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Scott A. Elias and Susan K. Short

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Article abstract

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PALEOECOLOGY OF AN INTERGLACIAL PEAT DEPOSIT, NUYAKUK, SOUTHWESTERN ALASKA, U.S.A.

Scott A. ELIAS and Susan K. SHORT, Institute of Arctic and Alpine Research, and Department of Anthropology and Institute of Arctic and Alpine Research, University of Colorado, Boulder, Colorado 80309, U.S.A.

ABSTRACT This paper reports the presence of interglacial beetle and pollen assemblages within a Pleistocene peat deposit exposed along the Nuyakuk River of southwestern Alaska. The fossil beetle assemblages contain a number of species not previously identified from eastern Beringian fossil assemblages. The Nuyakuk interglacial deposits are exposed within a 6-m-high terrace along the river, about 4 km beyond the moraine of the penultimate glaciation. Interglacial peat lies within the lowermost meter of the bluff and is overlain by fluvial gravel and loess. Insect fossils were extracted from five peat samples, yielding sixty-seven identified beetle taxa. The insect faunal diversity of the Nuyakuk assemblages is comparable to that found in regional Holocene peat samples. In contrast to assemblages of similar age from interior eastern Beringia, the Nuyakuk fauna contains significant numbers of aquatic, hygrophilous and riparian taxa. Four pollen samples from the Nuyakuk site were analyzed, providing spectra dominated by a few taxa, notably *Alnus, Betula, Picea*, Gramineae, Cyperaceae, Filicales, and *Sphagnum*, suggesting a rich alder-birch shrub tundra not much different from the modern regional vegetation. The pollen and insect fossil records also suggest climatic conditions similar to modern.

RÉSUMÉ *Paléoécologie d'un dépôt de tourbe interglaciaire à Nuyakuk, au sud de l'Alaska.* On rapporte la présence d'assemblages de coléoptères et de grains de pollen interglaciaires à l'intérieur d'un dépôt de tourbe du Pléistocène, situé le long de la Nuyakuk River. Ces assemblages de coléoptères fossiles renferment un certain nombre d'espèces qui n'avaient pas été encore identifiées dans les assemblages fossiles de la Béringie orientale. Les dépôts interglaciaires de Nuyakuk, à l'intérieur d'une terrasse de 6 m de hauteur le long de la rivière, située à environ 4 km au-delà la moraine de l'avant-dernière glaciation. La tourbe interglaciaire se trouve dans le dernier mètre de l'escarpement et est recouverte d'un gravier fluviatile et d'un loess. Les insectes fossiles ont été extraits de cinq échantillons de tourbe qui ont livré 67 taxons identifiés de coléoptères. La diversité faunique des insectes des assemblages de Nuyakuk est comparable à celle que l'on trouve dans les assemblages de tourbe de l'Holocène. Contrairement aux autres assemblages de la Béringie orientale de la même époque, la faune de Nuyakuk comprend un grand nombre de taxons aquatiques, hygrophiles et ripariens. Les quatre échantillons polliniques du site de Nuyakuk analysés ont livré des spectres dominés par quelques taxons, dont *Alnus, Betula, Picea*, Gramineae, Cyperaceae, Filicales et *Sphagnum*, reflétant ainsi une toundra à bouleau nain et à aulne, semblable à la végétation actuelle de la région. Les données polliniques et sur les insectes fossiles indiquent également des conditions climatiques semblables à celles d'aujourd'hui.

ZUSAMMENFASSUNG *Paläoökologie einer interglazialen Torfablagerung, Nuyakuk, südwestliches Alaska, U.S.A.* Dieser Artikel berichtet über interglaziale Käfer- und Pollen-Vorkommen in einer Torfablagerung aus dem Pleistozän entlang dem Nuyakuk-Fluß im südwestlichen Alaska. Diese Einheiten von Käfer-Fossilen enthalten eine Anzahl von Arten, die zuvor nicht in Fossil-Einheiten von Ost-Bering identifiziert worden sind. Die interglazialen Ablagerungen von Nuyakuk sind innerhalb einer 6 m hohen Terrasse den Fluß entlang ausgesetzt, etwa 4 km über die Moräne der vorletzten Vereisung hinaus. Interglazialer Torf liegt im untersten Meter des Steilhangs und ist von Flußkies und Löß überlagert. Aus fünf Torfproben wurden Insektenfossile entnommen, welche 67 identifizierte Käfer-Taxa lieferten. Die Vielfalt der Insekten-Fauna der Nuyakuk-Einheiten ist mit der, die man in regionalen Torfproben aus dem Holozän vorfindet, vergleichbar. Im Gegensatz zu Einheiten ähnlichen Alters vom Innern Ost-Berings enthält die Fauna von Nuyakuk eine bedeutende Zahl von Wasser-, Feuchtigkeits-liebenden und Ufer-Taxa. Vier Pollen-Proben vom Nuyakuk-Platz wurden analysiert und lieferten durch wenige Taxa dominierte Spektren, vor allem *Alnus, Betula, Picea*, Gramineae, Cyperaceae, Filicales und *Sphagnum*, welche auf eine reiche Erlen-Birken-Buschtundra schließen lassen, die sich nicht sehr von der modernen regionalen Vegetation unterschied. Die Pollen- und Insektenfossil-Belege lassen auch klimatische Bedingungen vermuten, die den heutigen ähnlich waren.

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INTRODUCTION

Pleistocene peats that contain pollen and/or macrofossil assemblages indicative of interglacial conditions are scattered throughout lowland basins of central Alaska and the northern Yukon Territory (Fig. 1). Until recently, Quaternary sedimentary basins in southwestern Alaska have received little stratigraphic and paleoenvironmental study. Consequently, the existence and character of interglacial deposits in this region of eastern Beringia has remained unknown.

This paper reports the presence of interglacial beetle and pollen assemblages within Pleistocene peat exposed along the Nuyakuk River of southwestern Alaska (Fig. 1). The fossil beetle assemblages are of particular ecological and biogeographical significance because they contain a large number of species not previously identified from eastern Beringia (*i.e.*, Alaska and the Yukon Territory west of the Mackenzie River). The interglacial character of the Nuyakuk peat is unique among Pleistocene deposits examined thus far from southwestern Alaska. The age of the deposit and its paleoenvironmental implications are evaluated in the broader context of interglacial deposits throughout eastern Beringia.

REGIONAL SETTING

PHYSIOGRAPHY AND GEOLOGY

The Nuyakuk site is located along the central reach of the Nuyakuk River, a major tributary of the Nushagak River in southwestern Alaska. The Nuyakuk River flows eastward from the glacially scoured trough of Tikchik Lake through the northern Nushagak lowland, a broad Quaternary basin east of the glaciated Ahklun Mountains (Fig. 1). Prominent moraine belts along the upper and central reaches of the Nuyakuk River record repeated advances of Pleistocene glaciers from the Tikchik trough into the lowland margin (Lea, 1989). Two inner moraine belts exhibit fresh hummocky morphology typical of deposits of the last glaciation (*ca.* 25,000(?)-12,500 BP; Lea, 1989). A third moraine further downstream is more subdued and represents the penultimate glaciation, dated in the southern Nushagak lowland at >40,000 BP (Lea, 1989). Beyond the moraines of the penultimate glaciation, the central Nushagak lowland is underlain by glaciolacustrine and glaciofluvial deposits and till of a still-older Pleistocene glaciation. This drift was deposited during an interval of extensive glaciation of the lowland, during which ice from the Ahklun Mountains and Alaska Peninsula locally coalesced (P. D. Lea, unpublished data, 1984; *cf.* Coulter *et al.*, 1965).

CLIMATE

The Nushagak and adjoining Bristol Bay lowlands lie within a zone of transitional maritime-to-continental climate, with cool, cloudy and wet summers and moderately cold winters. Mean annual air temperature at King Salmon (Fig. 1) is about +0.7°C, with mean January and July temperatures about −10.3°C and +12.5°C, respectively (National Oceanic and Atmospheric Administration, 1982). Mean annual precipitation within the lowland ranges from about 45 to 65 cm, with an average of 130-180 cm of snow per year.

