 100 miles west of Fairbanks in the Tofty mining district has yielded partially articulated specimens of carabid beetles, particularly *Cryobius*. In many specimens the male or female genitalia are preserved allowing positive specific identifications. The following species of the subgenus *Cryobius* were identified: *P. (Cryobius) similis* Mann., *P. (Cryobius) parasimilis* Ball, *P. (Cryobius) pinguedineus* Eschz., *P. (Cryobius) brevicornis* Kby., *P. (Cryobius) nivalis* Sahlb., *P. (Cryobius) mandibularoides* Ball, and *P. (Cryobius) tareumiut* Ball. Of these *parasimilis* and *similis* are thought by Ball (1966) to have been among the most recent to evolve. The sample comes from the base of the Wisconsin portion of the exposure (D. M. Hopkins 1966, personal communication). A radiocarbon analysis indicated an age greater than 39, 900 years B. P. (I-2248) for the fossiliferous horizon.

The evidence from the McGee cut thus indicates that *P. parasimilis*

Ball and *P. similis*   Mann. along with a few other species of *Cryobius* were in existence during early Wisconsin time. This evidence certainly does not confirm all of Ball's (1966) phylogenetic speculations concerning the time of evolutionary divergence within the subgenus *Cryobius*, but it does show that he was correct in those instances for which fossil evidence is now available. This enhances the probability that fossils of *Cryobius* in the oldest Wisconsin sample at Eva Creek do represent extant taxa. Unpublished work by the author dealing with Alaskan insect faunas much older than those reported on in this paper indicates that the other carabid taxa in the faunal list (table 1) have geologic longevities which greatly exceed the age of the oldest sample considered here (Eva 3-1A).

Derivation of Quantitative Data

In order that each of the three faunas might be compared quantitatively, the number of individuals represented by each taxon was tabulated. This number indicates the maximum number of individuals which could be represented by summing one diagnostic fragment (right elytron, pronotum, etc.). For example in Eva 3-3B the staphylinid genus, *Micralymma*, is represented by 36 heads. A tabulation of the elytra (seven right, six left) can account for only seven individuals. Thus, the greatest number of individuals (36) is represented by heads. In Eva 3-3C the staphylinid genus, *Stenus* is represented by six pronota, but an examination of *Stenus* elytra, which represent fewer than six individual beetles, indicates that two species are probably present. Therefore, the faunal list indicates six individuals of *Stenus* including at least two species.

The particular anatomical part that was used for tabulation varied from one group to another. The pronotum was used for all members of the genus *Pterostichus*, the elytra for members of the genus *Bembidion*, and in one exceptional case, *Silpha* sp. from Eva 3-3C, the scutellum was diagnostic. Only elytra were used for the tabulation of miscellaneous species. In many cases an elytron is represented by only a basal or apical fragment; therefore, tabulations were weighted so that two such fragments from the same beetle would not be counted as two individuals.

Coope (1961) has questioned the validity of using quantitative information for making faunal comparisons. His argument, based on tests, is that human bias is introduced during the extraction of fossils with the microscope. The biggest and most brightly colored species are often represented by the most fossils, while the small species are reciprocally under-represented. At Eva Creek this type of bias does not seem to be important. The largest and most spectacular species are often represented by very small fragments. Fortunately, such species (*Carabus trucaticollis* Eschz. is a good example) may be identified by examination of the small fragments, but very little may be said about individual abundance. Ten fragments could as easily have come from one insect as ten, but the faunal list must record the minimum number -- 1. The same situation applies to other large beetle fossils from the Eva Creek samples. Small fossils often are well preserved, and easily located at magnifications of 20X. While I do not claim that human bias of the type described by Coope (1961) is absent in this study, I do not believe that it is sufficiently significant to prohibit the use of quantitative data.

