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Late Quaternary Environments, Denali National Park and Preserve, Alaska

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ABSTRACT. Late Quaternary pollen, plant macrofossils, and insect fossils were studied from sites along three rivers in the foothills north of the Alaska Range in Denali National Park and Preserve. The aim was to carry out a reconaissance of late Quaternary organic sediments in the region, emphasizing the mid-Wisconsin, or Boutellier interstadial interval. Samples of probable early- to mid-Boutellier age (ca. 60 000 to 40 000 B.P.) from Unit 2 at the Toklat High Bluffs site indicate open boreal woodland with dense alder shrub vegetation. Organic Unit 1 at the Foraker River Slump site indicates open taiga with shrubs of probable Boutellier age. Fossil evidence from the youngest horizon in this unit indicates graminoid tundra environments, marking the transition from interstadial to late Wisconsin glacial environments. Early Holocene samples from the Foraker exposures suggest birch shrub tundra; coniferous forest apparently became established only after 6500 B.P. Local variations in forest composition at the Foraker and Sushana sites were probably the result of disturbances, such as fire.

Key words: Late Quaternary environments, Denali National Park, Alaska, pollen, insect fossils

RÉSUMÉ. Les grains de pollen et les pièces macrofossiles de plantes et d'insectes, caractérisant le quaternaire tardif, ont été étudiés dans des sites localisés le long de trois rivières coulant à proximité du versant nord de l'Alaska Range, dans le parc national et la réserve Denali. Cette étude porte essentiellement sur les sédiments organiques de la région, plus particulièrement ceux caractérisant l'intervalle interstadiaire Boutellier (milieu de la période du Wisconsin). Les échantillons récoltés dans l'unité numéro deux du site Toklat High Bluffs et datant probablement du début ou du milieu de l'intervalle Boutellier (60 000 à 40 000 BP) témoignent de la présence d'une forêt boréale ouverte avec couvert arbustif dense composé essentiellement d'aulnes. Les macrorestes et le pollen de l'unité organique numéro un du site Foraker River Slump témoignent, pour leur part, de la présence d'une taïga ouverte parsemée d'arbustes. Selon toute vraisemblance, cette taïga daterait de l'intervalle Boutellier. Les macrorestes et le pollen contenus dans l'horizon le plus jeune de cette unité indiquent que le paysage était constitué d'une toundra herbacée, marquant ainsi une transition entre la végétation caractérisant l'interstade Boutellier et celle de la fin de la période wisconsinienne. Les échantillons datant du début de la période holocène du site Foraker suggèrent la présence d'une toundra arbustive composée surtout de bouleaux. La forêt coniférienne ne se serait établie qu'après 6500 BP. Les différences observées au niveau de la composition forestière des sites Foraker et Sushana résultent probablement de l'impact de perturbations, tel le feu.

Mots clés: milieux du quaternaire tardif, parc national Denali, Alaska, pollen, insectes fossiles

INTRODUCTION

The Tanana–Kuskokwim Lowland includes the region immediately north of the Alaska Range in central Alaska. Several large rivers with headwaters in that range drain through the lowland, including the Foraker, Nenana, and Toklat Rivers (Fig. 1). Quaternary stratigraphic relationships in this lowland and adjacent areas are critical to the development of a late Quaternary paleoenvironmental framework for Eastern Beringia, because we lack published studies for this region. Recent studies have shown that the Tanana–Kuskokwim Lowland–north Alaska Range foothill area is of great importance to the Quaternary history of the region (Ten Brink, 1984). Paleoenvironmental information from this region is needed to complete long-distance correlation of late Quaternary stratigraphic records between coastal south western Alaska and the Alaskan interior and beyond and to allow for regional comparisons of paleoenvironmental records.

Information on Alaska Range Quaternary events, especially the late Wisconsin glacial chronology and stratigraphy, has been developing over the last two decades. Since 1978, nearly 100 radiocarbon dates on north central Alaska Range glacigenic, fluvial, and colluvial deposits have been determined, and stratigraphic studies have been made of most natural exposures in the area. Most of the recent information from this area was obtained during field studies conducted from 1977 to 1980 as part of the "North Alaska Range Project" (NARP), a multidisciplinary search for Paleo-Indian archeological sites sponsored by the National Geographic Society and the National Park Service (Ritter and Ten Brink, 1980; Ten Brink, 1983, 1984; Ten Brink and Waythomas, 1985). Our study developed paleoenvironmental reconstructions for this region.

We studied late Quaternary organic deposits (fossiliferous peat and silt) exposed in bluffs along three rivers in the Tanana–Kuskokwim Lowland–north Alaska Range foothill

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zone (Fig. 1). These localities provide an excellent opportunity for detailed paleoenvironmental studies involving paleoecology (insect fossils, plant macrofossils and pollen) and stratigraphy. Following the earlier field studies, we emphasized the mid-Wisconsin, or Boutellier interval (Hopkins, 1982). This time period is important from the standpoints of interstadial climatic change, biological community development, and glacial history, but relatively little was known about it in our study region.

Wisconsin Glacial History

Glacial deposits and river-bluff stratigraphy at numerous localities in the Tanana–Kuskokwim Lowland have been examined, and some detailed stratigraphic studies have also been performed (Ten Brink, 1984). Glacial deposits of the penultimate glaciation have been recognized and studied throughout the southern Tanana–Kuskokwim Lowland (Wahrhaftig, 1958; Péwé, 1975; Ten Brink, 1984; Thorson, 1986). Although the age of the penultimate glaciation in this part of Alaska is unknown, recent studies in southwestern Alaska suggest it predates the last interglacial (Waythomas, 1990). Several authors have suggested that penultimate glacial deposits throughout Alaska are of early Wisconsin age (e.g., Hamilton et al., 1986), but the widespread nature of those deposits seems inconsistent with amounts of ice cover predicted on the basis of the oxygen isotope record (Martinson et al., 1987).

Despite the well-preserved and extensive late Pleistocene glacial record of the northern Alaska Range, a number of important questions related to the non-glacial (ice-minimum) intervals remain unresolved. These include questions concerning chronology, climate, and biological communities of the early and mid-Wisconsin intervals.

MODERN VEGETATION AND CLIMATE

Open taiga and mesic shrub tundra are the dominant vegetation types of the present-day central Alaska Range (Viereck and Little, 1972). The taiga vegetation consists of relatively continuous to discontinuous stands of white and black spruce (*Picea glauca* and *P. mariana*, respectively), paper birch (*Betula papyrifera*), balsam poplar (*Populus balsamifera*), and alder (*Alnus* spp.). In this region the altitudinal tree-limit for spruce is about 950 m. Dwarf birch (*Betula nana* and *Betula glandulosa*) are important components of the shrub vegetation, along with willow (*Salix* spp.), heaths (Ericales [includes Ericaceae, Empetraceae, and Pyrolaceae]), and spirea (*Spiraea beauverdiana*). Understory vegetation is mainly Poaceae (grass family), Cyperaceae (sedge family), and a variety of herbs; mosses, especially *Sphagnum* spp., often form thick mats in moist sites. Mean annual temperature at Denali National Park headquarters is -2.8˚C, and the mean July temperature is 12.5˚C. Mean annual precipitation is 38 cm (Leslie, 1989).

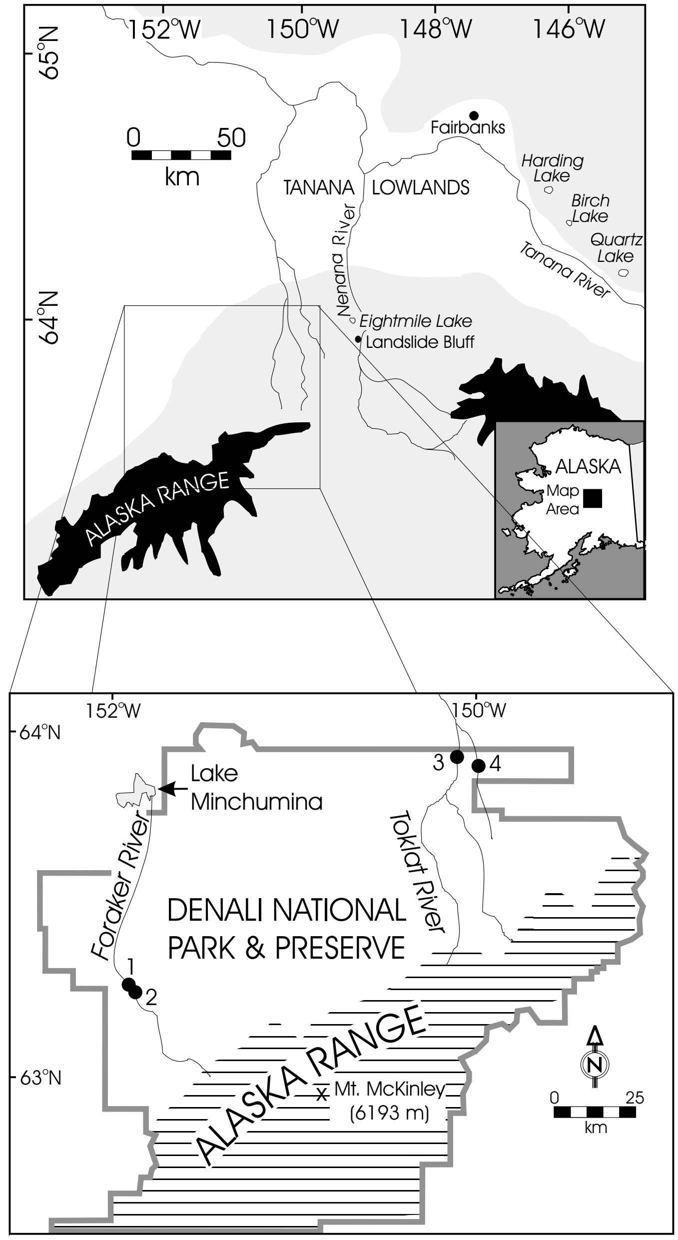

FIG. 1. Map of the Tanana-Kuskokwim Lowland, Alaska, and Denali National Park, showing major landmarks and fossil sites discussed in text (after Ager, 1984). 1, Foraker Ice Wedge site; 2, Foraker Slump site; 3, Toklat High Bluff site; 4, Sushana River site.