VEGETATION

The Nushagak lowland lies at the southwestern limit of boreal forest in Alaska and is covered by a mosaic of forest and shrub tundra (Fig. 2) (Viereck and Little, 1972). Closed-to-open forest, including white spruce (*Picea glauca*), paper birch (*Betula papyrifera*), and balsam poplar (*Populus balsamifera*), is generally confined to well-drained sites on Pleistocene outwash terraces or along major rivers. More poorly drained areas are mantled by mesic to wet shrub tundra, which includes tall shrubs of alder (*Alnus* spp.), willow (especially *Salix alaxensis* and *S. glauca*), and birch (*Betula glandulosa*). Low shrubs are also prevalent, including willow (*Salix* spp.), dwarf birch (*Betula nana*), and numerous species of heaths (Ericaceae). Grass (Gramineae) and sedge (Cyperaceae) meadows, which include a diverse assemblage of herbaceous taxa and ferns (Filicales), also make up a large proportion of the vegetation cover. Small *Sphagnum* bogs and *Eriophorum* (cotton grass) sedge fens are common. Bedrock uplands surrounding the Nushagak lowland display an altitudinal zonation above spruce treeline, from birch-shrub tundra with alder and willow thickets to alpine tundra dominated by open-ground herbs.

SITE STRATIGRAPHY

The Nuyakuk interglacial deposits are exposed within a 6-m-high terrace along the north side of a sharp meander bend in the central Nuyakuk River. The site (NY-13) is about 4 km beyond the moraine of the penultimate glaciation. The interglacial peat lies within the lowermost meter of the bluff and is overlain by fluvial gravel and loess (Lea, 1989).

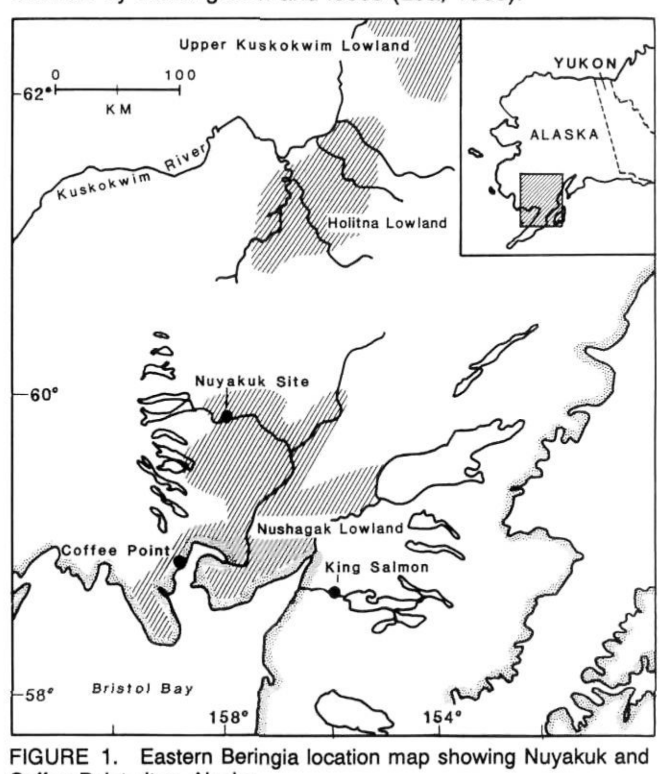

FIGURE 1. Eastern Beringia location map showing Nuyakuk and Coffee Point sites, Alaska.

Carte de localisation de la Béringie orientale montrant les sites de Nuyakuk et de Coffee Point, en Alaska.

OVERLYING UNITS

The terrace surface at the Nuyakuk site can be traced upstream to a recessional ice position associated with the last glaciation, and the facies association of the upper gravel unit is typical of the medial positions of outwash (Miall, 1977; Boothroyd and Nummedal, 1978). Based upon its similarities in lithology and weathering characteristics to the upper gravel unit, the lower gravel unit is also interpreted as outwash of the last glaciation. Both gravel units are oxidized, but a depositional hiatus between them is indicated by vertical, frost-oriented stones and small wedge casts, probably formed by frost cracking (*cf.* Hopkins *et al.*, 1955), at their contact. The composite outwash gravel sequence is capped by about 75 cm of oxidized massive silt, interpreted as loess of latest-Pleistocene and/or Holocene age (Lea, 1989).

INTERGLACIAL PEAT

At site NY-13, peat deposits lie atop a gently undulating surface which rises above and falls below midsummer river levels along the length of the exposure (Fig. 3). The base of the peat is exposed about 50 m from the upstream end of the bluff, where it gradationally overlies at least 30 cm of gray, generally inorganic, fine-grained diamicton (sandy silt with granules). The overall texture of the diamicton and its gradational contact with the overlying detrital peat suggest a colluvial origin (P. D. Lea, Geology Department, Bowdoin College, unpublished data).

The lowermost six centimeters of the peat is detrital and includes sand and granules which decrease in abundance upward. The basal detrital peat in turn grades upward into 27 cm of autochthonous peat, comprising matted, moderately humified, graminoid remains with subordinate moss and scattered shrub wood. The peat interfingers at the top with about 30 cm of dark-brown to yellowish-tan organic sandy silt, which contains near its center a thin (2- to 5-cm), discontinuous layer of peat. The organic sequence is separated from overlying fluvial gravel by a thin (1- to 3-cm) layer of massive medium sand. A sample from the uppermost three centimeters of autochthonous sedge peat yielded a radiocarbon age of >42,000 BP (GX-13,773; Fig. 3).

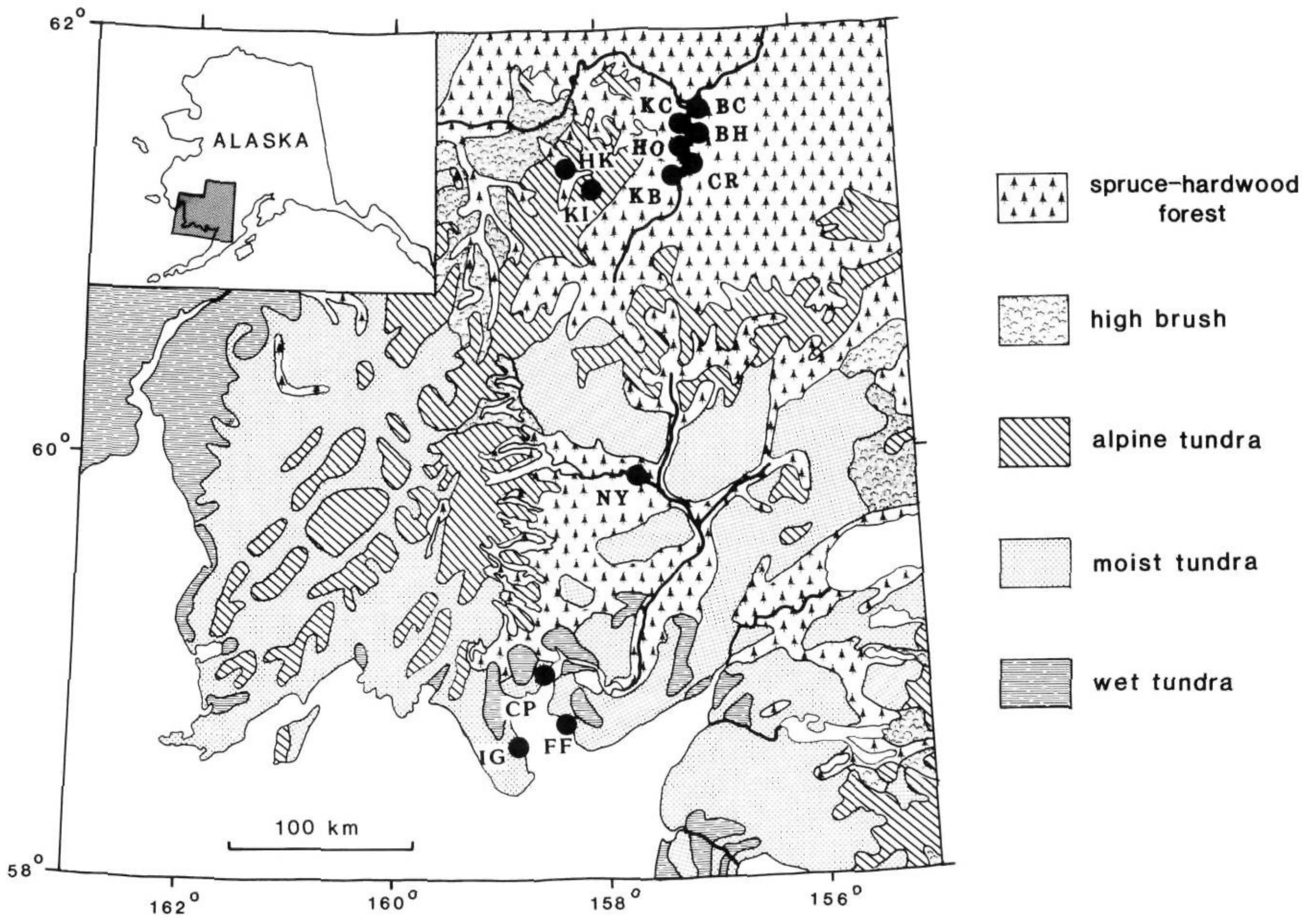

FIGURE 2. Map of southwestern Alaska, showing locality of moss polster samples in relation to modern vegetation zones and fossil localities discussed in text. Modern polster sites: BC, unnamed creek on Holitna River; BH, Beaverhouse Hill; CR, Crazy Raven Bluff; HO, Holitna River; HK, Holukuk Mountains; KB, Kulukbuk Bluffs; KC, unnamed creek on Holitna River; KI, Kioluk Mountain. Fossil localities: CP, Coffee Point, FF, Flounder Flat; IG, Igushik; NY, Nuyakuk.