Ecologic Classification of Fossils

In order that the environment represented by each fossil assemblage can be discussed those fossils which have been positively identified to species (Carabidae) are assigned to ecologic classes A, B or C according to the habitat preference of their living counterparts (see table 1). The letter A indicates that a species is an obligate tundra inhabitant. Some of those species listed in table 1 do not now occur on the alpine tundra of interior Alaska, but this is probably an artifact of limited collecting.

The letter B indicates that a particular species occurs both in tundra and woodland areas. The suffix "e" is attached when it is known that the species prefers "open" environments when it occurs below coniferous treeline. For example, I have collected *Diacheila polita* Fald. in the Fairbanks area. It is most often found on the tundra, but at Fairbanks it occurs in a *Carax* bog -- an open (treeless) habitat. In addition to those species such as *Pterostichus (Cryobius) trevicornis* Kby. which occur both in closed boreal forest and on tundra (Ba), class B includes many species which are known to occur on tundra but about which there is some doubt concerning their occurrence at lower elevations. These cases of uncertainty are designated by the suffix "x".

The species placed in class "C" are those which have never been collected above the limit of coniferous treeline. One of these species, *Agonum quinquepunctatum* Mtsch., occurs in wet, open habitats (bogs). Species which have been collected at Fairbanks or nearby at the same elevation are indicated in table 1 by the letter "F".

Fossil Evidence, excluding Insects, from Eva Creek

Other fossil evidence is available with which information yielded by fossil insects may be compared. Large mammal fossils from many late Pleistocene localities near Fairbanks include extinct taxa such as *Mammuthus* sp., *Equus* sp., *Camelops* sp., *Bison priscuc* (*sensu lato*) and others which presumably required an open grassy habitat (Guthrie 1968, Péwé 1966a) as well as extant taxa -- *Rangifer tarandus, Ovis nivicola*, and *Ovibos moschatus* -- that are now restricted to alpine or coastal tundra (Péwé 1966a). Small mammal fossils have been collected from the three sample intervals which yielded the coleopterous faunas reported in this paper. They, like fossils of large mammals indicate not only that the Wisconsin "mucks" of the Fairbanks area were deposited in an open, largely treeless environment, but specifically that the three samples (3-1A, 3-3B, 3-3C) at Eva Creek represent such an environment. Fossils of *Dicrostonyx* sp. and *Microtus gregalis* have been found in the three sampled intervals (Guthrie in press). Both of these microtines are now found on the tundra; however, neither occurs on the alpine tundra of the Tanana hills near Fairbanks.

Fossil pollen was extracted by the author from the silts of each of the three sampled levels. The pollen spectra from the three localities (table 6) are similar and indicate a treeless environment -- an environment too cold to support abundant dwarf birchs, alders, and ericaceous shrubs (Matthews MS).

Thus, fossils of vertebrates and pollen indicate that at the time dur-

which the three insect assemblages accumulated, treeline was significantly lower in interior Alaska. This conclusion will be compared with the environmental inferences derived from an analysis of the three fossil Coleoptera assemblages.

Discussion

The results presented in table 1 may be analyzed in two ways. One may compare the taxonomic content of each of the assemblages with the taxonomic composition of various contemporary Alaskan environments. The contemporary environment which most closely matches that of the fossil assemblage is judged to be the one that represents the paleoenvironment in which the fossils lived. This is the method that Coope has used in the analysis of fossil assemblages in England. Table 2 represents such an analysis using only specifically identified beetles from each assemblage. It is immediately apparent that the number of taxa available for a comparison of this type is small (maximum of 21 species). This results from the fact that specific determinations were possible only within the family Carabidae. In order to counter the effect of this small sample size I have chosen to compare the three assemblages quantitatively. The validity of the quantitative data presented in table 1 has been discussed in a previous section.

