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Fossil Pollen and Insect Evidence for Postglacial Environmental Conditions, Nushagak and Holitna Lowland Regions, Southwest Alaska

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ABSTRACT. This paper discusses the results of pollen and insect analyses of postglacial samples from the Nushagak and Holitna lowlands, southwest Alaska. Although radiocarbon dating control is poor, the samples can be arranged in a relative-age sequence based on stratigraphic occurrence. The fossil pollen data record the regional transition from a late-glacial dry graminoid tundra through the postglacial Birch, Alder, and Spruce zones. The lack of xeric insect species in the early postglacial suggests that the lowlands of southwest Alaska experienced maritime climatic conditions, in contrast to the interior. Rapid climatic warming is subsequently indicated by the fossil insect data, although the arrival of alder in the region postdates 8500 yr BP. There is no evidence for coniferous forest in the Nushagak lowland at any time in the postglacial, although spruce arrived in the Holitna lowland in the mid-postglacial.

Key words: pollen analysis, fossil insects, paleoenvironments, postglacial, southwest Alaska

RÉSUMÉ. Cet article traite des résultats d'analyses polliniques et d'insectes d'échantillons postglaciaires venant des basses-terres de Nushagak et d'Holitna, dans le sud-ouest de l'Alaska. Bien que le contrôle de la datation par le radiocarbone soit médiocre, les échantillons peuvent être classés en ordre d'âge relatif, d'après leur occurrence stratigraphique. Les données de pollens fossiles traduisent le passage de la région d'une toundra sèche de graminées datant de la fin de l'époque glaciaire, à des zones postglaciaires de bouleaux, d'aulnes et d'épicéas. L'absence d'espèces d'insectes xérophiles au début du postglaciaire donne à penser que les basses-terres du sud-ouest de l'Alaska ont connu des conditions climatiques maritimes, contrairement à l'intérieur. Les données sur les insectes fossiles permettent donc d'établir qu'il y a eu un réchauffement climatique rapide, bien que l'arrivée de l'aulne dans la région soit postérieure à 8500 ans avant le présent. On n'a pas de preuve de l'existence d'une forêt de conifères dans la basse-terre de Nushagak à un moment quelconque du postglaciaire, bien que l'épicéa fasse son arrivée dans la basse-terre d'Holitna au milieu du postglaciaire.

Mots clés: analyse pollinique, insectes fossiles, paléoenvironnements, postglaciaire, sud-ouest de l'Alaska

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Резюме. В статье обсуждаются результаты анализа пыльцы и насекомых из после-ледниковых отложений низменностей Нушагак и Холитна на юго-востеке Аляски. Несмотря на недостаточный контроль датировки отложений радиоуглеродным методом, их можно выстроить в относительной временной последовательности, основываясь на стратиграфических данных. Ископаемые остатки пыльцы показывают региональный переход от поздне-ледниковой сухой злаковой тундры к стадиям березы, ольхи и ели. Недостаток ксерофильных видов насекомых в начале после-ледниковья предполагает, что, в отличие от внутренних районов, низменности юго-восточной Аляски находились под влиянием морского климата. Быстрое потепление климата последовательно индицируется ископоаемыми остатками насекомых, хотя ольха появилась в регионе 8500 лет назад. Не найдены доказательства существования хвойных лесов на территории Нушагакской низменности на протяжении всего голоцена, однако ель появилась на низменности Холитна в середине после-ледниковья.

Ключевые слова: спорово-пыльцевой анализ, ископаемые остатки насекомых, палеоэкотопы, после-ледниковый, юго-восток Аляски.

INTRODUCTION

Paleoenvironmental research in Alaska has emphasized reconstructing the history of the Beringian environment and the postglacial development of modern vegetation. Recent summaries of the postglacial vegetation history of Alaska (Hopkins *et al.*, 1982; Ager, 1983; Ager and Brubaker, 1985; Barnosky *et al.*, 1987) are based mainly on data from the northern and central regions of Alaska and the Yukon Territory. However, the paleoenvironmental record of southwest Alaska has been little studied until recently (Lea, 1989; Elias and Short, 1992; Lea *et al.*, 1991; Waythomas, 1990).