Carte du sud-ouest de l'Alaska montrant les sites d'échantillonnage de coussinets de mousse en relation avec les zones de végétation modernes et les sites fossilifères dont on parle dans le texte. Sites modernes de mousse: BC, ruisseau sans nom sur la Holitna River; BH, Beaverhouse Hill; CR, Crazy Raven Bluff; HO, Holitna River; HK, Holukuk Mountains; KB, Kulukbuk Bluffs; KC, ruisseau sans nom sur la Holitna River; KI, Kioluk Mountain. Sites fossilifères: CP, Coffee Point; FF, Flounder Flat; IG, Igushik; NY, Nuyakuk.

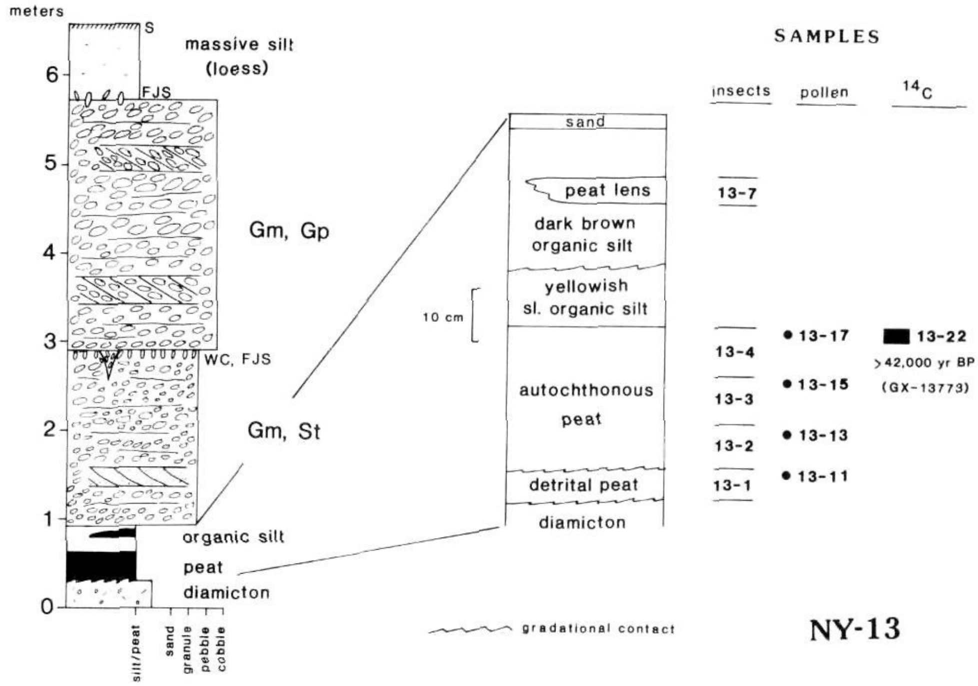

FIGURE 3. Site stratigraphy, Nuyakuk interglacial deposits, showing insect fossil and pollen sampling intervals (P. D. Lea, unpublished data). Gm, facies of granule-to-pebble-gravel in massive or crude horizontal beds; Sp and St, facies of subordinate cross-stratified coarse sand; Gp, facies of local planar cross-stratified units (after Miall, 1977).

Stratigraphie du site NY-13 dans les dépôts interglaciaires de Nuyaguk, montrant les intervalles de prélèvement des échantillons d'insectes fossiles et de pollen (P. D. Lea, données non publiées). Gm, faciès de graviers hétérométriques en lits horizontaux mal définis et massifs; Sp, et St, faciès secondaires de sables grossiers entrecroisés; Gp, faciès d'unités locales entrecroisées planes (selon Miall, 1977).

METHODS

INSECT FOSSIL ANALYSES

Insect fossils were extracted from five peat samples (Fig. 3). Sample 13-1, from the basal detrital peat, was sieved through a 300-micron mesh in the field, yielding about one liter of peat for insect fossil extraction in the laboratory. Samples 13-2, 13-3 and 13-4 represent successive 9-cm intervals through the overlying autochthonous sedge peat. About three liters of peat were taken from each sampling interval. Sample 13-7 came from a peaty zone within the upper organic-silt unit (Fig. 3), and was sieved in the field, yielding about three liters of organic material.

All of the samples were sieved in the laboratory to remove fine inorganic particles. The samples were then processed by the kerosene-flotation method (Coope, 1968) to concentrate and extract insect fossil parts from the plant detrital residue. The flotants were sorted in alcohol under a low-power binocular microscope. Robust specimens were mounted onto modified micropaleontology cards with water-soluble gum tragacanth. Fragile specimens and duplicates were stored in vials of alcohol.

Insect fossils were identified chiefly through comparison with modern and fossil specimens from the INSTAAR insect collection, and by comparison with modern specimens in the Canadian National Collection of Insects, Ottawa.

POLLEN ANALYSES

Four pollen samples from the Nuyakuk site were analyzed, from the upper portion of the basal detrital peat (13-11) and from three levels within the autochthonous sedge peat (13-13, 13-15 and 13-17; Fig. 3). For comparative purposes, we also report pollen analyses of moss polsters collected at a number of localities in southwestern Alaska (Fig. 2). The chemical treatment of the samples was conventional (Faegri and Iversen, 1975), and included sieving to remove coarse organics (250 μm screen), caustic soda, acetolysis, and hydrofluoric acid, with prolonged boiling time. A known weight of sample was prepared (Jørgensen, 1967), and prior to chemical pollen concentration, a tablet containing a known number of exotic marker grains (*Eucalyptus*) was added (Stockmarr, 1971). Thus, the pollen concentration data are discussed in number of grains per gram dry weight (gr/gdw) of sample. Pollen counts totaled at least 300 grains (pollen and spores) per slide. To facilitate comparison with other workers in Alaska, pollen percentages were recalculated exclusive of spores, most notably those of monolete ferns (Filicales), *Sphagnum* and *Lycopodium* spp. (clubmoss). The spores are reported as a percentage of the pollen sum.

Pollen identifications were made using the reference collection of the INSTAAR Palynology Laboratory with the additional aid of a number of keys and guides (McAndrews *et al.*, 1973; Moriya, 1976) and floras (Hultén, 1968). Twenty-two pollen taxa were identified. A reduced data set of nine taxa was used to construct the pollen diagrams (Figs. 4A and 4B); the minor taxa are listed in Table I.