A quantitative approach similar to that used with the qualitative data (table 2) would be desirable. Unfortunately this is impossible since it requires that carabid faunas of the major environments in Alaska have been analyzed quantitatively. No such studies have been attempted. In lieu of such information I have proceeded on the basis of several assumptions relating to the way in which a fossil assemblage might theoretically reflect the environment in which it was deposited. First, in the three assemblages of fossils, the numerically dominant species will be those which resided at the site of deposition. A minority of the fossils will represent beetles which lived in habitats other than those existing near to or at the site of deposition. Whether this latter group of fossils is in fact a minority depends on the former diversity of the beetle fauna at the site of deposition, the powers of dispersal of species in former neighboring habitats, and the proximity of those habitats to the site of deposition. For example, a community proximal to the site of deposition of a fossil assemblage and possessing a great number of actively flying beetles might have contributed more fossils to the assemblage than a community with a beetle fauna composed of non-flyers. The beetles from the neighboring community might well form the majority of the members of a fossil assemblage if the fauna of that community was taxonomically diverse and numerically abundant relative to the fauna at the site of deposition of the sample. It is unlikely that a large fraction of the carabid portion of each Eva Creek assemblage consists of fossils of such allochthonous beetles, since the dominant element of each assemblage is of the subgenus *Cryobius* (genus *Pterostichus*), all species of which are constantly flightless.

Interpretation of the fossil assemblages from Eva Creek is made more complex by the retransported or colluvial character of the fossil bearing sediments. Theoretically, insects which lived in habitats at

higher elevations on the slopes near Eva Creek and which were penecon-
temporaneous with insects at low elevations could have been retransported
with the silt into the valley bottom. Also, since deposition of sediments
in one area, usually implies erosion in another, some of the fossils in
each assemblage may have been derived from older sediments. Many
insect fossils would probably not survive this type of redeposition es-
pecially when the sediments from which the fossils were derived were
much older geologically than the sediments in which they were finally
deposited. Contamination of the fossil insect assemblages by penecon-
temporaneous mixing during accumulation of the assemblage can be eva-
luated only indirectly -- by examining the consistency of the environ-
mental implications of each assemblage.

TABLE 2. Abundance of species of Carabid beetles in each ecologic class.

Assemblage	Ecologic Class*						Total of A, B, and C
	A	Σ B	Be	Ba	Bx	C	
Eva 3-3C	4**	10	4	3	3	0	14
Eva 3-3B	5	7	1	3	3	1	13
Eva 3-1A	6	14	6	4	4	1	21

*   See text for explanation of class symbols.
** Number of species.

    Table 3 shows the relative abundance of beetles in each ecologic
class. The dominance of class B is partly related to its containing species
about which extralimital woodland occurrences are in doubt (class Bx).
If more detailed ecologic information were available, class A would no
doubt be larger and class Bx smaller. Nevertheless, the remarkable
feature of table 3 is the preponderance of fossils in classes A and B and
the paucity of fossils in class C.
    To duplicate any of the fossil assemblages with a collection of mod-
ern carabid beetles, one would have to go to a locality near to or above
the altitudinal or geographic limit of coniferous forest. A similar con-
clusion may be derived from the taxonomic analysis (table 2). But a
statement that each of the assemblages represents a tundra environment
might be challenged on the premise that all of the obligate tundra fossils
(group A) are allochthonous -- having been included in the fossil assem-
blages by retransportation with the silt from higher elevations. If this
were the case, the fossil assemblages might well have formed below
treeline in the Hudsonian Zone. This is clearly not the case since the
carabid fossils which would be expected to represent that zone are not
present in any of the fossil assemblages. For example, *Pterostichus adstrictus*

Eschz., *Calathus ingratius* Dej., *Asaphidion yukonense*·Wick., *Harpalus fulvilabris* Manh. *Bembidion mutatum* G. and H., *Carabus vietinghoffi* Adams, and *Trichocellus cognatus* Gyll., are common elements of the woodland carabid fauna of Alaska. Each of these beetles is morphologically distinct, they occur in a variety of habitats although most prefer open situations, and most of them range on to the tundra in parts of Alaska (Lindroth 1953, 1961, 1963a, 1963c, 1966). If any of the assemblages accumulated in a habitat which was below or near treeline, fossils of some of these species would be expected. They do not occur in any of the Eva Creek assemblages; therefore, all three of the assemblages no doubt represent a tundra environment. The position of coniferous treeline must have been below the present elevation of Eva Creek (230 m - 750 feet) during that part of Wisconsin time when each of the assemblages formed, and the Fairbanks area was largely, if not completely, treeless.