We analyzed a total of 14 moss and lichen polsters collected during the 1990 field season from four sites (Sushana, Toklat, Foraker, Landslide Bluff) north of the Alaska Range. The percentage pollen diagram for these surface samples is illustrated in Figure 2. The pollen spectra are dominated by *Alnus* (17–58%), *Betula* (17–75%), and *Picea* (4–59%). The variability recorded here reflects the complex vegetation mosaic of the region. The importance of alder and birch pollen in the modern pollen study is notable. Peak birch percentages are recorded in two polsters (3 and 7) collected from those sites with abundant paper birch trees. The peak alder value (polster 14) was recorded in a polster collected from an alder scrub

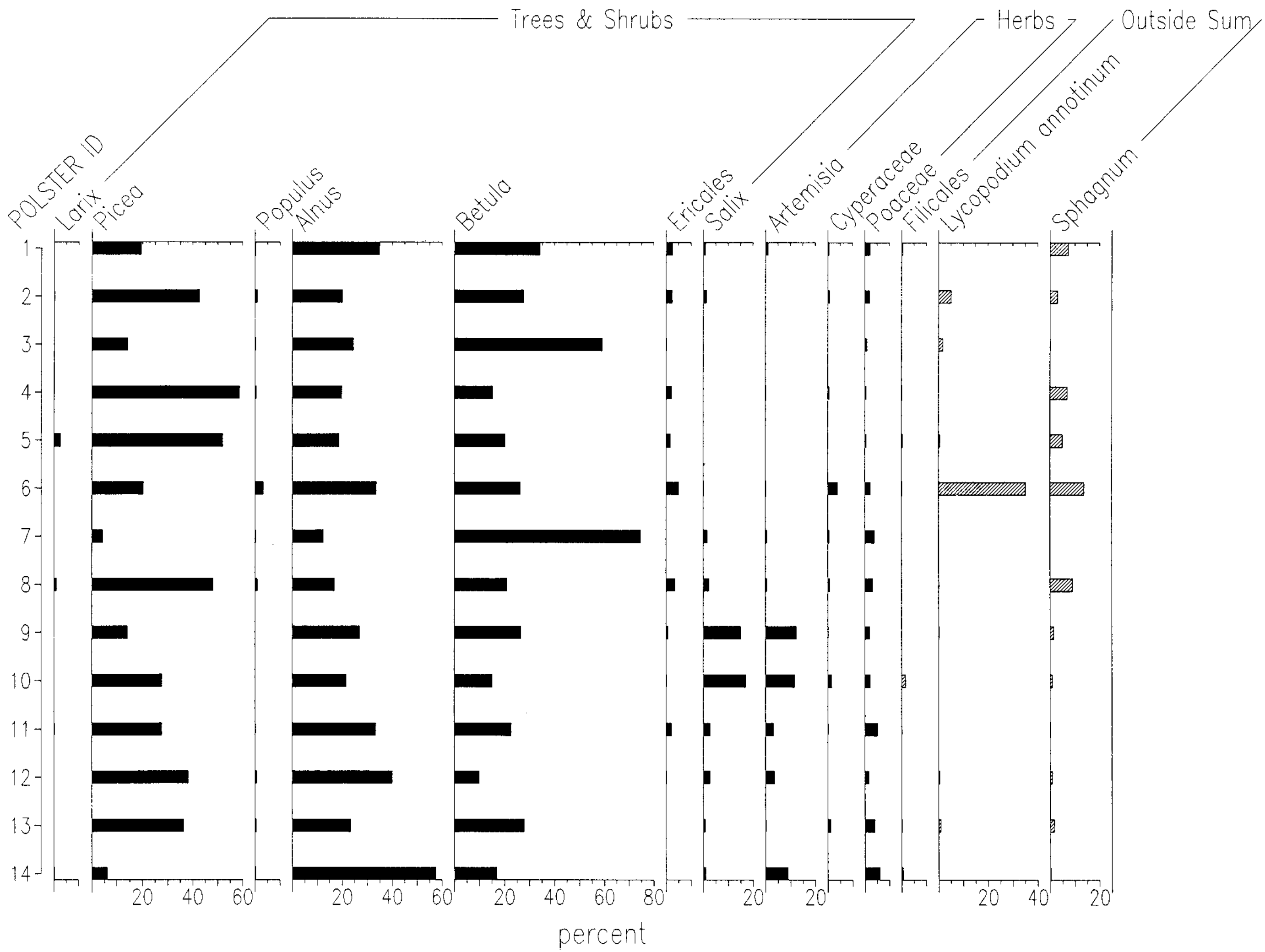

FIG. 2. Percentage pollen diagram, modern polster samples, North Alaska Range (reduced data set). Sites 1–3, Sushana River; sites 4–8, Foraker River; sites 9–12, Toklat River; sites 13–14, Landslide Bluff site.

vegetation plot. Poaceae is consistently represented with small values (0.6–6%) but *Populus*, *Larix* (larch), Cyperaceae, Ericales, Filicales (ferns and fern allies), and *Lycopodium annotinum* (stiff clubmoss) were sporadically recovered in the modern samples. Peak willow percentages are recorded in two polsters (9 and 10) collected from the dry willow/poplar forest at the Toklat High Bluff site. *Pinus* (pine) pollen is recorded in only two samples (<1%). The closest stands of pine are about 600 km southeast of the study sites.

SITE STRATIGRAPHY AND CHRONOLOGY

We sampled the Toklat High Bluff site (63˚37′N, 150˚07′W; elevation 366 m) (Fig. 1) in 1990. The site records a series of depositional units comprising eolian and fluvial deposits (Fig. 3). Wood and tephra are common throughout the section. The section records events beginning with the deposition of Nenana Gravel (Wahrhaftig, 1958). The Nenana Gravel was deposited during uplift of the Alaska Range in the Pliocene, ca. 5–3 million yr. B.P. (Ager et al., 1994). Of interest here are units 3 and 2 overlying the Nenana Gravel. Unit 3 records an interval of eolian sediment accumulation, associated with the migration of the Toklat River away from the site. This unit is about 12 m thick and contains a woody zone about 3 m above its lower contact. This woody zone probably reflects a minor stabilization of the eolian mantle by shrubs. Some of the silt is slightly organic rich, suggesting local slackening of eolian accumulation rates and soil development. A portion of the organic silt (sample site B) was sampled for fossil insects and pollen.

Unit 2 includes felted peat and silty peat with woody debris at the base; it has sharp upper and lower contacts. This deposit reflects complete stabilization of the surface by vegetation, tree growth, and generally warm climatic conditions.

The chronology of the sediments exposed at the Toklat High Bluff site is not well constrained. Many of the radiocarbon assays of organic detritus and wood from this exposure yielded infinite ages (e.g., > 42 900, > 35 800, and > 42 000 B.P.).

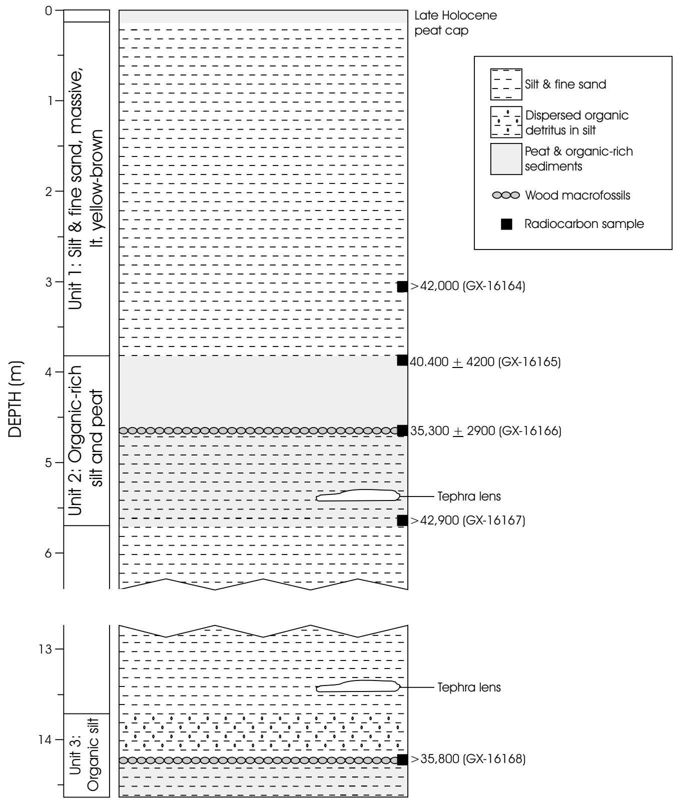

FIG. 3. Stratigraphic section, Toklat High Bluffs site.

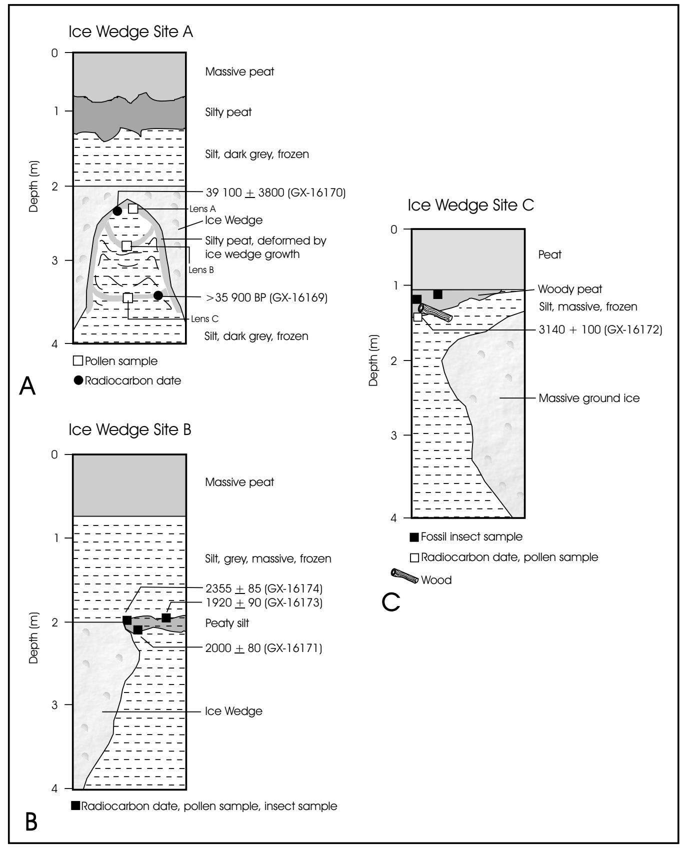

FIG. 4. Stratigraphic sections, Foraker Ice Wedge sites. A, site A stratigraphy; B, site B stratigraphy; C, site C stratigraphy.

Other radiocarbon ages from the section, while not infinite, are at least suspected to represent samples with too little radiocarbon activity to allow confidence in their seemingly finite age. We believe Unit 3 was deposited in a pre-Wisconsin interglacial or interstadial interval of indeterminate age. The organic-rich silt and peat deposits in Unit 2 may represent either a mid-Wisconsin interstadial interval or the last (Isotope stage 5e) interglacial interval. A thin tephra layer (THB-T3), collected just above the woody zone, was submitted for dating by the fission-track method, and yielded a pre-Quaternary age (Robert Walter, Berkeley Geochronology Center, pers. comm. 1993). This tephra was apparently reworked into much younger sediments, and its age tells us nothing about the age of the surrounding sediments. The rich macrofossil record of conifer wood and cones from this unit leads us to believe it was deposited when regional climates were at least as warm as today; this in turn suggests an interglacial rather than an interstadial interval. We believe the massive sandy silt of Unit 1 is most likely an eolian deposit of late Wisconsin age, and that the > 42 000 age is spurious.