RESULTS

INSECT FOSSIL ANALYSES

In order to compare Beringian insect fossil assemblages, the Nuyakuk fauna are discussed in relation to ecological groups. Figure 5 summarizes the relative faunal composition, defined on the basis of these groups. The groups generally follow Matthews' (1983) guidelines; however, notable exceptions are that his *Lepidophorus-Morychus* (xeric) group, the Silphid (carrion beetle) group and the *Aphodius* (dung beetle) group were not represented in the Nuyakuk assemblages. In contrast, the Nuyakuk fauna contains significant numbers of aquatic, hygrophilous and riparian taxa. We have added a *Stenus* group because of its regional importance and relatively great abun-

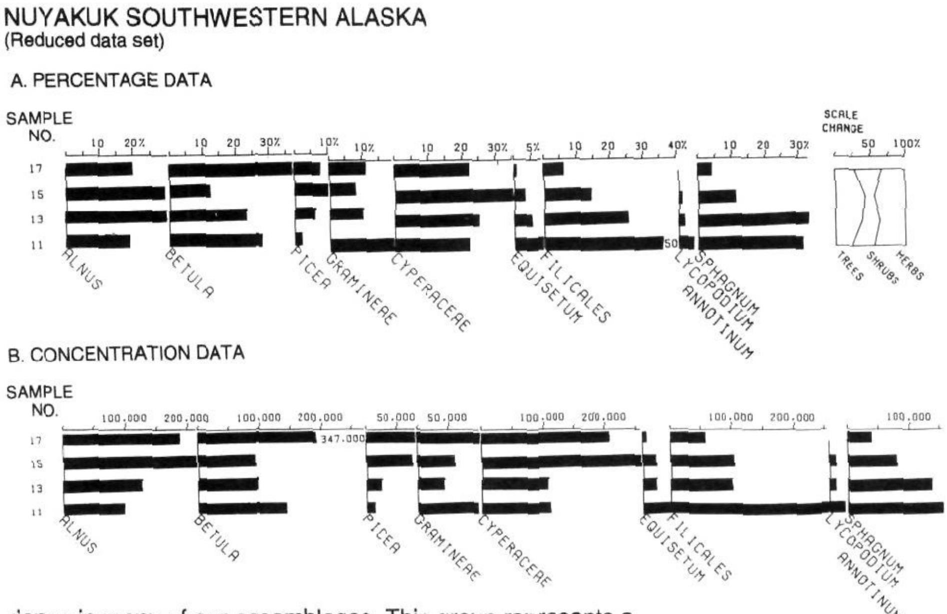

FIGURE 4. Nuyakuk peats (reduced data sets). A. Percentage pollen diagram (pollen sums excluded spores). B Pollen concentration diagram (numbers of pollen grains per gram oven dry weight).

Les tourbes de Nuyakuk. A. Diagramme sommaire des pourcentages polliniques (excluant les spores). B. Diagramme sommaire des concentrations polliniques (nombre de grains de pollen par gramme de poids sec).

dance in many of our assemblages. This group represents a genus of riparian rove beetles (Staphylinidae), for the most part found in close proximity to water. Also well represented in most of the Nuyakuk assemblages are the hygrophilous and aquatic groups. The *Cryobius* group, indicative of mesic tundra environments, is moderately-well represented in all sampled intervals. The *Cryobius* group taxa increase slightly in the uppermost sample (13-7, Fig. 3). This increase is coincident with the only record of another arctic tundra indicator, the *Tachinus* group (represented in this case only by the species *T. brevipennis*). Additional features of the Nuyakuk insect fauna are discussed more fully below.

Cryobius Group

The *Cryobius* group of the ground beetle genus *Pterostichus* is most often associated with mesic tundra habitats. During the Pleistocene, this group dominated many fossil beetle faunas from sites in southwestern Alaska during interstadials and the Holocene. In addition to the mesic tundra-associated ground beetles discussed in the text, we have included three staphylinid (rove beetle) species in this ecological group. These include *Olophrum latum, Boreaphilus henningianus* and *Holoboreaphilus nordenskioeldi*, all of which are associated with damp leaf litter, mosses and mesic substrates in open ground environments.

Hygrophilous-Riparian Group

This group includes species from a number of beetle families. All of the species in this group live in moist or wet habitats at the edges of water or in semi-emergent vegetation. Examples of this group include the hygrophilous ground beetles, *Diacheila arctica* and *Pterostichus circulosus*. Other hygrophilous taxa include semi-aquatic taxa, such as the leaf beetle genera *Plateumaris* and *Donacia* and the weevil, *Notaris aethiops.*

Omaliine Group

Matthews (1983) put the Omaliinae group of staphylinid beetles in his hygrophilous group. While this combination is ecologically sensible, we felt that the Omaliines should be separated into their own group, especially since they are a relatively important component of Southwestern Alaskan assemblages. This group shares ecological affinities with the *Cryobius* group, being found in mesic, open ground situations. It also forms a major part of Pleistocene tundra faunas throughout the northern hemisphere.

TABLE I

Minor taxa, Nuyakuk pollen samples

Artemisia	Sage (2)
Compositae-Tub.	Sunflower family (1)
Cruciferae	Mustard family (2)
Ericaceae	Heath family (4)
Pedicularis	Lousewort (1)
Pinus	Pine (1)
Potentilla	Cinquefoil (2)
Ranunculaceae	Buttercup family (1)
Rosaceae type	Rose family (4)
Rubus chamaemorus	Cloudberry (1)
Salix	Willow (2)
Thalictrum	Meadow-rue (3)
Umbelliferae	Parsley family (1)

All taxa present at ≤1%
(n) indicates presence in n sample(s)

Stenus Group

The habitat requirements of most *Stenus* species are poorly studied in North America, but as far as is known all the species of *Stenus* found in southwestern Alaskan assemblages are strictly riparian, occurring on moist banks of standing and running water. We collected numerous specimens of *Stenus* along the banks of the Holitna River (about 100 km north of the Nuyakuk site) in damp mud with a thin cover of mosses, within 2 m of the water's edge (locality no. 17 in Elias, 1987).

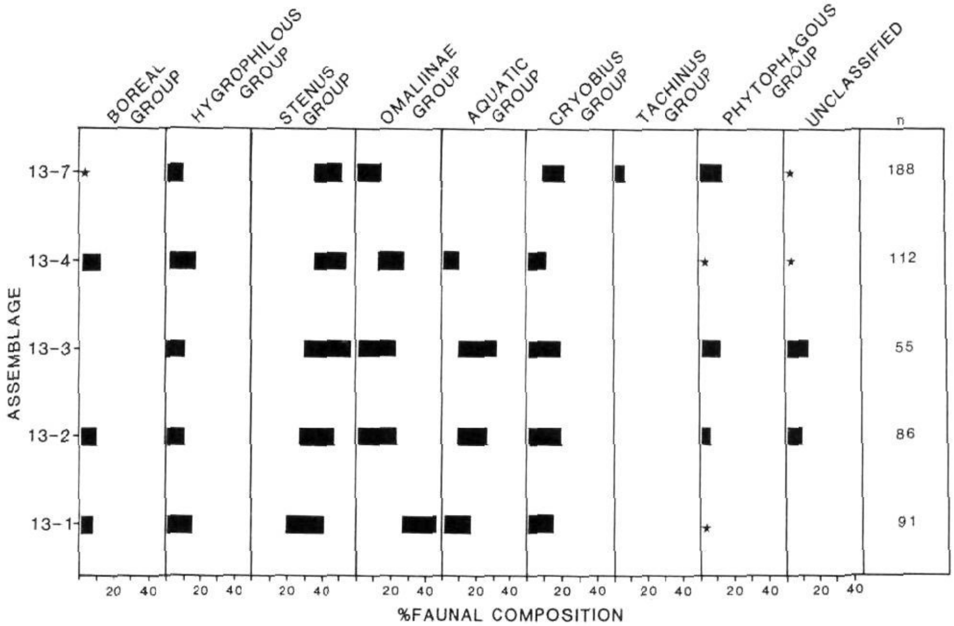

FIGURE 5. Percentage composition of fossil beetle groups, shown in 95% confidence intervals, and minimum numbers of individuals per group for the Nuyakuk fossil assemblages.

Assemblages fossiles de Nuyakuk: composition en pourcentages des groupes de coléoptères fossiles, selon des intervalles à 95 % de fiabilité, et nombres minimaux d'individus par groupe.

Boreal Group

This group is rather limited in southwestern Alaskan assemblages, including the Nuyakuk interglacial assemblages. The boreal-associated beetle species that comprise this group are not obligate tree-dwellers or tree-feeding taxa, such as bark beetles, but rather predators that occur today in the boreal regions of Canada and Alaska. As with other southwestern Alaskan fossil faunas, the boreal species from the Nuyakuk assemblages are only found as lone individuals in given assemblages, and we do not consider their presence in these assemblages indicative of either boreal forest vegetation or of macroclimatic parameters associated with the modern boreal zone.

Tachinus Group

The only representative of this group from the southwestern Alaskan Pleistocene faunas is *Tachinus brevipennis*. This is an essentially amphi-beringian species, although it has also been taken from two localities west of the Lena River in Siberia. Modern specimens have been collected primarily from coastal tundra regions, but recently Campbell (1988) has collected specimens from elevations over 300 m on the north slope of the Brooks Range. The most frequent collecting localities are stream and pond banks, and in beach gravel in close proximity to the water, along the arctic coast of northern Alaska. Campbell (pers. comm., 1987; Campbell, 1988) notes that the water in such situations is only mildly brackish, and that many other freshwater insects inhabit these waters. The larvae of *T. brevipennis* probably prey on maggots found in fish and bird carrion in beach flotsam. The *Tachinus* group is an important element of full glacial-age faunas in southwestern Alaskan sites (Elias and Short, 1987). Geomorphic and palynological data from organic horizons containing fossils of *T. brevipennis* suggest that it is characteristic of periglacial conditions with cold, dry climate.