This conclusion agrees with the alternate fossil evidence presented earlier. The colder climate which must have been responsible for the lowered treeline is also indicated by inactive or remnant ice wedges in the sediments at Eva Creek. Currently such features are forming only in those areas where the mean annual temperature is at least 2 C colder than the present mean annual temperature of Fairbanks (Péwé 1966b).

TABLE 3. Abundance of individuals of carabid beetles in each ecologic class.

Assemblage		Ecologic Class*					Total of A, B, & C
	A (%)	Σ B (%)	Be	Ba	Bx	C (%)	
Eva 3-3C	20**(25.0)	60(63.7)	9	14	37	0 (00)	80
Eva 3-3B	22 (45.8)	24(49.9)	1	11	12	2(4.1)	48
Eva 3-1A	43 (42.1)	58(56.7)	21	19	18	1(0.9)	102

* *See text for explanation of class symbols.*
** *Number of individuals.*

Though all three of the fossil assemblages were evidently deposited in a tundra environment, each of the assemblages possesses certain distinctive characteristics. Statistical tests (table 4) are used to establish the mutual relationship, if any, of the assemblages, and an attempt is made to provide environmental interpretations for the observed differences among the three fossil assemblages.

Several of the statistical comparisons in table 4 indicate that samples Eva 3-3B and 3-3C are more closely related to each other than either is to Eva 3-1A. The basis for this conclusion is the lack of statistically significant differences between 3-3B and 3-3C. The failure of a com-

parison of two samples to be statistically significant implies that the two
samples could have been drawn from the same parent population. In this
paper such a conclusion will be taken to imply that the two compared as-
semblages represent the same type of paleoenvironment.

TABLE 4. Statistical tests*.

Type of comparison	N	Comparison	Computed $\chi 2$	$\chi 2$ .05
Relative preservation of Carabidae skeletal elements in each assemblage				
Pronota -	180	3-3B, 3-3C	8.772	3.841
	262	3-1A, 3-3C	*0.046* **	3.841
	196	3-1A, 3-3B	10.315	3.841
Right elytra -	198	3-3B, 3-3C	17.370	3.841
	129	3-1A, 3-3C	*3.637*	3.841
	179	3-1A, 3-3B	5.628	3.841
Left elytra -	189	3-3B, 3-3C	13.459	3.841
	237	3-1A, 3-3C	7.755	3.841
	190	3-1A, 3-3B	*1.427*	3.841
Number of individuals in Coleoptera families common to all assemblages	759	3-3B, 3-3C	66.640	12.592
	730	3-1A, 3-3C	120.250	12.592
	609	3-1A, 3-3B	79.962	12.592
Number of taxa in families of Coleoptera common to all assemblages	112	All three	*3.931*	21.026
Number of individuals of Curculionidae in each assemblage	819	3-3B, 3-3C	*0.108*	3.841
	805	3-1A, 3-3C	65.093	3.841
	652	3-1A, 3-3B	61.025	3.841
Number of individuals in the genera *Pterostichus, Amara* and *Bembidion*	197	3-3B, 3-3C	*0.788*	5.991
	260	3-1A, 3-3C	12.480	5.991
	205	3-1A, 3-3B	15.990	5.991
Number of individuals in the species groups of *Pterostichus (Cryobius)*	120	3-3B, 3-3C	*0.480*	9.488
	173	3-1A, 3-3C	25.431	9.488
	139	3-1A, 3-3B	17.375	9.488