The sampling localities on the Foraker River (63˚22′N, 151˚51′W; elevation 418 m) (Fig. 1) are cutbank exposures. Previous investigations (Ten Brink, pers. comm. 1990) revealed an 8 m section of frozen silt and peat. Peat at 4 m depth was dated at > 35 000 B.P. (A-2164). One pollen sample from this peat was analyzed by Ager (pers. comm. 1996). This locality (the Foraker Ice Wedge site) was resampled during our field season in 1990, in addition to another exposure about 200 m upstream (the Foraker Slump site).

The Foraker Ice Wedge site consists of a series of exposures along a bluff that is retreating from the river's edge as underlying frozen silt and ground ice melt back each summer. The site was visited by Ten Brink and Ager in 1978, and the face of the bluff has since retreated approximately 20 m (Ten Brink, pers. comm. 1990). Therefore, we are uncertain how the units Elias, Short, and Ten Brink sampled in 1990 relate to the stratigraphic units originally sampled. Three exposures (A, B, and C) were sampled at this locality when it was revisited. Ice Wedge Site A (Fig. 4A) consists of organic silt laterally deformed by massive ground ice (Fig. 5). Our field observations indicated that these sediments accumulated in a small pond that formed on a stabilized surface, probably during the Boutellier interstadial interval. Organic plant remains scraped from Lens A yielded a ^{14}C date of > 35 900 B.P. (GX-16169), but the actual age of the sediments is problematical. Ice Wedge Site B (Fig. 4B) primarily represents an accumulation of organic detritus and peat that filled a space left when an ice body melted. This wedge of organic material is inset into frozen silt and rests unconformably on a massive ice wedge. An organic-rich lens in the frozen silt was sampled approximately 1 m below the ice melt-out fill; it was also beyond the range of radiocarbon dating (> 41 700 B.P. [GX-16175]). Ice Wedge Site C (Fig. 4C) is a 1 m thick lens of peat and wood macrofossils at the top of the section. It lies unconformably above late Pleistocene ice and frozen silts, and the basal 30 cm are frozen.

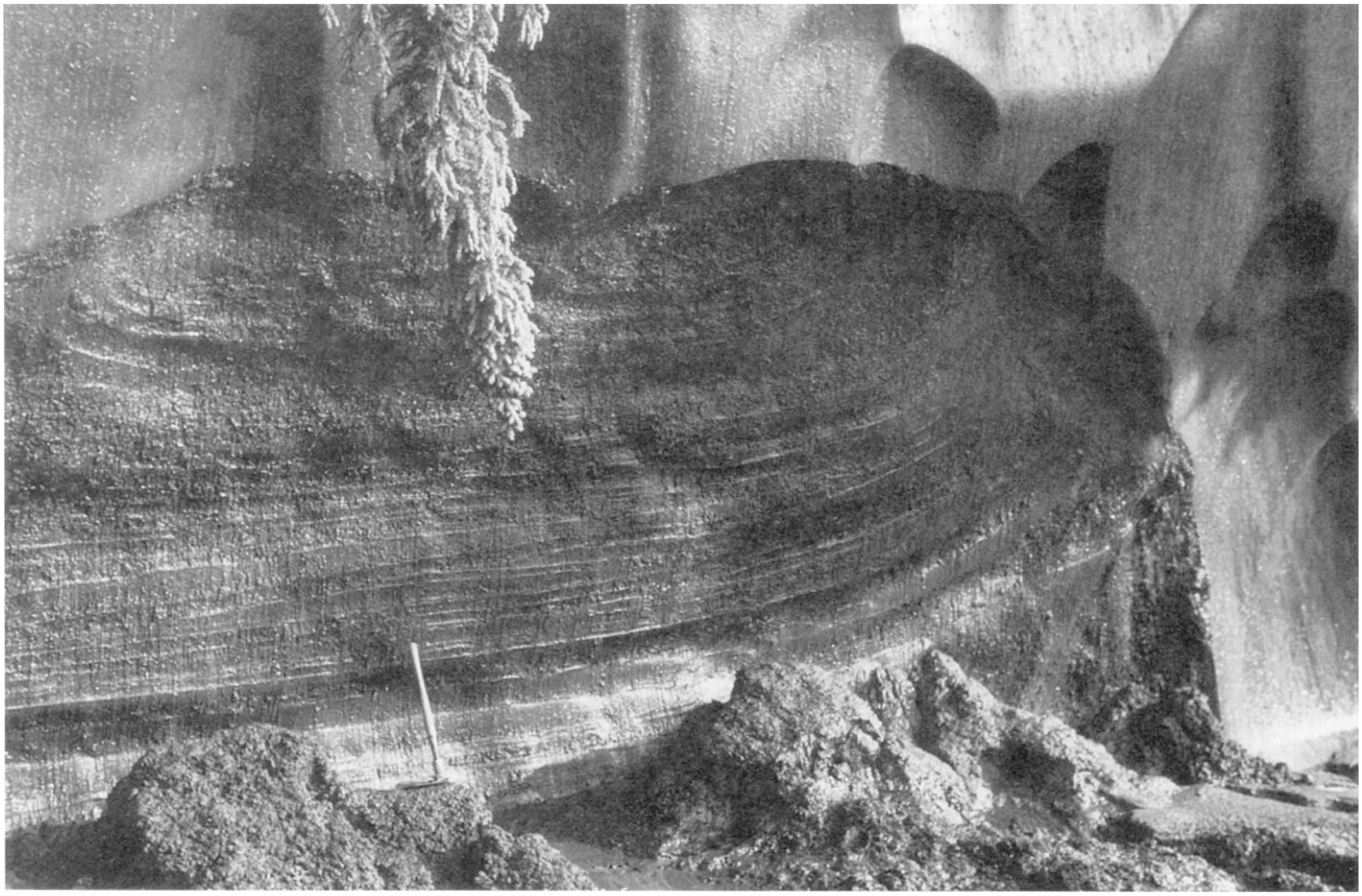

FIG. 5. Photograph of Foraker Ice Wedge, Sample Site A. Note deformation of sediments by surrounding ground ice. Spruce treetop visible in photo is hanging over exposure from the modern surface (out of view). Photo by Susan Short.

Radiocarbon dates indicate that the ice melt-out fill at Ice Wedge Site B and the base of the upper peat capping frozen silt at Ice Wedge Site C were of late Holocene age.

The Foraker Slump site consists of exposures made when the Foraker River undercut frozen sediments, causing a massive slump of material into the river. A composite stratigraphic column of the sedimentary sequence at sites A and B consists of alternating sections of silt and organic-rich silt and peat (Fig. 6). We did not sample the basal organic silt at Slump site A because it was too close to the river and we were unable to reach it. Organic Unit 1, the lowest sampled at this site, was dated at greater than 42 000 B.P. (GX-16176). At the same site, the peat cap (Peat 3), presumed to be late Holocene, was not submitted for dating. Organic Unit 2 represents a complicated suite of organic-rich silts and peats at Slump Site B. Two radiocarbon dates place its development between 8075 (GX-16178) and 6540 B.P. (GX-16177). Our interpretation of the sedimentology and chronology of this stratigraphic column leads us to believe that the massive, frozen silt underlying the Holocene-age sediments was deposited during the late Wisconsin glacial interval (i.e., about 30 000 to 15 000 B.P.). Underlying this frozen silt is a peaty silt that we interpret as a Boutellier interstadial deposit. Since the associated radiocarbon age was > 42 000 B.P., this organic deposit must have accumulated sometime during the early Boutellier interval, which began about 60 000 B.P. (Matthews, 1982). Underlying this organic deposit was another massive silt that is similar in all respects to loess deposits of late Wisconsin age. We interpret that this deposit probably accumulated during the penultimate glaciation of the Alaska Range region, > 60 000 yr. B.P. The peaty silt at the bottom of the exposure may have accumulated during the last interglacial interval (if the penultimate glaciation occurred during early Wisconsin times), or during a prior nonglacial interval (if the penultimate glaciation occurred prior to the last interglacial period).

Organic lenses exposed at the base of the Ice Wedge site were preserved in frozen silts deformed by the growth of massive ground ice at Ice Wedge Site A. Organic plant remains scraped from Lenses A and C yielded ^{14}C dates of 39 100 ± 3800 (GX-166170) and > 35 900 B.P. (GX-16169). Frozen organic-rich silt at Ice Wedge Site B also was beyond the range of radiocarbon dating (> 41 700 B.P. [GX-16175]).

The Sushana River site (64°06′N, 149°55′W; elevation 366 m) is an accumulation of reworked, organic-rich silt beds interspersed with two distinct wood beds and associated peaty deposits (Fig. 7) that overlie fluvial basal

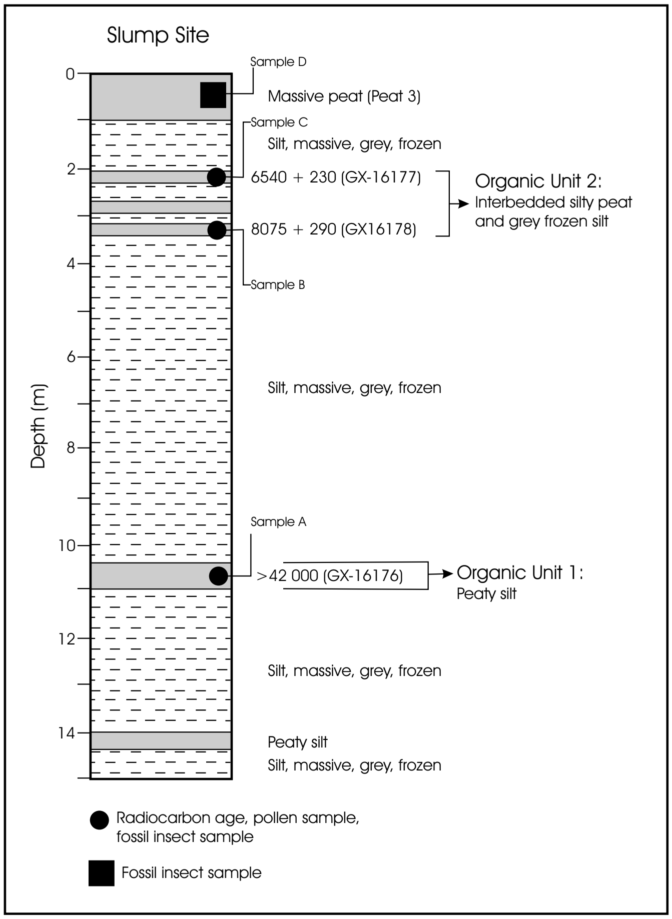

FIG. 6. Stratigraphic section, Foraker Slump site.