This paper presents the results of pollen and insect analyses on postglacial sediments from two major regions in southwest Alaska (Fig. 1). Postglacial environments of southwest coastal Alaska are represented by data from the southern Nushagak lowland, while interior southwest Alaska is represented by data from the Holitna lowland, the upper Kuskokwim lowland, and other localities in the nearby Chuilnuk and Kioluk mountains.

REGIONAL SETTING

Physiography and Climate

The Nushagak lowland of coastal southwest Alaska forms a broad depositional basin between the high, glaciated peaks of the northern Aleutian Range (to 2300 m) to the southeast and the lower Ahklun Mountains (to 1500 m) to the northwest (Lea, 1989). The Holitna lowland is located about 300 km northeast of the Nushagak lowland and is a broad intermontane basin containing more than 20 m of unconsolidated Quaternary sediment. The Holitna lowland abuts the foothills of the northwestern Alaska Range on its southwest side and is elsewhere enclosed by low hills and formerly glaciated uplands (Waythomas, 1990).

During late Pleistocene glaciation, ice advanced into both lowlands from the south and east, forming broad piedmont lobes along the northwestern sector of the Cordilleran ice sheet. A glacier complex covering the Ahklun Mountains expanded

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into the Nushagak lowland from the west and coalesced with the Cordilleran ice sheet during all but the last glaciation (Muller, 1953; Coulter *et al.*, 1965; Lea, 1984). In the Nushagak lowland, moraines and ice-thrust ridges form the major topographic features, exhibiting relief to 90 m. Elsewhere the landscape is dominated by low-relief (< 20 m) rolling tundra, underlain by postglacial peat and late-Pleistocene eolian deposits. Permafrost is discontinuous in both lowlands, but indicators of continuous permafrost within Pleistocene sediments (e.g., ice-wedge casts) provide evidence for colder periglacial climates in the past.

The Holitna lowland was less severely affected by Pleistocene glaciation. The area functioned as a depositional basin, receiving mainly periglacial eolian and fluvial sediments during the late-Quaternary (Lea and Waythomas, 1990; Waythomas, 1990). Postglacial deposits in both lowlands are exposed in river and seacoast bluffs and consist mainly of loess, organic silt, and peat that form capping deposits over much of the landscape.

The modern climate of the study area is transitional between maritime and continental, with cool, cloudy, and wet summers and moderately cold winters (Péwé, 1975; National Oceanic and Atmospheric Administration, 1980). The mean annual temperature at Aniak (1951-71) on the Kuskokwim River is –2.2°C, whereas the mean annual temperature at King Salmon (1951-77) on the Nushagak Bay coast is –3.7°C. At both sites mean annual precipitation is around 50 cm (Waythomas, 1990).

Modern Vegetation, Pollen, and Insect Spectra

The southern Nushagak lowland lies at the southwestern limit of boreal forest in Alaska (Viereck and Little, 1972). Trees are typically confined to well-drained sites on modern floodplains and gravelly Pleistocene deposits. Localized open stands of white spruce (*Picea glauca*) extend to the northern shore of Nushagak Bay. Dense but localized forests of white spruce and paper (tree) birch (*Betula papyrifera*) are found inland from the coast (Viereck and Little, 1972). Open-canopy spruce hardwood forest is the most common vegetation in the Holitna lowland.

Poor surface drainage is characteristic of the lowlands and extensive tracts of muskeg and bog dominate these areas. The dominant vegetation is mesic to wet shrub tundra (Viereck and Little, 1972), with tall shrubs of alder (*Alnus crispa*), willow (especially *Salix alaxensis* and *S. glauca*), and birch (*Betula glandulosa*). Low shrubs also are common and include willow (*Salix* spp.), dwarf birch (*Betula nana*), and numerous species of heaths (Ericaceae). A large proportion of the vegetation cover consists of grass (Gramineae) and sedge (Cyperaceae) meadows, which include a rich assemblage of herbs and ferns (Filicales).