  *   *$\chi 2$ test of independence for binomial and multinomial populations.*
  ** *Nonsignificant $\chi 2$ values are in italics.*

Differential preservation of certain fossils could bias conclusions concerning the taxonomic and numerical relationships of 3-3B and 3-3C. To test this contingency I have made a statistical comparison of the preservation of carabid fossils in the three assemblages (table 4). The results of these comparisons indicate that differential preservation does exist; however, the relationships of the three assemblages based on preservation are different from those based on qualitative and quantitative taxonomic composition. Thus, the qualitative-quantitative comparisons showing 3-3B and 3-3C to be related are probably not initially biased by differences in preservation of the fossils. It is interesting that the two samples which are shown to be related by the statistical analyses represent the same sub-unit in the Wisconsin portion of the Eva Creek exposure.

Samples Eva 3-3C and 3-1A display the greatest degree of taxonomic and quantitative difference. Some of the major differences cannot be explained at this time, yet their existence, established in part by the statistical tests, is assumed to be evidence of paleoenvironmental differences. For example, the obvious difference between the two assemblages is indicated in the miscellaneous species section of table 1. There are very few species common to both assemblages 3-1A and 3-3C. The relative abundance of individuals of curculionid beetles (weevils) is also markedly different in the two assemblages, but only one curculionid, *Lepyrus gemellus* Kby. was identified specifically, and this species is rare in all three assemblages.

Finally, Eva 3-3C differs from 3-1A (and 3-3B) by its relative abundance of fossils of the scarabaeid genus *Aphodius*. In England, Coope has observed a correlation of concentrations of large mammal fossils with an abundance of *Aphodius* fossils, the explanation being that *Aphodius* has copraphogous habits (Coope & Sands 1966). But Landin (1961) pointed out that some species of *Aphodius* are not coprophagous, and of the few species that are known from Alaska, some are associated with small mammals such as *Marmota* rather than ungulates (W. J. Brown 1967, written comm.). Thus, at the present time and until specific identifications are forthcoming, I am hesitant to invoke Coope's explanation for the abundance of *Aphodius* fossils.

Those differences between 3-1A and 3-3C which are subject to interpretation occur within the family Carabidae. The greatest contrast is within the subgenus *Cryobius*, genus *Pterostichus* . In 3-3C (and 3-3B) the species *P. (Cryobius) kotzebuei* Ball is abundant. In Eva 3-1A this species is rare, and *P. (Cryobius) nivalis* Sahlb. is abundant (see table 1). *P. (Cryobius) kotzebuei* Ball has been collected by Ball (1967, personal communication) on rather dry tundra, and since it is a dominant element in the carabid fauna of Eva 3-3C, I conclude that dry tundra was probably present at the site of deposition of that assemblage approximately 24,400 years ago. Supporting this conclusion is the presence in 3-3C (and 3-3B) of individuals of the species *Bembidion dauricum* Mtsch.which inhabits xeric tundra sites that are almost devoid of vegetation (Lindroth 1963b). *Notiophilous semistriatus* Say, occurring in both 3-1A and 3-3C, occupies similar habitats (Lindroth 1961) and *Cymindis* sp. represented by one fossil in 3-3C, often occurs in xeric habitats (Ball 1963b).