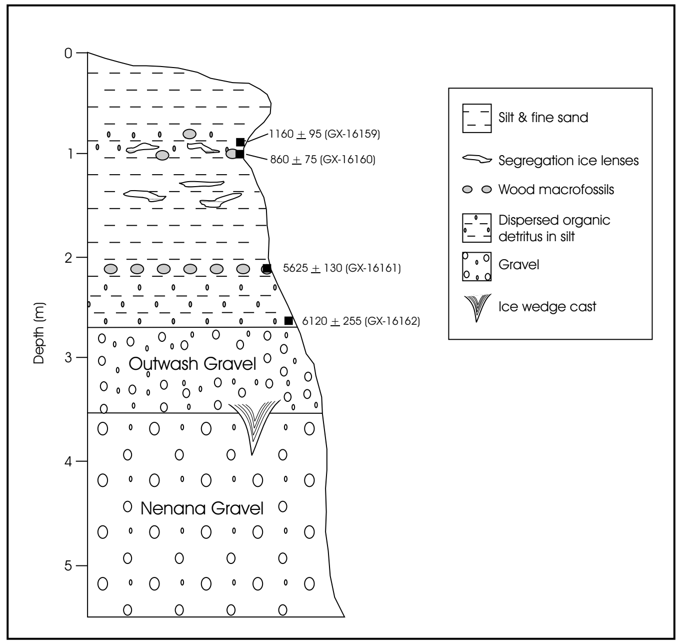

FIG. 7. Stratigraphic section, Sushana River site.

gravels. Both wood beds contained charcoal, and the upper bed (Wood Bed 1) contained spruce logs up to 10 cm in diameter. There was evidence of recent ice melt-out in the section with considerable slumping.

Four dates were submitted from the Sushana River locality; they range from late to mid-Holocene (Table 1). Both wood and organics from Peat 1 were dated. The wood sample dated younger (860 ± 75 [GX-16160]) than the peat sample (1160 ± 95 [GX-16159]), suggesting that some peat dates in this region may be slightly too old. Alternatively, the mixture of radiocarbon dates may suggest retransport of the wood or peat. The dates need to be interpreted cautiously, because melting permafrost can redeposit the wood and peat in much younger sediments.

METHODS

Pollen samples include peats, organic silts, and moss and lichen polsters. Laboratory processing included sieving to remove coarse organics (> 0.25 mm), caustic soda, acetolysis, and hydrofluoric acid (Faegri and Iversen, 1975; Nichols, 1975), with extended boiling times because of the elevation of the laboratory. A tablet containing a known number of exotic tracer grains (*Eucalyptus*) was added to a weighed sample prior to chemical concentration, allowing calculation of pollen concentrations as number of grains per gram dry weight (g/gdw) of sample (Jørgensen, 1967; Stockmarr, 1971).

Pollen counts ranged from 50 to 500 grains (pollen + spores) per sample; pollen percentages were calculated exclusive of spores (Filicales [monolete ferns], *Sphagnum*, *Lycopodium* spp. [clubmoss]). Spores are reported as a percentage of the pollen sum. Pollen identifications were made using the INSTAAR Palynology Laboratory reference collection plus keys and floras (Hultén, 1968; McAndrews et al., 1973; Moriya, 1976). An attempt was made to separate black and white spruce pollen grains on the basis of size measurements. There was substantial overlap in the measurements, which suggests that both species may have been present, and all grains are reported as *Picea* in this study. Discrimination between shrub and tree birch pollen grains was also attempted on the basis of size measurements, but this technique failed to consistently separate these taxa in the modern samples. Therefore, all *Betula* grains were combined in one category.

Material for fossil insect and plant macrofossil analyses was collected as bulk peat samples or was concentrated from organic silts by field-sieving of up to 50 kg of material through a 0.42 mm screen in the river. These materials were processed in the laboratory by the standard kerosene flotation method (Coope, 1986; Elias, 1994) to concentrate and extract insect sclerites from plant macrofossil residues. Fossil insect specimens were mounted with gum tragacanth (a water-soluble glue) onto modified micropaleontology cards. Duplicate specimens were stored in vials of alcohol. Insect fossils were identified with the aid of taxonomic literature and by comparison with modern specimens at the Institute of Arctic and Alpine Research, University of Colorado. A few specimens were referred to taxonomic specialists, as noted in the acknowledgements. Table 1 records all fossil insects recovered in this study.

TABLE 1. Fossil insect fauna, Toklat and Foraker River sites, in minimum number of individuals per sample.

TAXON	SAMPLE[1]							
	A	B	C	D	E	F	G	H
COLEOPTERA								
CARABIDAE								
Notiophilus semistriatus Say	-	-	-	-	-	1	-	-
Dyschirius nigricornis Mots	-	-	-	-	-	1	-	-
Dyschirius sp.	-	2	-	-	-	-	-	-
Bembidion spp.	-	2	-	-	-	-	-	-
Pterostichus brevicornis Kby.	-	1	-	-	-	1	-	-
Pterostichus (*Cryobius*) spp.	3	4	-	1	1	3	3	-
Amara discors Kby.	1	-	-	-	-	-	-	-
Amara cf. *laevipennis* Kby.	-	1	-	-	-	-	-	-
Agonum cf. *gratiosum* Mannh.	-	1	-	-	-	-	-	-
Agonum spp.	-	2	-	-	-	-	-	-
DYTISCIDAE								
Agabus sp.	2	2	-	-	2	-	-	-
Hydroporus sp.	2	2	-	-	3	-	-	-
Acilius sp.	-	1	-	-	-	-	-	-
GYRINIDAE								
Gyrinus sp.	-	1	-	-	-	-	-	-
LIMNEBIIDAE								
Ochthebius sp.	-	3	-	-	-	-	1	1
HYDROPHILIDAE								
Hydrobius fuscipes (L.)	1	5	-	-	-	-	-	-
Helophorus sp.	-	1	-	-	-	-	-	-
Enochrus/Cymbiodyta sp.	-	4	-	-	-	-	-	-
STAPHYLINIDAE								
Eucnecosum spp.	6	3	-	-	5	-	-	-
Olophrum boreale Gyll.	1	-	-	-	-	-	-	-
Olophrum consimile Gyll.	6	6	-	-	-	-	-	-
Olophrum rotundicolle Sahlb.	1	2	-	-	-	-	-	-
Olophrum spp.	19	18	-	-	1	-	-	-
Bledius sp.	-	3	-	-	-	-	-	-
Oxytelinae	1	-	-	-	-	-	-	-
Lathrobium sp.	3	1	-	-	-	-	-	-
Quedius sp.	4	1	-	-	-	-	-	-
Stenus cf. *ageus* Csy.	-	-	-	-	1	-	-	-
Stenus cf. *austini* Csy.	-	-	-	2	1	-	-	-
Stenus cf. *coriaceus* Puthz	-	-	-	-	1	-	-	-
Stenus cf. *kryzhanovskii* Puthz	-	-	-	-	1	-	-	-
Stenus cf. *vinnulus* Csy.	-	-	-	1	-	-	-	-
Stenus sp.	1	3	-	1	2	-	-	-
Mycetoporus sp.	-	-	-	-	-	-	-	2
Tachinus brevipennis (Sahlb.)	-	-	-	1	-	-	1	-
Bolitobiinae indet.	-	1	-	-	-	-	-	-
Lathrobium sp.	-	-	-	1	-	2	1	-
Quedius (*Raphirus*) sp.	-	-	-	-	-	1	2	1
Aleocharinae indet.	-	3	-	-	-	-	-	-
Genus et sp. indet.	1	-	-	-	-	-	-	-
SCARABAEIDAE								
Aphodiinae indet.	-	3	-	-	-	-	-	-
BYRHHIDAE								
Simplocaria tessellata LeC.	-	-	-	-	-	1	-	-
ELATERIDAE								
Ctenicera cf. *kendalli* (Kby.)	-	-	-	-	-	1	-	-
Genus et sp. indet.	-	2	-	-	-	-	-	-
CANTHARIDAE								
Genus et sp. indet.	-	-	-	-	-	1	-	-
COCCINELLIDAE								
Scymnus sp.	-	-	-	-	-	-	-	1
LATHRIDIIDAE								
Corticaria sp.	-	-	-	-	-	-	-	3
Genus et sp. indet.	1	1	-	-	-	-	-	-
CHRYSOMELIDAE								
Donacia cf. *hirticollis* Kby.	-	-	-	-	-	-	1	-
Plateumaris germari (Mannh.)	-	-	-	2	1	-	-	-
Plateumaris (*Shoemakeri*) sp.	-	3	-	-	-	-	-	-
Pyrrhalta sp.	-	2	-	-	-	-	-	-
CURCULIONIDAE								
Apion sp.	-	1	-	-	-	1	-	1
Lepidophorus lineaticollis Kby.	-	5	-	-	-	-	-	-
SCOLYTIDAE								
Polygraphus rufipennis (Kby.)	1	-	-	-	-	-	-	-
Phloeotribus piceae Swaine	1	-	-	-	-	-	-	-
Pityophthorus sp.	-	-	-	-	-	-	1	1
TRICHOPTERA								
Genus et sp. indet.	-	1	-	-	146	-	-	-
HEMIPTERA								
CICADELIDAE								
Genus indet.	-	1	-	-	-	-	-	-
HYMENOPTERA								
FORMICIDAE								
Camponotus herculeanus L.	-	-	-	-	-	-	-	3
Formica (*Fusca*) sp.	-	-	-	-	-	-	-	1
Myrmica alaskensis Whlr.	1	8	3	-	2	1	1	4
Hymenoptera parasitica indet.	-	1	-	-	-	-	-	-
ARACHNIDA								
ACARI								
PROSTIGMATA								
LABIDOSTOMMATIDAE								
Genus et sp. indet.	-	-	-	-	-	-	-	1
ORIBATEI								
ORIBATULIDAE								
Phauloppia sp.	1	4	-	-	-	-	-	-
PELOPPIIDAE								
Ceratopia bipilis (Herm.)	-	2	-	-	1	-	-	-
Ceratopia sp.	-	-	-	-	-	-	-	1
CERATOZETIDAE								
Diapterobates humeralis (Herm.)	-	6	-	-	1	-	1	-
Sphaerozetes nr. *castaneus* (Herm.)	-	-	-	-	1	-	-	-
CRUSTACEA								
CLADOCERA								
Daphnia sp.[2]	-	+	-	-	+	-	-	-

[1] Samples: A, Toklat Unit 2, 0–80 cm; B, Toklat Unit 2, 90–180 cm; C, Toklat Unit 3; D, Foraker Slump, Sample A; E, Foraker Slump, Samples B and C; F, Foraker Slump, Sample D; G, Foraker Ice Wedge B; H, Foraker Ice Wedge C.