Modern altitudinal tree line in the region lies between 300 and 360 m. Upland areas beyond the tree line support a diverse alpine tundra assemblage of lichens, mosses, grasses, low shrubs, and heaths (including *Vaccinium uliginosum* [bog blueberry], *Betula nana*, *Empetrum nigrum* [crowberry], *Ledum decumbens* [Northern Labrador-tea], and *Arctostaphylos alpina* [alpine bearberry]) and some mat-forming plants (e.g., *Silene acaulis* [moss campion] and *Dryas*).

Modern surface pollen data were obtained from moss polsters collected from three coastal localities near Nushagak Bay and eleven interior sites in the Holitna lowland (Waythomas, 1990; Elias and Short, 1992:Fig. 5). The coastal sites register high pollen percentages of *Alnus* (21-34%), *Betula* (16-32%), and Gramineae (11-52%) and smaller percentages of Cyperaceae, Ericaceae, and Filicales. *Picea* pollen is rare in these samples (< 2%), despite the proximity of spruce tree line 20 km to the north. The low spruce percentages may reflect the persistence of strong southerly (onshore) winds during times of spruce pollination.

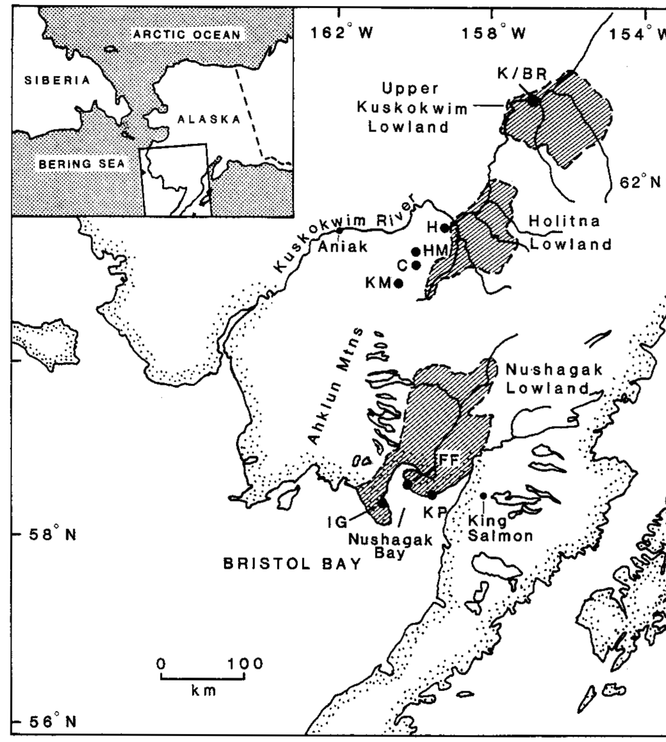

FIG. 1. Location map, Nushagak, Holitna and upper Kuskokwim lowlands, southwest Alaska. Fossil sites: FF = Flounder Flat 3, IG = Igushik 1, KP = Kvichak Peninsula 5. Modern polster sites: HM = Holukuk Mountain, K/BR = Kuskokwim/Big River, H = Lower Holitna, C = Chineekluk Creek, KM = Kioluk Mountain.

The surface samples from the interior Holitna lowland–Chuilnuk/Kioluk mountains region constitute an altitudinal transect from low-elevation spruce forest to middle-elevation birch-spruce forest to tree-line and high-elevation shrub tundra. Along this transect, three main pollen spectra can be defined. Group I is represented by four samples from the low-elevation forest and is characterized by maximum *Picea* (20-25%) and moderate *Betula* (27-52%) percentages. Group II contains four samples from the middle-elevation forest and is dominated by *Betula* percentages (*ca.* 60%). Group III is represented by three samples from the high-elevation tundra and is dominated by *Alnus* values (*ca.* 50%). All three groups contain significantly higher proportions of *Picea* pollen (> 10%) than do the coastal polster samples.