The five insect samples yielded beetle (Coleoptera) faunas generally similar in taxonomic composition and ecological implications, and are therefore discussed as a group. Sixty-seven beetle taxa were identified, representing nine families and including 46 species determinations (Table II). The insect faunal diversity of the Nuyakuk assemblages is comparable to that of Holocene peat samples from the Nushagak and Holitna lowlands of southwestern Alaska, based on a comparison of the number of species with the minimum number of individuals per sample (Fig. 6).

POLLEN ANALYSES

Although no polsters or modern pollen samples were collected at the Nuyakuk site, collections were made at eleven interior and three coastal localities in the region (Fig. 7). The coastal polsters exhibit high percentages of *Alnus* (21-34%), *Betula* (16-32%), and Gramineae (11-52%), with smaller percentages of Cyperaceae (1-14%), Ericaceae (3-14%) and Filicales (3-14%). *Picea* pollen is rare in these samples (<2%), despite the proximity (<20 km) of spruce treeline to the north. These low values may reflect, at least in part, a persistence of strong southerly (onshore) winds during times of spruce pollination. The interior samples constitute an altitudinal transect from spruce forest through birch-spruce forest to altitudinal treeline and shrub tundra. These pollen spectra can be divided into three main groups, dominated by *Picea* (25-20%) (Group I), *Betula* (*ca.* 60%) (Group II), or *Alnus* (*ca.* 50%) (Group III). All three groups contain significantly higher proportions of *Picea* pollen (>10%) than the coastal samples.

The four Nuyakuk fossil samples are dominated by a few taxa, notably *Alnus* (19-30%), *Betula* (12-37%), *Picea* (2-10%), Gramineae (8-19%), Cyperaceae (22-35%), Filicales (6-50%), and *Sphagnum* (4-33%) (Fig. 4A). Maximum spore percentages are recorded in the two basal samples but values drop off markedly upsection. *Picea* percentages are very low (2%) in the basal sample but increase (5-10%) in the higher samples. *Alnus* percentages peak in the middle two samples, corresponding to lower *Betula* percentages in those levels.

Pollen concentration values are illustrated in Fig. 4B. Total numbers of pollen grains range from *ca.* 700,000 to 1,000,000 gr/gdw. Spore values register a trend similar to the

TABLE II

Taxonomic list of insect fossils from the Nuyakuk assemblages, in minimum number of individuals per sample

Taxon	Group	Sample* 1	2	3	4	7
Coleoptera						
Carabidae						
Nebria metallica Fisch.	Unclass					1
Diacheila arctica Gyll.	Hygro				1	
Diacheila polita Fald.	Cryob					7
Dyschirius nigricornis Mots.	Cryob					4
Dyschirius sp.	Unclass					1
Patrobus sp.	Unclass					1
Trechus apicalis Mots.	Boreal	1			1	2
Bembidion concretum Csy.	Boreal				2	
Bembidion fortestriatum Mots.	Boreal	1	4		4	
Bembidion grapii Gyll.	Ripar	1				2
Bembidion spp.	Unclass		1			1
Pterostichus agonus Horn	Cryob	1				
Pterostichus brevicornis Kby.	Cryob				12	
Pterostichus circulosus Ball	Hygro		2		1	
Pterostichus kotzebuei Ball	Cryob	1				1
Pterostichus pinguedineus Eschz.	Cryob					1
Pterostichus tareumiut Ball	Cryob					1
Pterostichus (Cryobius) spp.	Cryob	4	6	3	3	
Agonum gratiosum Mannh.	Cryob	1	2	2		
Agonum sp.	Unclass	1			2	
Amara sinuosa Csy.	Boreal	1				
Dytiscidae						
Hygrotus nr. *picatus* Kby.	Aquat	1		1		
Hydroporus cf. *boreus* Gordon	Aquat	2				
Hydroporus sp.	Aquat	2	5	4	6	
Agabus (Clavicornis) sp.	Aquat		1			
Agabus cf. *colymbus* Leech	Aquat		1			
Agabus sp.	Aquat	1				
Ilybius (Angustior) sp.	Aquat		1	1		
Ilybius nr. *discedens* Sharp	Aquat	4	8	5	1	
Hydrophilidae						
Hydrobius fuscipes L.	Hygro	1				
Genus indet.	Unclass	1		1		
Hydraenidae						
Hydraena angulicollis Notm.	Hygro		1	1	9	1
Gyrinidae						
Gyrinus sp.	Aquat		1			
Staphylinidae						
Arpedium/Eucnecosum sp.	Omal				7	1
Olophrum consimile (Gyll.)	Omal	1			1	
Olophrum latum Mäkl.	Cryob	12	2	3	2	4
Olophrum rotundicolle Sahlb.	Omal	1	4		2	4
Olophrum spp.	Omal	20	7	4	13	11
Acidota crenata (Fab.)	Boreal				1	1
Acidota quadrata (Zett.)	Omal					1
Omaliinae sp. indet.	Omal		2			
Boreaphilus henningianus (Sahlb.)	Cryob					3
Holoboreaphilus nordenskioeldi (Mäkl.)	Cryob	1				4
Stenus ageus Cas.	Stenus			6		
Stenus alexanderi Puthz	Stenus	1				
Stenus austini Cas.	Stenus		4			4
Stenus canaliculatus Gyll.	Stenus					4
Stenus hyperboreus Sahlb.	Stenus	9	5	6	6	
Stenus jacuticus Popp.	Stenus					3
Stenus juno Payk.	Stenus	8				
Stenus latipennis Sahlb.	Stenus	1		6		
Stenus mammops Cas.	Stenus					3
Stenus melanarius Er.	Stenus		7			3
Stenus plicipennis Cas.	Stenus	2	3			
Stenus cf. *rossi* Sand.	Stenus		1			
Stenus vinnulus Cas.	Stenus	4	6	5	6	7
Stenus spp.	Stenus	1	7		40	58
Lathrobium spp.	Unclass	2	3	2	1	3
Tachinus brevipennis (Sahlb.)	Tachin					13
Mycetoporus sp.	Unclass					1
Gymnusa sp.	Hygro	1			2	1
Scarabaeidae						
Aegialia lacustris LeC	Ripar		1			
Chrysomelidae						
Plateumaris (Pusilla) sp.	Hygro	1				
Curculionidae						
Apion alaskanum Fall	Phyto					19
Apion sp.	Phyto	1	2	2	1	
Notaris aethiops Fab.	Hygro					8
Genus indet.	Unclass	1				

* 1 = 84NUY 13-1; 2 = 84NUY 13-2; 3 = 84NUY 13-3; 4 = 84NUY 13-4; 7 = 84NUY 13-7.

pollen percentages with maximum numbers of grains recorded in the basal two samples. *Picea* numbers are relatively low in the basal two samples, but increase to moderate values above, following a general trend in the non-spore taxa toward increasing pollen influx upsection.

DISCUSSION

The stratigraphic position, pollen spectra and fossil insect assemblages suggest that the Nuyakuk peats were deposited in conditions associated with interglacial climate. The interglacial character of the Nuyakuk peats is unique among late-Pleistocene organic deposits studied thus far in southwestern Alaska.

The regional distribution of organic-bearing sediment and peat in stratigraphic context is of limited extent in southwestern Alaska. Sedimentary sequences in the Nushagak, Holitna and upper Kuskokwim lowlands are mainly eolian sand sheets and loess that date to the last and penultimate glaciations (*ca.* 25,000-12,500 and >40,000 BP, respectively).