[2] + = species present.

Plant macrofossils were stored in vials of alcohol. Identifications (Table 2) were made with the aid of taxonomic literature and modern specimens in the INSTAAR Paleoentomology Laboratory.

RESULTS

Pre-Holocene Environments

This group of samples includes those with both infinite dates and "old" dates (> 35 000 B.P.) with large errors. We believe that all of these samples are Boutellier in age (60 000 to 30 000 B.P.) or older. This interpretation is based on the paleoecological reconstructions of the sites, as follows.

Unit 2 at the Toklat High Bluffs site can be divided into two zones in both the fossil pollen (Fig. 8) and fossil insect data. Both, however, record the presence of conifers in the region. The presence of both dytiscid and hydrophilid water beetles in the samples suggests that this was a mire that was consistently well-vegetated at its edges, but maintained open water throughout the interval represented in Unit 2. The presence of *Plateumaris* aquatic leaf beetles at 140–150 cm and 170–180 cm depth in Unit 2 indicates the establishment of semiaquatic vegetation, such as rushes or sedges, which served as host plants for these beetles. In addition, *Typha latifolia* (cattail) pollen was recovered at the 20 cm depth; this species grows along the Tanana River today (Hultén, 1968).

Boreal or boreo-arctic species dominate each insect fossil assemblage. The samples yielding the strongest indications of boreal conditions were from depths of 0–10 cm and 40–50 cm in Unit 2. These samples contained boreal zone and boreo-arctic insects. With the exception of the bark beetles, the boreal zone insects recovered in Unit 2 are characterized by their association with open ground habitats within forests. None rely on trees. This suggests that conifers were scattered and widely spaced across the landscape; the development of a mire (first sedge fen, then *Sphagnum* bog) fostered more riparian shrubs and trees, including alder and birch, at the expense of spruce.

The pollen spectra (Fig. 8) from the upper 80 cm (Zone II) are characterized by large *Alnus* (59–81%) and moderate *Picea* (3–25%) percentages and large pollen concentration values (17 000–123 000 g/gdw), suggesting an open boreal woodland with dense alder shrub vegetation on or around the bog. This pollen spectrum is similar to the modern spectrum but with more alder and less birch (Fig. 2). It is also comparable to modern altitudinal treeline pollen samples from the Dalton Highway (Short et al., 1985: Fig. 3). Black spruce cones and needles were found in every sample from Unit 2, and white spruce macrofossils were also recovered in several samples (Table 2).

Zone I is characterized by maximum Poaceae (7.5–19%) and Cyperaceae (7–44%) percentages and decreased pollen concentrations below 90 cm (Fig. 8). *Betula* percentages peak (25%) at the peat/silt boundary (90 cm), sustaining moderate values (≤11%) to the base. Filicales and *Sphagnum* spores increase upsection, reaching moderate to large values at the top of the section (38% and 37%, respectively). However, *Picea* percentages increase to 25% at the120 cm level, and white spruce twigs and a cone were recovered at the 100 cm level (Table 2). The insect data indicative of cooler climatic conditions come from the base of Sample Section A, at 140–150 and 170–180 cm. While the difference between these assemblages and those from stratigraphically higher horizons is minimal, these contain a greater proportion of boreo-arctic species and are lacking in obligate forest-dwellers. Intervening samples (70–80 cm and 90–100 cm) represent a gradation between the basal and upper faunas. The presence of *Lepidophorus lineaticollis* and *Pterostichus brevipennis* in the intervals 90–100 and 170–180 cm also supports the interpretation that dry tundra environments were proximal to the site. These data indicate a graminoid tundra with abundant shrubs and ferns. We also believe that the pollen and plant macrofossil data indicate that spruce trees were near the site. At least during the earlier parts of the record documented in Section A, the site may have been at or near the ecotone between spruce forest and mesic shrub tundra.

Zone I is also characterized by peaks in *Pinus*, with 18% at 140 cm, declining to low values at the base. Several grains of exotic deciduous tree taxa were recovered: *Juglans cinerea* (white walnut) and *Ulmus* (elm) (not shown in Fig. 8). Pine pollen grains are well suited to long-distance transport, but the values registered here are larger than those observed in modern pollen databases from the region (Fig. 2, this study; Short et al., 1985; Anderson and Brubaker, 1986). Pine was a dominant conifer in Alaska during the Miocene and Pliocene (Leopold and Liu, 1994), and we believe these taxa represent reworking via windblown silt from the Suntrana Formation of early middle Miocene age.

Five pollen samples were processed from the slightly organic silt lens at Unit 3 at Toklat High Bluffs. Pollen recovery was poor. The pollen spectra (Fig. 9A) are dominated by Poaceae (26–34%) and Cyperaceae (34–45%) pollen. In contrast to Unit 2, *Picea* is present in small percentages (< 5%). *Pinus* is also consistently recovered at this site, but values are small (3–9%). *Alnus* (0–5%) and *Betula* (0–11%) register small-to-moderate values. The pollen, insect, and macrofossil data all support the interpretation of graminoid tundra with willow, birch, and perhaps scattered alder shrubs. The presence of fossil remains of the ant, *Myrmica alaskensis* (Table 1), suggests that the treeline was not more than a few kilometers away from the site.

Sample Site A, Organic Unit 1, at the Foraker Slump is dated > 42 000 B.P. (GX-16176). This sample contained the arctic rove beetle, *Tachinus brevipennis*, as well as elytra of the ground beetle group *Pterostichus* (*Cryobius*) (Table 1). The pollen sample (Fig. 9B) is dominated by *Alnus* (22.2%), *Betula* (35%), *Picea* (24%), and *Sphagnum* (145.2%) (not shown in Fig. 9B), and compares well with the modern pollen spectra (Fig. 2), suggesting an open forest and shrub environment. The sample also yielded spruce twigs and needles, providing further evidence for the proximity of spruce trees to the site at the time of deposition. Therefore, we

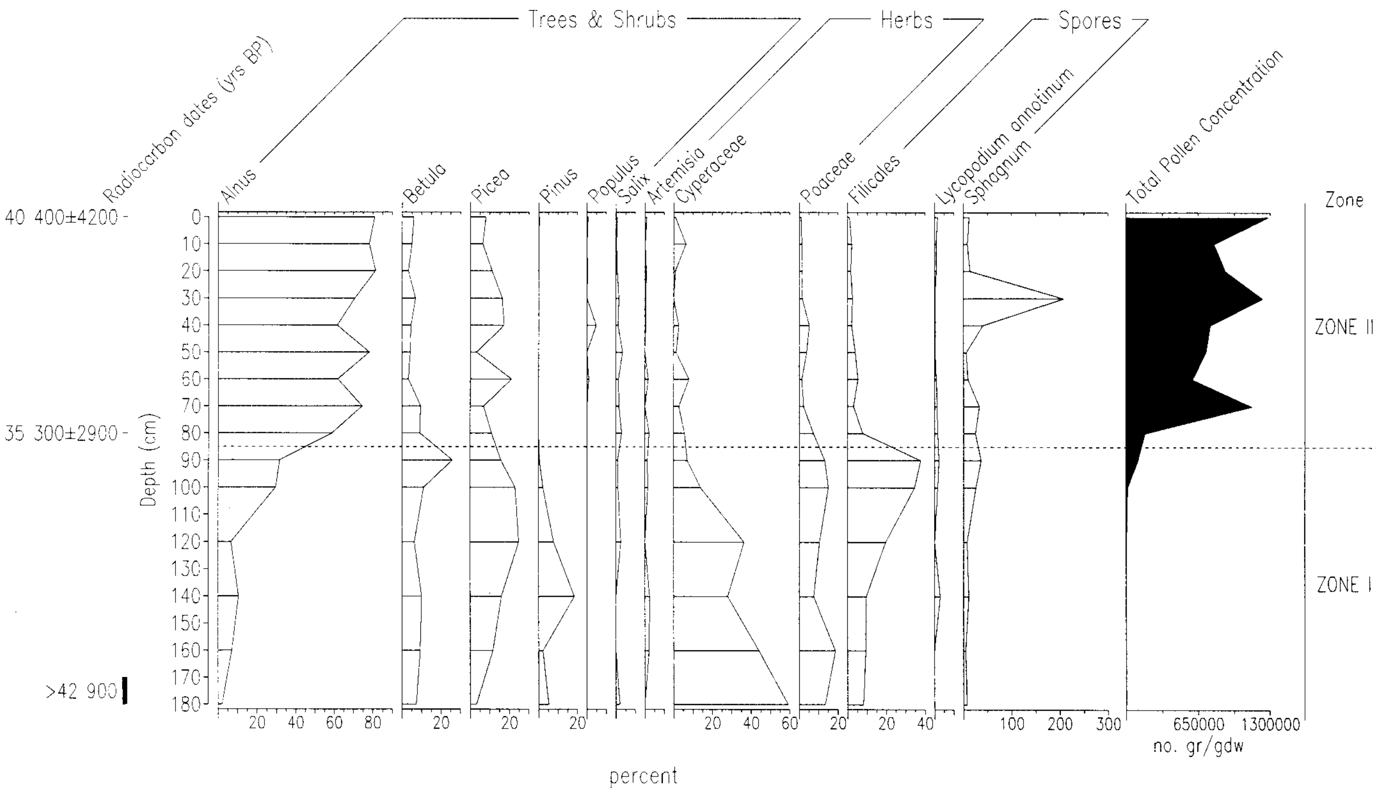

FIG. 8. Percentage pollen diagram, Toklat High Bluffs, Unit 2 (reduced data set).

believe that the landscape was characterized by open taiga; the presence of graminoid pollen (8.7%) and "tundra" beetles indicates the presence of open, meadow areas. We interpret the climate as having been cooler than the modern climate. Its stratigraphic position overlying massive silts of probable Early Wisconsin (Happy Interval) (Hopkins, 1982) age and underlying massive silts of probable Late Wisconsin (Duvanny Yar) (Hopkins, 1982) age indicate that this organic horizon probably represents part of the Boutellier Interval.