P. (Cryobius) nivalis Sahlb. has been collected on rather dry tundra, but

Ball (1966) states that it is also associated with "deep moss". The or-
ganic residue from which the fossils of 3-1A were extracted possessed
an abundance of moss fragments. *P. (Cryobius) nivalis* Sahlb. evidently lived
in the environment at the site of deposition of 3-1A -- hence its abun-
dance in the fossil assemblage. *P. (Cryobius) tareumiut* Ball and *P. (Cryobius)
similis* Mann., both of which occur in 3-1A and probably not in 3-3C are
found presently on rather moist tundra (Ball 1963c, 1966). Several of
the carabid fossils from assemblage 3-1A indicate that an aquatic en-
vironment may have existed near the site of deposition. *Bembidion arcticum*
Lth. occurs now along the barren and gravelly margins of small streams
(Lindroth 1963b). Both species of *Elaphrus* listed in table 1 for the one
Elaphrus fossil in 3-1A are found in a similar habitat -- areas, usually
near streams or ponds, which are devoid of vegetation (Lindroth 1961).
Agonum quinquepunctatum Mtsch. is a hygrophilous species. It may not have
lived at the site of deposition of 3-1A, but its presence in the assemblage
is further evidence for the existence of an environment near by which was
favorable for its survival. It is of interest that Lindroth (1966) lists
Dischirius nigricornis Mtsch., another beetle restricted to assemblage 3-1A,
as a contemporary associate with *Agonum quinquepunctatum* Mtsch. in a bog
near Edmonton, Alberta. Eva 3-3C contains a fossil of an aquatic beet-
le, *Colymbetes*, but the absence of any other identified beetles which indi-
cate an aquatic or near aquatic environment suggests that *Colymbetes* does
not represent a community near the site of deposition of 3-3C.

With the exception of the fossils of *P. (Cryobius) kotzebuei* Ball and *P.
(Cryobius) nivalis* Sahlb. the differences between the carabid portions of the
two assemblages, 3-1A and 3-3C, are subtle; consequently, the environ-
mental interpretations are somewhat speculative. A more definite con-
cept of the meaning of the variation of the two assemblages might be ob-
tained if they could be compared quantitatively and qualitatively with data
from contemporary environments. As I have said earlier no such infor-
mation is available, but the fossil assemblage from McGee Cut near
Tofty, Alaska (fig. 1) is suitable for such a comparison (table 5).

Many of the beetle fossils extracted from the peaty silt at the McGee
cut were partially articulated, and almost only those that were so pre-
served are included in table 5. Thus the assemblage is made up of those
beetles which lived at or very near the site of deposition of the peaty
silt. The fact that many of the fossils are better preserved than dead
specimens collected in the contemporary environment indicates that some
of the fossil beetles probably died during hibernation.

Pollen analysis of the sediments from which McGee fossils were ex-
tracted reveals an unusual pollen spectrum consisting of more than 70%
sedge pollen and 20% willow pollen (Matthews MS). This is a clear case
of over-representation in the pollen spectrum by elements of the local
fossil plant community; that is, the plants growing at the site of depo-
sition -- the habitat in which the fossil beetles originally lived.

Assemblage 3-1A is more similar to the McGee assemblage than is
3-3C. I consider this to be further evidence that the environment re-
presented by assemblage 3-1A was more moist than that represented by
assemblage 3-3C. The differences between 3-1A and the McGee assem-
blage are best explained by the depositional histories of the two samples.

The McGee assemblage, consisting of well preserved fossils derived from peaty silt, represents a local, monotypic habitat. The Eva 3-1A assemblage derived as it is from colluvial silt no doubt represents a polytypic habitat. This explains the association in 3-1A of fossils of *Pterostichus haematopus* Dej., *Carabus chamissonis* Fisch., *Notiophilus semistriatus* Say, and *Notiophilus borealis*Harr. (beetles normally found in areas of scant vegetation) with fossils of beetles indicative of a moist tundra habitat. The implication is that the taxonomic diversity of the carabid fauna of 3-1A is a reflection of the diversity of the paleoenvironment in which the fossil beetles lived. Compared to assemblage 3-1A the carabid fauna of 3-3C is much less taxonomically diverse, even though the sample size of 3-3C is larger and the diversity at the familial level is greater. Perhaps this implies that the paleoenvironment represented by 3-3C was both drier and more uniform than that represented by 3-1A.