PALYNOLOGY

The pollen spectra from the Nuyakuk assemblages suggest a rich alder-birch shrub tundra possibly with scattered spruce trees regionally, at least in the upper half of the section, suggesting an environment and vegetation similar to the present. There is no exact "fit" with any of the modern pollen samples; comparisons can best be made with the coastal samples and the treeline community interior (Group III) samples. The presence of alder shrubs in the Nuyakuk samples suggests substantially warmer conditions (similar to present) than do any of the Boutellier samples analyzed in a larger study (Lea *et al.*,

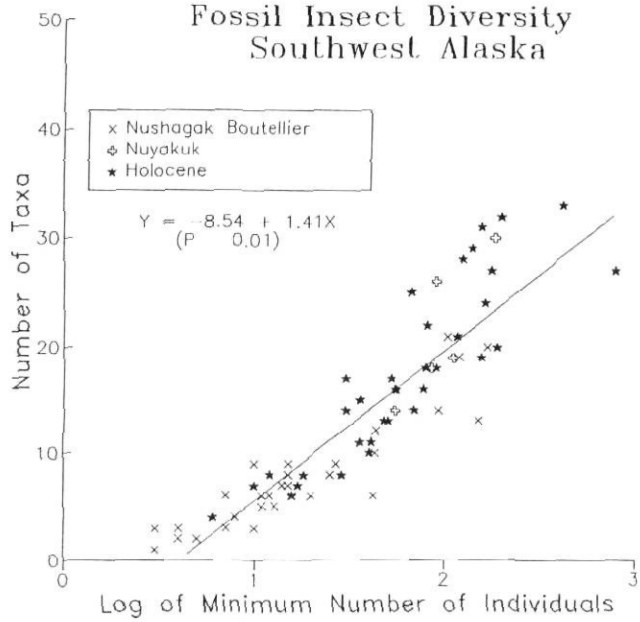

FIGURE 6. Insect fossil species diversity of southwestern Alaskan insect fossil samples, shown by a linear regression of number of insect taxa on the log of the minimum number of individuals from the Nuyakuk interglacial-age assemblages, and from Boutellier- and Holocene-age assemblages from other southwestern Alaskan sites (Short *et al.*, 1992).

La diversité des espèces d'insectes fossiles à partir des échantillons d'insectes fossiles du sud-ouest de l'Alaska, illustrée par une régression linéaire du nombre de taxons d'insectes sur le nombre minimal d'individus, fondées sur les assemblages interglaciaires de Nuyakuk et les assemblages de l'intervalle de Boutellier et de l'Holocène en provenance d'autres sites du sud-ouest de l'Alaska (Short et al., *1992).*

1991). Twenty-nine regional samples assigned to the Boutellier have been analyzed to date. In contrast to the Nuyakuk samples, the pollen spectra from Boutellier-age sediments are dominated by Gramineae (*ca.* 40%) and Cyperaceae (25-40%). *Artemisia* (sage), *Salix*, and *Sphagnum* are important in some of the Boutellier samples, but percentages are variable. *Alnus*, *Betula*, and *Picea* pollen are rare or absent in the majority of the samples. Table III lists percentage values from four Boutellier-age samples from Coffee Point, 100 km to the southwest. Pollen concentration values are variable within this large group of samples but generally are an order of magnitude smaller than those recorded in the Nuyakuk samples. In general, the Boutellier-age pollen spectra from southwest Alaska suggest a diverse graminoid tundra with a mosaic of willow shrubs in localized areas. The importance of shrub pollen, fern and *Sphagnum* spores in some Boutellier-age samples indicates that at least local and perhaps regional conditions were somewhat mesic and warmer than during full glacial time. Similarly, the fossil beetle assemblages within these same organic deposits are of a different character than the Nuyakuk assemblages, in that they generally lack taxa of the Boreal and Hygrophilous groups and exhibit lower percentages of *Stenus*.

INSECT PALEOECOLOGY

As discussed above, mesic tundra beetles are an important element in the Nuyakuk assemblages. Among these are the ground beetles, *Pterostichus brevicornis, P. kotzebuei*, and *P. tareumiut*. All of these are presently found in arctic tundra habitats of Alaska, although Lindroth (1966) notes that *P. brevicornis* ranges south into forested country, mostly near the forest-tundra ecotone. *P. kotzebuei* is usually found among

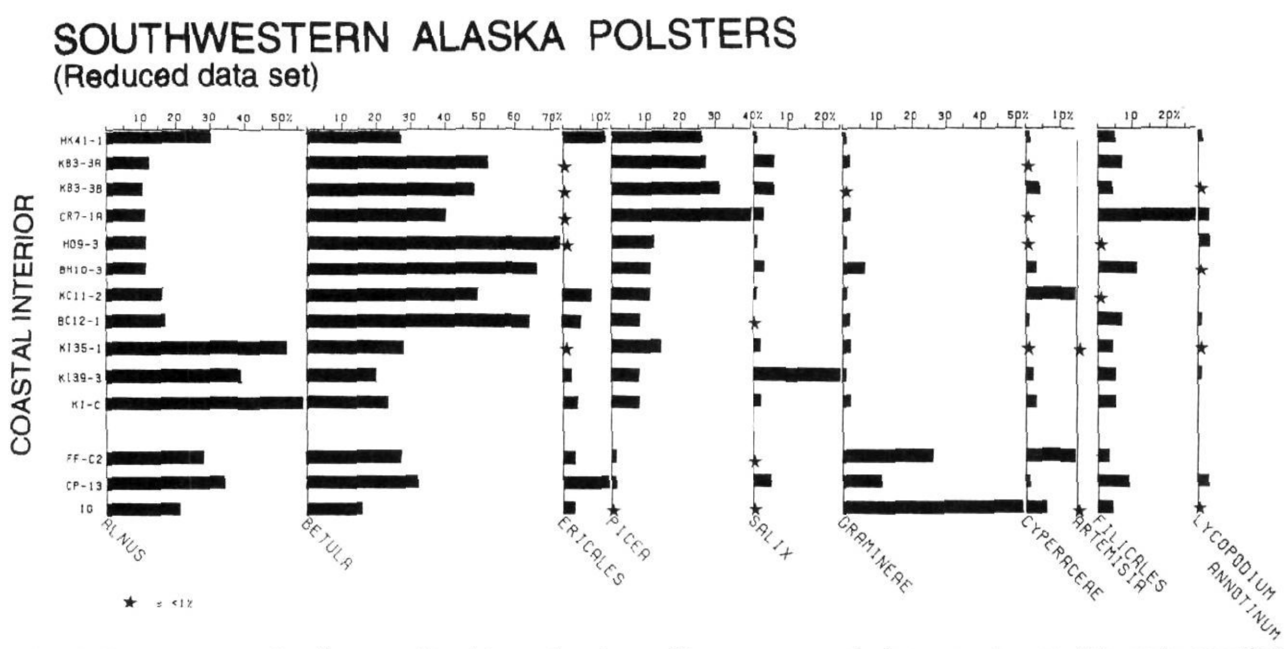

FIGURE 7. Percentage pollen diagram, polster data, southwestern Alaska (reduced data set). Pollen sum excludes spores. The interior Alaskan sites are arranged along an altitudinal transect from sea level to altitudinal treeline.

Diagramme sommaire des pourcentages polliniques des coussinets de mousse du sud-ouest de l'Alaska (excluant les spores). Les sites de l'intérieur de l'Alaska sont réparties le long d'un transect altitudinal, tracé à partir du niveau de la mer jusqu'à la limite altitudinale des arbres.

TABLE III

Mean percentage data, selected taxa, Coffee Point, Boutellier-age samples

	Sample Number			
	2-2	2-6A	2-7A	2-8A
Alnus	0.8	0	0	0
Betula	0.8	2.8	6.2	0.2
Picea	2.5	0.4	0.2	0
Salix	4.1	5.2	17.0	2.4
Artemisia	4.1	4.8	11.5	3.6
Gramineae	52.9	53.2	25.4	58.3
Cyperaceae	19.8	19.8	28.9	28.9

leaves under *Salix* bushes or in dense moss on both peaty and gravelly soil. *P. tareumiut* lives on wet, peaty soil and today is found mainly in coastal regions, while *P. brevicornis* frequents heathlands or rather dry meadows, especially among grasses and leaf litter (Lindroth, 1966).

Diacheila polita is another ground beetle in the mesic tundra group. This species usually inhabits peaty soil on the open tundra, but is found in habitats ranging from the damp edges of sedge-lined pools to drier, upland localities with rich shrub and herbaceous vegetation (Lindroth, 1961). Another carabid, *Agonum gratiosum*, is not strictly a tundra species (occurring as far south today as Indiana and Oregon), but it lives in open ground situations, on moist, peaty soils among sedges or *Sphagnum* mosses. Within the context of the fossil locality, it appears that this beetle was a member of the regional mesic tundra communities of the late Pleistocene. Another mesic tundra indicator, *Olophrum latum*, is the most northerly distributed species of *Olophrum* today. In North America it is found only in arctic and subarctic regions west of Hudson Bay. On the whole, the *Cryobius* ecological group is not important in the Nuyakuk assemblages, except in the uppermost sample.