Sample Site A at the Foraker Ice Wedge site contained a series of organic lenses in frozen silt, deformed laterally by massive ground ice (Fig. 4A). Two radiocarbon dates were recovered from Lens A and Lens C, but both can be considered as infinite dates. Pollen recovery was poor in the three organic lenses sampled at this site, but a count of > 200 grains was achieved for each sample. The pollen spectra are similar (Fig. 9C), and are dominated by *Salix* (5–20%), Poaceae (12.7–25.2%), and Cyperaceae (27–53%). *Alnus*, *Betula*, *Picea*, Filicales, and *Sphagnum* register small values (< 8%). The vegetation was a graminoid tundra with willow shrubs.

Early Holocene Environments

Organic Unit 2 from Foraker Slump Site B is early Holocene in age, with a basal date of 8075 ± 290 B.P. (GX-16178) and an upper date of 6540 ± 230 B.P. (GX-16177). The insect fauna (Table 1) from the basal sample included numerous water beetles (the predaceous diving beetle, *Hydroporus*, and the whirligig beetle, *Gyrinus*) and caddis fly larvae, all indicative of an aquatic environment. The aquatic leaf beetle *Donacia* cf. *hirticollis* is indicative of emergent vegetation. It feeds mostly on *Potamogeton* (pondweed) and other plants with floating leaves. The upper part of Organic Unit 2 contained *Sphagnum* mosses and *Betula* seeds and some small twigs. The insect fauna, similar to the basal sample, contained numerous aquatic taxa. The rove beetle genus *Stenus* is generally found along the margins of streams and lakes. The aquatic leaf beetle, *Plateumaris germari*, is found today in *Carex* (sedge), *Scirpus* (bulrush), and *Eleocharis* (spike-rush) vegetation along the margins of streams and ponds (Askevold, 1991).

The pollen spectra from four levels in Organic Unit 2 are quite similar (Fig. 9D). *Betula* (50–66%), *Alnus* (2.2–13.7%), Poaceae (11–20%), Cyperaceae (5.5–17%), and *Sphagnum* (10–19%) dominate the spectra. Conifer pollen is rare (< 2%). These data suggest a birch shrub tundra with scattered alder, but with no conifers locally.

Middle to Late Holocene Environments

Organic Unit 3 from Foraker Slump Site B is presumed late Holocene in age, overlying a massive, frozen silt that may have been deposited during the Neoglacial period. This unit contained abundant *Sphagnum* peat with many small conifer twigs. The insect fauna included *Pterostichus brevicornis*, *Notiophilus semistriatus,* and *Dyschirius nigricornis* (Table 1).

TABLE 2. Plant macrofossil list, North Alaska Range sites.

TAXON	SAMPLE[1]						
	A	B	C	D	E	F	G
BRYOPHYTA							
Sphagnaceae							
Sphagnum sp.	+	-	+	+	+	+	-
Amblystegiaceae							
Drepanocladus	+	-	-	+	-	-	-
GYMNOSPERMAE							
Pinaceae							
Picea glauca (Moench)	+	-	-	-	-	-	-
Picea mariana (Mill)	+	-	-	-	-	-	-
Picea sp.	-	-	+	+	+	-	+
ANGIOSPERMAE							
Betulaceae							
Betula sp.	+	+	-	+	+	-	-
Cyperaceae							
Carex sp.	+	+	-	+	+	-	+
Ericaceae							
Ledum groenlandicum Oeder	-	-	-	-	+	-	-
Menyanthaceae							
Menyanthes sp.	+	-	-	-	-	-	-
Nymphaeaceae							
Nymphaea cf. *tuberosa*	-	-	-	+	-	-	-
Ranunculaceae							
Caltha sp.	+	-	-	-	-	-	-
Rosaceae							
Rubus sp.	+	-	-	-	-	-	-
Salicaceae							
Populus sp.	-	-	-	-	-	-	+

[1] Samples: A, Toklat, Unit 2; B, Toklat, Unit 3; C, Foraker Slump, Sample A; D, Foraker Slump, Sample B; E, Foraker Ice Wedge B; F, Foraker Ice Wedge C; G, Sushana.

In contrast to the early Holocene samples, the late Holocene peats from the Foraker Slump site contain moderate values of *Picea* pollen (14% and 12%), although *Alnus* (27% and 36%) and *Betula* (26% and 36.6%) dominate the spectra (Fig. 9E). Indeed, with the importance of Ericales pollen and *Sphagnum* spores (not illustrated), the pollen spectra resemble the modern polster spectra from the Foraker River region (Fig. 2). Taken together, the beetle and pollen data suggest boreal forest conditions, but with extensive shrubs and open ground.

At the Foraker Ice Wedge site, sample Site B, a small lens of organic-rich silt dated to the late Holocene, yielded woody organic detritus with *Sphagnum* mosses, spruce needles, *Ledum* leaves, and *Carex* and *Betula* seeds. The base of the lens (Sample Level 1) contained a few head capsules of the ant, *Myrmica alaskensis*. The middle of the lens (Sample Level 2) contained a combination of tundra and forest insects, including *Tachinus brevipennis* and the bark beetle (Scolytidae), *Pityophthorus*, as well as an elytron on *Pterostichus* (*Cryobius*). This mixture of faunal elements suggests that the sediment was reworked, containing insects from both cold and warm environments. It also suggests that the pollen and plant data may also be from mixed assemblages. The uppermost sample from the lens (Sample Level 3) contained a few insect specimens, but none that are diagnostic of any particular environmental regime, except for the ant, *Myrmica alaskensis*, which is a boreal forest dweller, ranging north to the treeline in Alaska.

The four pollen samples from this site (Fig. 9F) record similar spectra dominated by *Alnus* (55–75%), *Betula* (10–32.6%), *Picea* (4.4–8.4%), and *Sphagnum* (14.4–38.5%). There is no evidence of reworked or degraded pollen grains in these samples. The late Holocene sample from Site C is also dominated by *Alnus* pollen (68%). These large alder percentages contrast with the modern pollen samples (Fig. 2) from the Foraker area and the late Holocene pollen spectra from the nearby Foraker Slump site, which record generally higher birch and spruce values and more moderate alder percentages. The importance of alder in the vegetation at the Foraker Ice Wedge site ca. 2000–3000 B.P. probably reflects a local vegetation pattern, perhaps a disturbance such as fire. The two insect samples (Sample Levels 2 and 3) contained a boreal insect fauna, including coniferous bark beetles and boreal ants.

At the Sushana River section, pollen samples were collected from the modern peat cap, Peat #1, Wood Bed 2, basal disseminated organics, and from two levels above and below the peat lens. Samples for fossil insect analyses were collected from Peat #1 and from between Wood Bed 2 and the disseminated organics at the base of the section; these samples proved barren of fossils, however. The Sushana paleoenvironmental record is entirely Holocene in age, dating from 6120 B.P. to the late Holocene. Although demonstrating some variability, the six pollen samples record similar pollen spectra (Fig. 9G). They are dominated by *Alnus* (15.7–27.8%), *Betula* (21.6–55.8%), *Picea* (15–52%), Poaceae (4–16.3%) and *Sphagnum* (5.9–72.6%). These values are similar to the modern polster record from this site (Fig. 2) and record an open spruce-shrub forest environment.

Discussion of Selected Insect Species

The Toklat High Bluff and Foraker insect assemblages yielded 70 arthropod taxa, mostly insects (Table 1). Most of the species identified in the assemblages represent boreal zone habitats and have been collected in the Alaskan interior in recent times. The assemblages include upland, riparian, mire, and open-water species.

The ground beetles (Carabidae) identified from the Toklat site include both mesic tundra and boreal forest species. *Pterostichus brevicornis* is a widely distributed, arctic and alpine species. In Alaska, it is found today on heath or in dry arctic meadows. It ranges south to the treeline and just beyond, into the forest-tundra ecotone regions, living in alder leaf litter (Lindroth, 1966). *Amara discors* is a boreal ground beetle that ranges across coniferous forests in Canada and down into the Rocky Mountains as far south as Colorado. It lives in open, sandy habitats with sparse vegetation cover (Lindroth, 1968). *Amara* cf. *laevipennis* is another boreal species. It also ranges across coniferous forest regions of Canada and south along the Rockies to Colorado. Modern specimens have not been collected on either arctic or alpine tundra (Lindroth, 1968). Like *A. discors*, *A. laevipennis* lives in open country with herbaceous vegetation. *Agonum gratiosum* lives today in the boreal and northern temperate

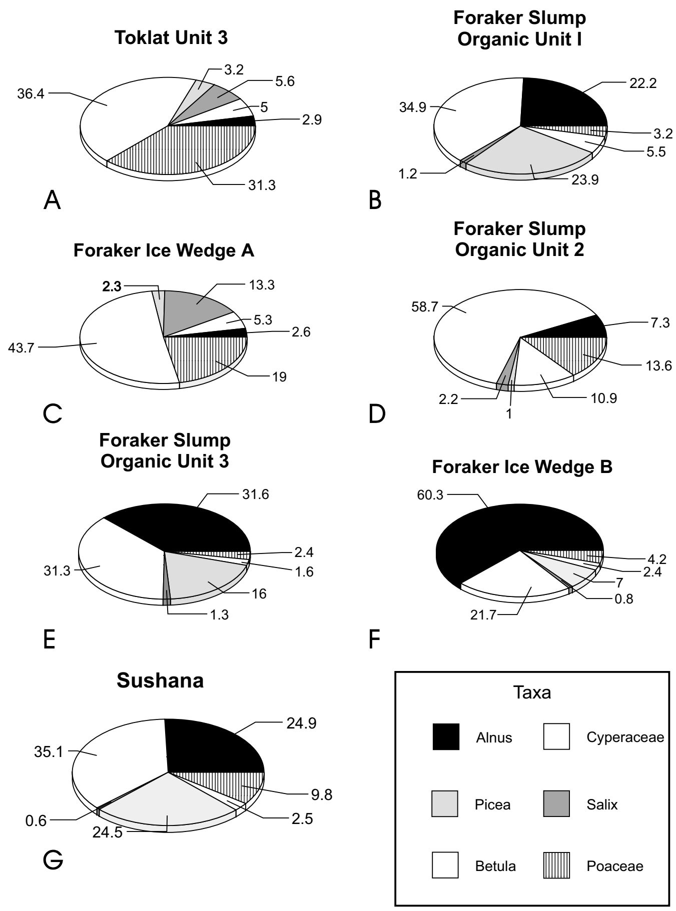

FIG. 9. Circle graphs showing mean pollen percentages for six major taxa at three sites, Denali National Park and Preserve. A, Toklat High Bluffs, Unit 3; B, Foraker Slump, Organic Unit 1; C, Foraker Ice Wedge A; D, Foraker Slump, Organic Unit 2; E, Foraker Slump, Organic Unit 3; F, Foraker Ice Wedge B; G, Sushana River.

zones of North America, ranging south as far as Indiana and Oregon. Similar to the other ground beetles from the Toklat assemblages, *A. gratiosum* prefers open ground situations. It is associated with more mesic and damp habitats, however, including moist, peaty soils or sedge patches (Lindroth, 1966).