TABLE 5. Fossil Coleoptera from the McGee cut.

Taxa	Number of individuals
Carabus truncaticollis Eschz.	3
Diacheila polita Fald.	4
Pterostichus (Cryobius) pinguedineus grp.	6
Pterostichus (Cryobius) ochoticus subgrp.	1
Pterostichus (Cryobius) tareumiut Ball	2
Pterostichus (Cryobius) similis subgrp.	10
Pterostichus (Cryobius) similis Mann.	22
Pterostichus (Cryobius) parasimilis Ball	11
Pterostichus (Cryobius) pinguedineus Eschz.	4
Pterostichus (Cryobius) ventricosus grp.	1
Pterostichus (Cryobius) ventricosus Eschz.	1
Pterostichus (Cryobius) brevicornis Kby.	13
Pterostichus (Cryobius) mandibularoides Ball	3
*Pterostichus (Cryobius) nivalis*Sahlb.	1
Agonum quinquepunctatum Mtsch.	1
Amara alpina Payk.	8
Total	91

Fossil assemblage 3-3B from Eva Creek was shown by the statistical tests to be allied with 3-3C; however, in some respects it differs from both 3-3C and 3-1A. Of these differences, one, fewer taxa in 3-3B, is probably related to the smaller sample size of 3-3B. Other characteristics of 3-3B may not be explained so easily. For example, it contains an abundance of fossils of the staphylinid genus *Micralymma*, the species of which are tundra inhabitants (M. Sanderson 1967, written communi-

cation) and the byrrhid genus, *Curimopsis*, presently a very rare insect.
Though these differences are not subject to detailed environmental inter-
pretation, I do believe they indicate that the paleoenvironment of Eva
Creek was not identical when assemblages 3-3C and 3-3B accumulated.
Minor differences in the content of plant macrofossils and the pollen
spectra of 3-3C and 3-3B tend to support this conclusion (Matthews MS).

To what extent are the different tundra environments represented
by the fossil insect assemblages indicative of climatic change? Paly-
nologists working in arctic Alaska have found that late Pleistocene clim-
atic changes produced only subtle modifications of the composition of
former tundra plant communities (Colinvaux 1964, Livingston 1955).
Also, there is abundant evidence that world wide climatic oscillations
occurred in the time interval during which the three Eva Creek insect
assemblages were deposited. These facts seem to imply that the ob-
served variability of the insect assemblages is a reflection of such cli-
matic change.

It is necessary to refer to evidence of fossil pollen in order to test
this implication. Because pollen is more easily and more widely dis-
persed than insects, fossil pollen provides a more generalized picture
of the environment of a region such as interior Alaska, and it is changes
in the general environment which are coupled with macroclimatic change.
Though the three pollen spectra associated with the insect fossils are
not identical (table 6), they are similar enough to be placed in the same
pollen zone according to the system of pollen zonation now in use in nor-
thern Alaska (Livingston 1955). This means that similar climates ex-
isted in the Fairbanks area when each insect assemblage formed. Ac-
cordingly, the differences among the insect assemblages cannot have
major climatic significance. More than likely those differences reflect
features of a local environment such as the Eva Creek watershed. The
position of permafrost, proximity of water, exposure to sunlight, amount
of vegetation cover, and rate of deposition of loess are just a few of the
variables in such a local environment which may have influenced the com-
position of the insect assemblages.

TABLE 6. Fossil pollen spectra associated with Eva Creek fossil in-
sect assemblages.

| | Percentage of pollen types | | |
	Eva 3-3C	Eva 3-3B	Eva 3-1A
Spruce	-	+	-
Birch	+	9	12
Alder	+	4	9
Willow	10	26	24
Sedge	36	22	19
Grass	11	11	12
Artemisia	16	7	
Misc. pollen	10	9	7
Misc. spores	13	7	15

- Indicates only a trace of pollen seen.   + Indicates less than 3%.

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