One of the hygrophilous species from Nuyakuk is the ground beetle, *Diacheila arctica*, a cryptic species that is extremely rare in modern collections and in North American fossil assemblages (Elias, 1982). *D. arctica* is circumpolar today, but only known from two modern localities in Alaska. It lives in quagmire moss carpet vegetation at the outer margins of lakes and ponds (Lindroth, 1961). Another hygrophilous carabid, *Pterostichus circulosus*, is known only from a few localities in Alaska. It has been found on very wet, soft mud among sedges in a small marsh (Lindroth, 1966). The chrysomelid (leaf beetle), *Plateumaris (Pusilla)* sp., represents a group of beetles with aquatic larvae that feed on emergent vegetation. The weevil, *Notaris aethiops*, is a semi-aquatic species that feeds on *Sparganium* (bur-reed). The hygro-riparian group is best represented in assemblage 13-4. In addition, the riparian staphylinid genus, *Stenus*, was abundant in the all the Nuyakuk assemblages, suggesting the availability of moist, riparian habitats throughout the time of peat deposition. The Omaliine staphylinids, included here in the *Cryobius* group, are most abundant in sample 13-2, and then decline towards the top of the section.

The boreal group includes three species from the Nuyakuk assemblages. The carabid, *Trechus apicalis* occurs today only within the boreal regions of Canada and Alaska. While it is not specifically tied to forest trees, living under damp deciduous leaf litter or in the drier parts of sedge marshes, it is not an open ground species *per se*, and it is not found on the tundra (Lindroth, 1963). In southwestern Alaska, we collected *T. apicalis* from riparian habitats along the Holitna River (Elias, 1987), in a region of closed spruce-hardwood forest (Viereck and Little, 1972). *Amara sinuosa* is another boreal ground beetle, found across Canada and southern Alaska. It ranges onto coastal tundra in Newfoundland and up to timberline in the mountains of northern British Columbia (Lindroth, 1968).

Acidota crenata is a widely distributed, boreal species of rove beetle. It lives in a multitude of habitats, including mosses in wet forest regions, in wet bog meadows and in dry upland regions of pine forests (Campbell, 1982). The boreal species from the Nuyakuk assemblages are only found as lone individuals in three assemblages (Fig. 6), and we do not consider their presence in these assemblages indicative of either boreal forest vegetation or of macroclimatic parameters associated with the modern boreal zone.

The *Tachinus* group, while an important element of full glacial-age faunas in other southwestern Alaskan sites (Elias and Short, 1987; Elias, 1992), is represented only in the uppermost sample from Nuyakuk.

The trends in the Nuyakuk insect assemblages are as follows. The basal sample shows a mixture of mesic tundra and boreal species. Beetles commonly associated with deciduous leaf litter (the Omaliinae group) occur in large numbers within this sample. This assemblage probably represents an open ground community with mesic vegetation, including *Salix*, *Alnus*, and *Betula* shrubs. Climatic conditions may have been similar to modern parameters, or slightly cooler.

Samples 13-2, 13-3 and 13-4 contain assemblages with maximum numbers of aquatic and riparian taxa, suggesting expansion of aquatic habitats. Minor fluctuations in boreal and mesic tundra beetles suggests that the temperature regime may have remained fairly stable. Toward the top of the peat sequence, the aquatic group decreases, and eventually disappears from the uppermost assemblage. This youngest fauna shows a lack of thermophilous indicators, a decrease in deciduous leaf litter-associated taxa, an increase in the mesic tundra group to maximum levels, and the only record of the *Tachinus* group, regionally indicative of colder, drier climatic regimes (*e.g.*, during full glacial intervals). The combination of these changes suggests climatic cooling and drying. This may signal the beginning of full glacial conditions or perhaps only a temporary climatic deterioration.

COMPARISONS WITH OTHER EASTERN BERINGIAN SITES

Figure 8 illustrates the relative composition of major ecological groups in fossil beetle assemblages of comparable age from the Nuyakuk and Ch'ijee's Bluff (Bluefish Basin) localities of eastern Beringia, as well as the composition of major pollen taxa from these sites and from Imuruk Lake, Koyukuk and

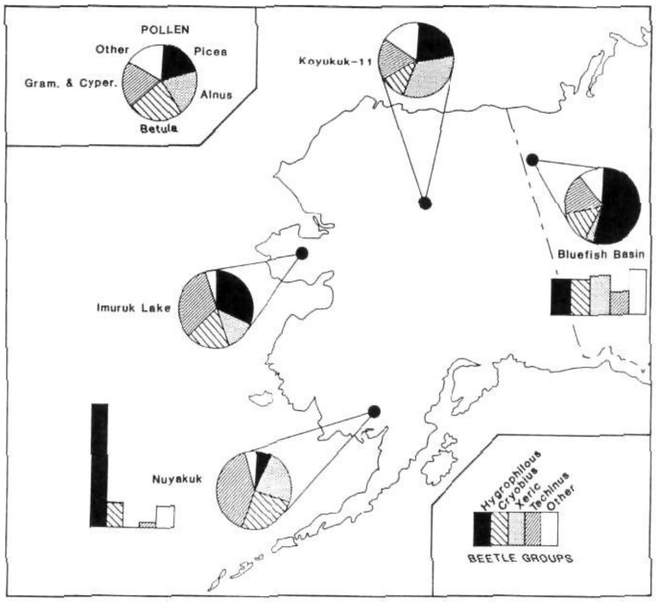

FIGURE 8. Correlative pollen and beetle group percentage diagrams for sites in eastern Beringia. Imuruk Lake pollen data from Colinvaux (1964); Koyukuk-11 data from Schweger (1982); Bluefish Basin pollen data from Lichti-Federovich (1974) and Schweger and Matthews (1985); Bluefish Basin insect data from Matthews *et al.*, (1990).

Diagrammes corrélatifs des pourcentages polliniques et des groupes de coléoptères des sites de la Béringie orientale. Les données polliniques de Imuruk Lake sont de Colinvaux (1964); données de Koyukuk-11 de Schweger (1982); données polliniques de Bluefish Basin de Lichti-Federovich (1974) et de Schweger and Matthews (1985); données sur les insectes de Bluefish Basin de Matthews et al., *(1990).*

Bluefish Basin. The stratigraphic position of the deposits compared here (and in some cases their stratigraphic position relative to the Old Crow tephra), in addition to their interglacial character, suggests that they are generally correlative. However, several considerations need to be made in order to make meaningful comparisons. First is the question of chronologies.

Various age estimates of the Old Crow tephra place its deposition between 86,000 yr BP (Wintle and Westgate, 1986) and 149,000 yr BP (Westgate, 1988). Schweger and Matthews (1985) considered that a series of fossil assemblages overlying the tephra at Imuruk Lake, the Yoyukuk region, the Fairbanks region, Bluefish Basin and the Old Crow Basin are indicative of interglacial type climate that suggest an early Middle Wisconsinan age (*i.e.*, early Stage 3) warm episode (their "Koy-Yukon thermal event"). However, Westgate's (1988) fission track date supports the view that forest beds deposited just above the Old Crow tephra relate to the last interglacial and not an Early Wisconsinan warm event. Hamilton (1991) has reviewed the stratigraphic data from ten Alaskan sites containing the Old Crow tephra, noting that in some localities (Palisades, Fairbanks, Ky-12. and the Holitna Lowland), the tephra lies below organic horizons or spruce pollen peaks that represent a distinctive warm interval, while at other sites (Birch Creek, Halfway House, and Hogatza Mine), the tephra lies just above or within conspicuous paleosols. The multiple paleosols or spruce maxima that occur within or above the Old Crow tephra horizons may be indicative of multiple warming intervals within isotope stage 5, hence, there may be no single warm "signature" attributable to a unique last interglacial maximum. Hamilton's estimate for the age of the tephra falls between 130,000 and 135,000 yr BP.

INSECT FOSSIL ASSEMBLAGES

The interglacial insect faunal assemblages from the Nuyakuk site show some similarities to the Ch'ijee's Bluff assemblages from the last interglacial. Matthews *et al.* (1990) describe interglacial assemblages with substantial numbers of mesic and hygrophilous taxa (including the *Cryobius* group, indicative of mesic tundra environments). However, there are some differences between the two faunas. The Bluefish Basin faunas include significant percentages of xeric (*Lepidophorus-Morychus*) group and *Tachinus* group species, while the Nuyakuk fauna is lacking in the former group, and has only small numbers of *Tachinus* specimens. Given these differences, the Nuyakuk assemblages appear to represent more mesic to moist conditions than those seen from the interior of eastern Beringia. The faunal uniformity of the five Nuyakuk samples suggests a long-lived bog maintained under relatively stable environmental conditions.