Three species of the rove beetle (Staphylinidae) genus *Olophrum* were found in the Toklat assemblages. The ecological requirements of all three species are remarkably alike. They live in damp habitats, including deciduous leaf litter, and clumps of moss and sedge (Campbell, 1983). *O. boreale* is widely distributed across the boreal regions of North America. Isolated populations have been found in montane forests in Utah, Wyoming, and Montana. In Alaska, it ranges north onto the arctic tundra on the north side of the Brooks Range. *O. consimile* is a holarctic, boreal species. In North America, it ranges across the boreal forest regions of Canada and Alaska, and its range extends south along the Sierra Nevada and Rocky Mountains to Arizona. It has not been collected beyond the treeline (Campbell, 1983). *O. rotundicolle* is found in boreal regions of Canada and Alaska. Unlike the other two species, it has not been found in montane forests to the south of Canada, although subfossil specimens have been collected from late Holocene sites in Colorado (Elias et al., 1986).

The aquatic leaf beetles in the *Shoemakeri* species group of the genus *Plateumaris* range across various parts of the temperate and boreal zones in North America. They feed on semiaquatic vegetation, such as sedges and rushes (Askevold, 1991).

The only weevil (Curculionidae) species identified from the Toklat assemblages was *Lepidophorus lineaticolis*. This species is common on sandy floodplains in Alaska and the Yukon Territory, and is one of the most common species associated with dry, poorly vegetated habitats in Pleistocene assemblages from Eastern Beringia (Matthews, 1983).

Two species of coniferous bark beetles (Scolytidae) were found in the fossil assemblages. *Polygraphus rufipennis* is a generalist, attacking all species of conifers across the boreal regions of North America. *Phloeotribus piceae* attacks spruce trees across boreal regions of North America (Bright, 1976).

Myrmica alaskensis is one of the most widely distributed ant species in Alaska. It ranges from the southern flank of the Brooks Range south throughout the interior, in both boreal and tundra regions (Nielsen, 1987). It has been collected from tussocks in swamps, decayed logs, and in mosses.

Two species of oribatid mites were identified, *Ceratopia bipilis* and *Diapterobates humeralis*. Both of these are common species in subarctic and boreal regions of Alaska today (Behan-Pelletier, pers. comm. 1992).

The ground beetles (Carabidae) from the Foraker sites (Table 1) include both boreal and arctic tundra species. *Dyschirius nigricornis* is found today across the boreal regions of Canada and Alaska, but it also ranges north onto arctic tundra in western Alaska (Lindroth, 1961). It lives on moist, peaty soil with *Sphagnum* and other mosses. *Notiophilus semistriatus* is more widely distributed across the entire boreal forest region, with additional populations in montane forests of the Rocky Mountains and the Appalachians. It lives on open, dry ground with thin, low vegetation (Lindroth, 1961). *Pterostichus brevicornis* was also found in the Foraker assemblages.

The rove beetle, *Tachinus brevipennis*, is an inhabitant of arctic tundra in Alaska and eastern Siberia. It has been found along the northern coast of Alaska and east to the Mackenzie Delta region. Campbell (1988) also described specimens from the north slope of the Brooks Range, the first record from an interior locality. This beetle and its close relative, *T. apterus*, are frequently found in glacial stadial deposits from Eastern Beringia (Matthews, 1979; Lea et al., 1991; Elias, 1992).

Plant Macrofossils

Table 2 summarizes the results of the plant macrofossil analyses. Many of the taxa are typically found on boggy or moist substrates today, for example, *Caltha* (marsh-marigold), *Rubus* (raspberry), and *Menyanthes* (buckbean). Spruce cones and wood are common throughout the Toklat section, and spruce wood and needles were also found in most of the Foraker and Sushana samples. Fossil cones assigned to *P. mariana* were recovered from Toklat Unit 2, and *P. glauca* cones were identified from Toklat Unit 3 samples. *Populus* twigs and bark were recovered from the Sushana site, and

Betula macrofossils (twigs, seeds, and leaves) were found in both of the Toklat fossil units, Foraker Slump site B, and Foraker Ice Wedge Site B.

REGIONAL COMPARISONS

The most detailed pollen studies in interior Alaska have been carried out at sites in the Tanana River Valley and adjacent parts of the Yukon–Tanana Uplands near Fairbanks, and in the northern foothills of the Alaska Range (Ager, 1975, 1982, 1983; Ager and Brubaker, 1985; Barnowsky et al., 1987). Data are most complete for the late Wisconsin and Holocene, and the pre-16 000 yr. record is fragmentary.

The middle Wisconsin (Boutellier) interval is represented by data from only a few scattered localities, and these allow only a first-order reconstruction of the vegetation history of the region. The *Picea-Alnus-Betula*-Ericaceae-Cyperaceae pollen assemblage from Harding Lake (Fig. 1) in the Tanana Valley is interpreted as a spruce muskeg-bog environment (Ager, 1975). The pollen spectra from Harding Lake and from Isabella Basin near Fairbanks indicate that the forest was less extensive than today and that treeline was somewhat lower (Matthews, 1974; Ager, 1975; Nakao et al., 1980). Organic sediments of interglacial character were reported at Landslide Bluff (Fig. 1), a large earthflow in foothills of the north central Alaska Range (Waythomas et al., 1989). Fossil pollen and insect analyses indicate forested conditions at the site followed by either a cooling or a drying climate and replacement by a sedge and grassland-dominated vegetation. Other possible interglacial sites in the north Alaska Range region are rare and have not been studied in detail. Interglacial pollen spectra dominated by *Picea*, *Alnus*, and *Betula* are reported from the Little Delta River valley (63°57′N, 146°52′W) and from the outer Teklanika River valley (64°10′N, 149°39′W) (Ager, 1984). In this study, Sample A from the Foraker Slump exposure records an open taiga environment that probably dates to part of the Boutellier Interval.

Three samples from outcrops in the Alaska Range are also assigned to the Boutellier Interval, but because radiocarbon dates on these samples are infinite, they may represent conditions that existed prior to the mid-Wisconsin interstadial (Ager, 1987). The vegetation in the foothills is interpreted as a herbaceous tundra with occasional willow and dwarf birch shrubs (Ager, 1982); the treeline was interpreted as below 600 m (versus 950 m today). The pollen spectrum recorded at Foraker Ice Wedge Site A reported here also records a herbaceous tundra vegetation. The dating at this site, believed to date to the transition from Late Boutellier to Duvanny Yar, is also in question.

No data from the late Wisconsin interval were recovered in this study. The region of the Alaska Range (Ager, 1987) as well as the lowlands of the Tanana Valley (Ager, 1975) were dominated by sparse, discontinuous herbaceous tundra (i.e., “steppe-tundra”). Climate was significantly colder and more arid than at present; it was probably more continental as well, with short, warm summers and long, severe winters.

A composite pollen percentage diagram for the Tanana Valley for the last 16 000 yr. (Ager and Brubaker, 1985: Fig. 7) records the succession from a herbaceous tundra (full glacial), through a birch-heath shrub tundra (14 000 B.P.), to a cottonwood-willow woodland (11 000 B.P.), to a spruce-birch gallery forest (9500 B.P.), to the modern boreal forest with white (and black?) spruce, alder, and birch at ca. 8400 B.P. Thus, the establishment of spruce predates that of alder by about 1100 yr. in that interior region, in contrast to other regions of Alaska.

At the higher (648 m) Eightmile Lake site (Fig. 1) near the Alaska Range, the birch invasion is dated somewhat later, ca. 13 000 B.P., and *Picea* and *Alnus* appear to have invaded simultaneously at about 7500 B.P. (Ager, 1984; Ager and Brubaker, 1985). Ager (1976) described an 8700-year pollen record from a sediment core from Lake Minchumina (Fig. 1), located in the Tanana–Kuskokwim Lowland north of Denali National Park. At this site, *Alnus* invaded about 7500 B.P., but *Picea* delayed until 5700 B.P. In some lake records from the Tanana Valley, there is evidence of a possible regional decline in *Picea* pollen percentages between ca. 8000 and 6000 B.P. (Ager, 1975, 1983), perhaps related to an episode of warm, dry climate (Hypsithermal) in interior Alaska.

These data and data from other sites in interior Alaska clearly demonstrate a pattern of Holocene spruce migration from north to south, from east to west, and from lower to higher elevations in the North Alaska Range. Dates of spruce establishment range from 9200 B.P. in the Tanana area, 7500 B.P. at Eightmile Lake, and 5700 B.P. at Lake Minchumina; at the Foraker River, the spruce invasion is not well dated, but spruce evidently moved into the area between 6500 and ca. 3000 B.P. This episode is more closely constrained by the paleoenvironmental record from the Sushana River, 110 km northeast of the Foraker River sites. The Sushana site records an open spruce woodland in its basal sediments, which date to 6120 ± 255 B.P. (GX-16161).

The pattern for alder is more complex. In the Tanana sites, alder postdates spruce by 1000 years, but to the south and west the pattern changes. At Eightmile Lake, spruce and alder arrived simultaneously at ca. 7500 B.P., or 1000 years later than in the Tanana Valley; a similar date for the alder invasion is seen at Lake Minchumina and at the Foraker River. The low to moderate alder percentages at the latter, however, suggests that this taxon was not important in the local vegetation until after 6000 B.P. Alder is an important component of the pollen spectra of the Sushana River site from the base (6120 B.P.) to the present.

CONCLUSIONS

The late Quaternary organic deposits studied from the Foraker, Sushana, and Toklat Rivers in Denali National Park and Preserve reveal the presence of various boreal and arctic communities through at least the last 50 000 years. Unit 2 at the Toklat High Bluffs site records open boreal woodland with dense alder shrub vegetation developed around a bog.

This unit is beyond the range of reliable radiocarbon dating, but probably formed during the early to mid-Boutellier interval (ca. 60 000 to 40 000 B.P.). A lower level of this stratigraphic unit, Pollen Zone I, is probably much older, perhaps early- to mid-Pleistocene. It contained pine, walnut, and elm pollen redeposited from Miocene pollen-bearing sediments. The oldest organic unit exposed at the Toklat site (Unit 3) contained pollen, plant macrofossils, and insects indicative of graminoid tundra with scattered birch or alder. Organic Unit 1 at the Foraker River Slump site indicates open taiga with shrubs of probable Boutellier age. The youngest horizon in this unit indicates graminoid tundra environments, marking the transition from interstadial to late Wisconsin glacial environments. Early Holocene samples from the Foraker exposures suggest birch shrub tundra; coniferous forest apparently became established only after 6500 B.P. Local variations in forest composition at the Foraker and Sushana sites were probably the result of disturbances, such as fire.