PALYNOLOGICAL COMPARISONS

The pollen data presented in Figure 8 reflect several different modern environments, and hence the pollen percentages are not directly comparable. However, the pollen spectra have been interpreted as indicative of vegetation and climatic regimes as warm or warmer than present (see summary in Schweger and Matthews, 1985). At Imuruk Lake, Colinvaux's (1964) benchmark study from the central Seward Peninsula, *Picea* frequencies in subzone i_1 are higher than in any other Imuruk zone, including the Holocene, and also higher than modern surface spruce values. Together with higher *Alnus* frequencies, this period suggests the westward expansion of boreal forest vegetation toward the lake during a time when the climate was at least as warm as today.

Koyukuk locality 11 features the Old Crow tephra near the base of a thick sequences of lacustrine silt overlain by a peat containing *Picea* wood dated >56,000 BP. The pollen spectrum from that level records maximum *Alnus* and *Picea* frequencies. The former value is higher than in most modern pollen surface samples from boreal woodland regions (Nelson, 1979), and the pollen spectra, along with spruce macrofossils, has been interpreted as indicating boreal forest vegetation and warmer climatic conditions than at present (Schweger and Matthews, 1985).

Several lowland areas in the Old Crow region of northern Yukon record extensive stratigraphic sections containing tephra which extend at least into the Early Wisconsinan. Figure 8 summarizes the pollen spectra from units containing the tephra at the Old Crow and Bluefish Basins; the differences point up again the problem of chronology with these sites. The large *Picea* frequencies in Zone D from Bluefish Basin have been interpreted by Schweger and Matthews (1985) as representative of boreal forest. In addition, macrofossils of plants (and insects) imply summer climate that was warmer than present during deposition. The Old Crow pollen data, however, suggest a climate similar to today, and there is reason now to doubt that disconformity "A" is equivalent to Zone D from Bluefish Basin.

Edwards and McDowell (1991) have recently published the results of palynological analyses of last interglacial deposits at Birch Creek, Yukon Flats basin, northeastern Alaska. The assemblage, representing a boreal forest dominated by *Picea, Alnus,* and *Betula,* is the same as that which characterizes Holocene records of the region, although the relative abundances are subtly different. Recent evidence suggests that the last interglacial was exceptional in its warmth and characterized by a rapid onset (see also Bartlein and Prentice, 1988; Heusser and King, 1988); Edwards and McDowell believe that the Birch Creek assemblage supports this conclusion.

INSECT ZOOGEOGRAPHY

The modern distributions of the Nuyakuk fossil insect species represent 11 different patterns, with no pattern dominant. Five species, including *Tachinus brevipennis* (Fig. 9, A) are amphi-beringian, that is, they occur in eastern Siberia and in Alaska and the Yukon Territory regions west of the Mackenzie River. Four species are found today only in eastern Beringia (*i.e.*, they are not found in Siberia), including *Pterostichus kotzebuei* (Fig. 9, B). *Nebria metallica* is the only species from the Nuyakuk assemblages that is currently found only in the Pacific Northwest region, extending along the southern coast of Alaska as far west as Kuskokwim Bay (Fig. 9, C). Sixteen species are currently boreo-arctic in North America, as typified by *Notaris aethiops* (Fig. 9, D). Only three species are found across all of arctic North America, while species such as *Olophrum latum* (Fig. 9, E) are found at high latitudes only west of Hudson Bay. Ten species are either boreal or boreomontane and subarctic, such as *Hydraena angulicollis* (Fig. 9, F), a species that is apparently absent from Alaska today.

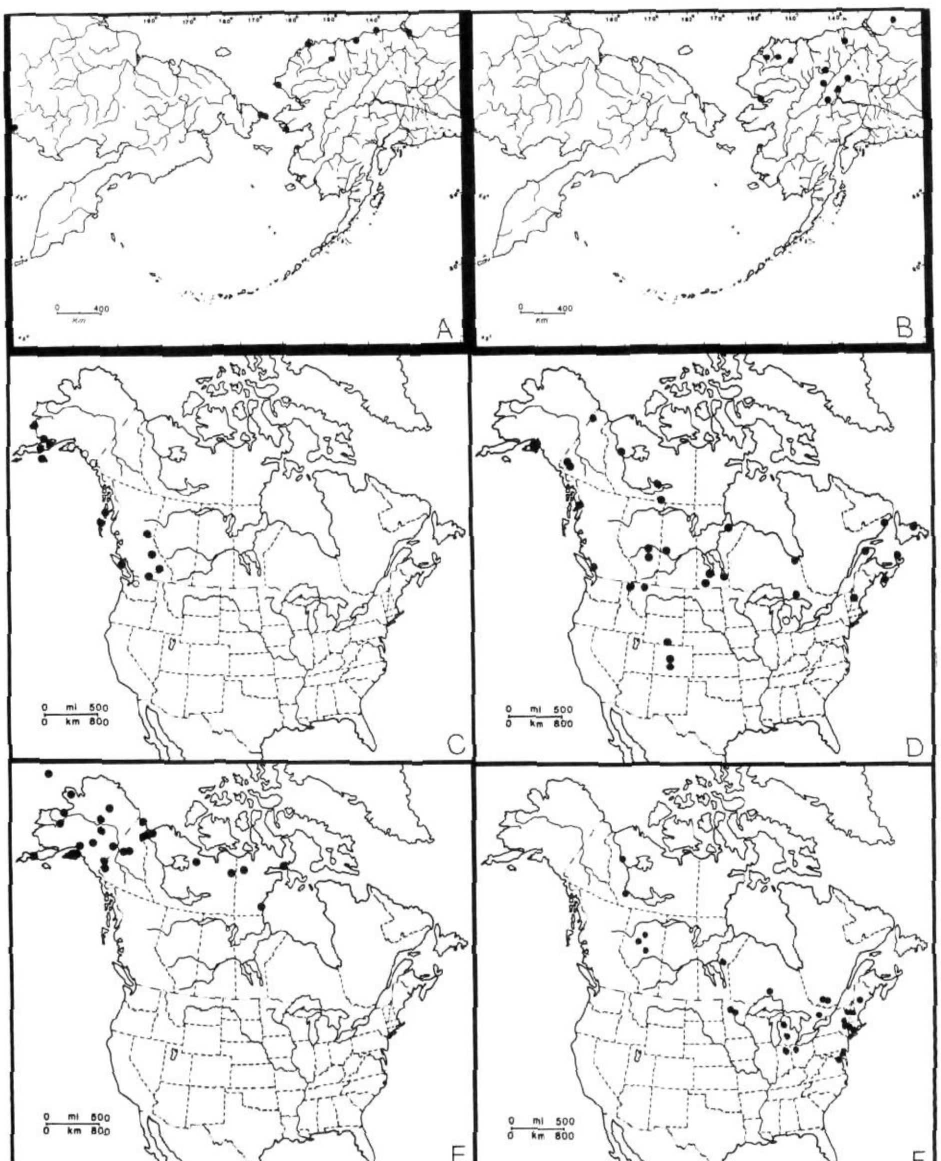

FIGURE 9. Known modern Beringian and North American distributions of beetle species discussed in text. A. *Tachinus brevipennis* (after Campbell, 1988); B. *Pterostichus kotzebuei* (after Lindroth, 1966); C. *Nebria metallica* (after Lindroth, 1961); D. *Notaris aethiops* (after Buchanan, 1927 and records from Canadian National Collection, Ottawa); E. *Olophrum latum* (after Campbell, 1983); F. *Hydraena angulicollis* (after Perkins, 1980).

Répartitions modernes connues des espèces de coléoptères traitées dans le texte, en Béringie et en Amérique du Nord. A. Tachinus brevipennis *(selon Campbell, 1988); B.* Pterostichus kotzebuei *(selon Lindroth, 1966); C.* Nebria metallica *(selon Lindroth, 1961); D.* Notaris aethiops *(selon Buchanan, 1927 et de la collection du Canadien National, à Ottawa); E.* Olophrum latum *(selon Campbell, 1983); F.* Hydraena angulicollis *(selon Perkins, 1980).*

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