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REFERENCES

AGER, T.A. 1975. Late Quaternary environmental history of the Tanana Valley, Alaska. Columbus, Ohio: Ohio State University Institute of Polar Studies, Report 54.

———. 1976. Holocene vegetation history of the Lake Minchumina area, Mt. McKinley quadrangle, Alaska. Tempe, Arizona: American Quaternary Association, Sixth Biennial Meeting, Program and Abstracts. 96.

———. 1982. Vegetational history of western Alaska during the Wisconsinan glacial interval and the Holocene. In: Hopkins, D.M., Matthews, J.V., Jr., Schweger, C.E., and Young, S.B., eds. Paleoecology of Beringia. New York: Academic Press. 75–94.

———. 1983. Holocene vegetational history of Alaska. In: Wright, H.E., ed. Late Quaternary environments of the United States. Vol. 2. The Holocene. Minneapolis: University of Minnesota Press. 128–140.

———. 1984. An outline of the Quaternary history of vegetation in the North Alaska Range. In: Ten Brink, N., ed. North Alaska Range Project final report on 1978–1982 geoarcheological studies. Allendale, Michigan: National Geographic Society and the National Park Service.

———. 1987. Quaternary history of vegetation in the North Alaska Range: A preliminary outline. Unpubl. ms. Copy on file with S.A. Elias, Institute of Arctic and Alpine Research, University of Colorado, Boulder, Colorado 80309-0450, U.S.A.

AGER, T.A., and BRUBAKER, L.B. 1985. Quaternary palynology and vegetational history of Alaska. In: Bryant, V.M., and Holloway, R.G., eds. Pollen records of Late-Quaternary North American sediments. Dallas, Texas: American Association of Stratigraphic Palynologists Foundation. 353–385.

AGER, T.A., MATTHEWS, J.V., Jr., and YEEND, W. 1994. Pliocene terrace gravels of the ancestral Yukon River, Circle, Alaska: Palynology, paleobotany, paleoenvironmental reconstruction and regional correlation. Quaternary International 22/23: 185–206.

ANDERSON, P.M., and BRUBAKER, L.B. 1986. Modern pollen assemblages from northern Alaska. Review of Palaeobotany and Palynology 46:273–291.

ASKEVOLD, I.S. 1991. Classification, reconstructed phylogeny, and geographic history of the New World member of *Plateumaris* Thompson, 1859 (Coleoptera: Chrysomelidae: Donaciinae). Memoirs of the Entomological Society of Canada No. 157. 175 p.

BARNOWSKY, C.W., ANDERSON, P.M., and BARTLEIN, P.J. 1987. The northwestern U.S. during deglaciation: Vegetational history and paleoclimatic implications. In: Ruddiman, W.F., and Wright, H.E., Jr., eds. Geology of North America Volume K-3, North America and adjacent oceans during the last deglaciation. Boulder, Colorado: Geological Society of America. 289–321.

BRIGHT, D.E. 1976. Bark beetles of Canada and Alaska (Coleoptera: Scolytidae). Canada Department of Agriculture Publication 1576. The insects and arachnids of Canada, Part 2. 241 p.

CAMPBELL, J.M. 1983. A revision of the North American Omaliinae (Coleoptera: Staphylinidae): The genus *Olophrum* Erichson. Canadian Entomologist 115:577–622.

———. 1988. New species and records of North American *Tachinus* Gravenhorst (Coleoptera: Staphylinidae). Canadian Entomologist 120:231–295.

COOPE, G.R. 1986. Coleoptera analysis. In: Berglund, B.E., ed. Handbook of Holocene palaeoecology and palaeohydrology. New York: John Wiley & Sons. 703–713.

ELIAS, S.A. 1992. Late Quaternary beetle fauna of southwestern Alaska: Evidence of a refugium for mesic and hygrophilous species. Arctic and Alpine Research 24:133–144.

———. 1994. Quaternary insects and their environments. Washington, D.C.: Smithsonian Institution Press.

ELIAS, S.A., SHORT, S.K., and CLARK, P.U. 1986. Paleoenvironmental interpretations of the Late Holocene, Rocky Mountain National Park, Colorado, U.S.A. Revue de Paléobiologie 5:127–142.

FAEGRI, K., and IVERSEN, J. 1975. Textbook of pollen analysis. New York: Hafner Press.

HAMILTON, T.D., REED, K.M., and THORSON, R.M. 1986. Glaciation in Alaska – The Geologic Record. Fairbanks: Alaska Geological Society.

HOPKINS, D.M. 1982. Aspects of the paleogeography of Beringia during the late Pleistocene. In: Hopkins, D.M., Matthews, J.V., Jr., Schweger, C.E., and Young, S.B., eds. Paleoecology of Beringia. New York: Academic Press. 3–28.

HULTÉN, E. 1968. Flora of Alaska and neighboring territories. Stanford, California: Stanford University Press.

JØRGENSEN, S. 1967. A method of absolute pollen counting. New Phytologist 66:489–493.

LEA, P.D., ELIAS, S.A., and SHORT, S.A. 1991. Stratigraphy and paleoenvironments of Pleistocene nonglacial units in the Nushagak Lowland, southwestern Alaska. Arctic and Alpine Research 23:375–391.

LEOPOLD, E.B., and LIU, G. 1994. A long pollen sequence of Neogene age, Alaska Range. Quaternary International 22/23:103–140.

LESLIE, L.D. 1989. Alaska climate summaries. Alaska Climate Center Technical Note 5:257.

LINDROTH, C.H. 1961. The ground beetles of Canada and Alaska, part 2. Opuscula Entomologica Supplement No. 20. 1–200.

———. 1966. The ground beetles of Canada and Alaska, part 4. Opuscula Entomologica Supplement No. 29. 409–648.

———. 1968. The ground beetles of Canada and Alaska, part 5. Opuscula Entomologica Supplement No. 33. 649–944.

MARTINSON, D.G., PISIAS, N.G., HAYS, J.D., IMBRIE, J., MOORE, T.C., Jr., and SHACKLETON, N.J. 1987. Age dating and the orbital theory of ice ages: Development of a high-resolution 0 to 300,000-year chronostratigraphy. Quaternary Research 27:1–29.

MATTHEWS, J.V., Jr. 1974. Wisconsinan environment of interior Alaska: Pollen and macrofossil analysis of a 27 meter core from the Isabella Basin (Fairbanks, Alaska). Canadian Journal of Earth Sciences 11:828–841.

———. 1979. Fossil beetles and the Late Cenozoic history of the tundra environment. In: Gray, J., and Boucot, A.J., eds. Historical biogeography, plate tectonics, and the changing environment. Corvallis, Oregon: Oregon State University. 317–378.

———. 1982. East Beringia during Late Wisconsin time: A review of the biotic evidence. In: Hopkins, D.M., Matthews, J.V., Jr., Schweger, C.E., and Young, S.B., eds. Paleoecology of Beringia. New York: Academic Press. 127–150.

———. 1983. A method for comparison of northern fossil insect assemblages. Géographie physique et Quaternaire 37:297–306.

McANDREWS, J.H., BERTI, A.A., and NORRIS, G. 1973. Key to the Quaternary pollen and spores of the Great Lakes region. Toronto: Royal Ontario Museum, Life Sciences Miscellaneous Publications.

MORIYA, K. 1976. Flora and Palynomorphs of Alaska. Tokyo: Kondasha Company. In Japanese.

NAKAO, K., LA PERRIERE, J., and AGER, T.A. 1980. Climatic changes in interior Alaska. In: Nakao, K., ed. Climatic changes in the Interior Alaska: Report of the Alaskan Paleolimnology Research Project - 1977/78/79. Hokkaido, Japan: Laboratory of Hydrology, Department of Geophysics, Hokkaido University.

NICHOLS, H. 1975. Palynological and paleoclimatological study of the late Quaternary displacement of the boreal forest-tundra ecotone in Keewatin and Mackenzie, N.W.T., Canada. Institute of Arctic and Alpine Research, Occasional Paper No. 15. 87 p.

NIELSEN, M.G. 1987. The ant fauna (Hymenoptera: Formicidae) in northern and interior Alaska. Ecological News 98:74–88.

PÉWÉ, T.L. 1975. Quaternary geology of Alaska. U.S. Geological Survey Professional Paper 835. 145 p.

RITTER, D., and TEN BRINK, N.W. 1980. Glacial chronology of the north central Alaska Range and its implication for discovery of early-man sites. Geological Society of America, Abstracts with Programs 12:1534.

SHORT, S.K., ANDREWS, J.T., and WEBBER, P.J. 1985. Pollen, vegetation and climate relationships along the Dalton Highway, Alaska, U.S.A.: A basis for Holocene paleoecological and paleoclimatic studies. Arctic and Alpine Research 18:57–72.

STOCKMARR, J. 1971. Tablets of spores used in absolute pollen analysis. Pollen et Spores 13:615–621.

TEN BRINK, N.W. 1983. Glaciation of the northern Alaska Range. In: Thorson, R.M., and Hamilton, T.D., eds. Glaciation in Alaska – Extended abstracts from a workshop. University of Alaska Occasional Paper No. 2. 82–91.

———. 1984. North Alaska Range Project final report on 1978–1982 geoarcheological studies. Allendale, Michigan: National Geographic Society and National Park Service.

TEN BRINK, N.W., and WAYTHOMAS, C.F., 1985. Late Wisconsin glacial chronology of the north-central Alaska Range: A regional synthesis and its implications for early human settlements. In: Swanson, W., ed. North Alaska Range Early Man Project. National Geographic Society Research Reports 19[1978]. 15–32.

THORSON, R.M. 1986. Late Cenozoic glaciation of the northern Nenana Valley. In: Hamilton, T.D., Reed, K.M., and Thorson, R.M., eds. Glaciation in Alaska – The Geologic Record. Fairbanks: Alaska Geological Society. 99–121.

VIERECK, L.A., and LITTLE, E.L. 1972. Alaska trees and shrubs. United States Forest Service Handbook No. 410. 265 p.

WAHRHAFTIG, C. 1958. Quaternary geology of the Nenana River Valley and adjacent parts of the Alaska Range. U.S. Geological Survey Professional Paper 293-A. 66 p.

WAYTHOMAS, C.F. 1990. Quaternary geology and late-Quaternary environments of the Holitna Lowland, and Chuilnuk-Kiokluk Mountains Region, interior southwestern Alaska. Ph.D. dissertation, Department of Geological Sciences, University of Colorado, Boulder, Colorado. 268 p.

WAYTHOMAS, C.F., SHORT, S.K., and ELIAS, S.A. 1989. Deposits of interglacial character, Nenana Valley, Alaska. Current Research in the Pleistocene 6:95–98.