Modern beetle assemblages from the southern Nushagak lowland (Elias, 1988, unpubl. data) are characterized by moderate to high percentages (15-50%) of the *Cryobius* group, indicators of mesic tundra conditions, and low to moderate percentages (5-25% each) of the *Stenus* group, typical of riparian habitats, and the Omaliinae group, found in moist habitats and mesic tundra (see Lea *et al.*, 1991, for ecological groups). Other hygrophilous and boreal taxa are present in low but persistent percentages (< 10% each). The Xeric and *Tachinus* groups, typical of cold tundra environments, are nearly absent from the modern fauna. The Unclassified group includes taxa identified only to the family or generic level and taxa that do not fit any of the other categories.

PALEOECOLOGICAL METHODS

Pollen Analyses

Sediments sampled for fossil pollen analysis include peat and organic silts. Laboratory treatment included sieving to remove coarse organics (> 0.250 mm), 10% sodium hydroxide, acetolysis, and 48% hydrofluoric acid (Faegri and Iversen, 1975; Nichols, 1975). Boiling times were increased due to the elevation of the laboratory (1650 m) and ranged from 40 min for acetolysis to 1 h for hydrofluoric acid.

Pollen identifications were made by Short with the aid of a reference collection housed in the INSTAAR Palynology Laboratory and a number of keys and floras (Hultén, 1968; McAndrews *et al.*, 1973; Moriya, 1976). Pollen sums ranged from 108 to 989 pollen grains per slide; only six samples fell below 150 grains, and the most common range was 200-400 grains. The pollen sum is exclusive of spores, particularly those of monolete ferns (Filicales), *Sphagnum*, and club moss (*Lycopodium* spp.). Spores are reported as a percentage of the pollen sum (Figs. 2-4). In this study 39 taxa were recovered. Only major pollen and spore types are illustrated in the pollen diagrams; minor pollen types are listed in Table 1.

Fossil Insect Analyses

Samples for insect fossil analysis consisted of bulk peat or organic silt, which was sieved through a 0.300 mm mesh screen in the field and laboratory. Yields of concentrated organic matter ranged from 0.5 to 8.0 L. Extraction of insect fossil fragments followed the standard kerosene-flotation method (Coope, 1968). The beetle fossils were identified by Elias through comparison with modern specimens from the INSTAAR insect collection and the Canadian National Collection of Insects, Ottawa. Williams identified fossil caddisfly specimens by comparison with modern material at the University of Toronto and the Royal Ontario Museum. Results are listed in Table 2, and selected fossils are illustrated in Figures 5 and 6.

Following the methodology of Matthews (1983), the fossil beetle assemblages have been grouped into broad ecological and taxonomic categories (Fig. 9) to facilitate comparison of samples. Major categories are broadly representative of 1) aquatic to moist substrates (Hygrophilous and Riparian groups), 2) mesic tundra conditions (*Cryobius* group), 3) dry, poorly vegetated substrates (Xeric group), 4) plant-feeders (Phytophagous group), 5) cold-tundra climates (*Tachinus* group), 6) boreal climates (Boreal group), and 7) carrion-feeders (Carrion group).

PALEOECOLOGICAL RESULTS

Pollen Data

Nushagak Lowland and Bristol Bay Coast: Forty-seven samples for pollen analyses were collected from Flounder Flat (sections 1 and 3) (11), Kvichak Peninsula (15), and Igushik (21) (Fig. 1). Three groups can be distinguished from the pollen spectra (Figs. 2-4).

1) Transition Zone: All three sites record a basal pollen spectrum characterized by high herb pollen percentages, especially *Artemisia* (sage, wormwood) and graminoid taxa, and moderate shrub pollen percentages. This spectrum has been labeled the Transition Zone.

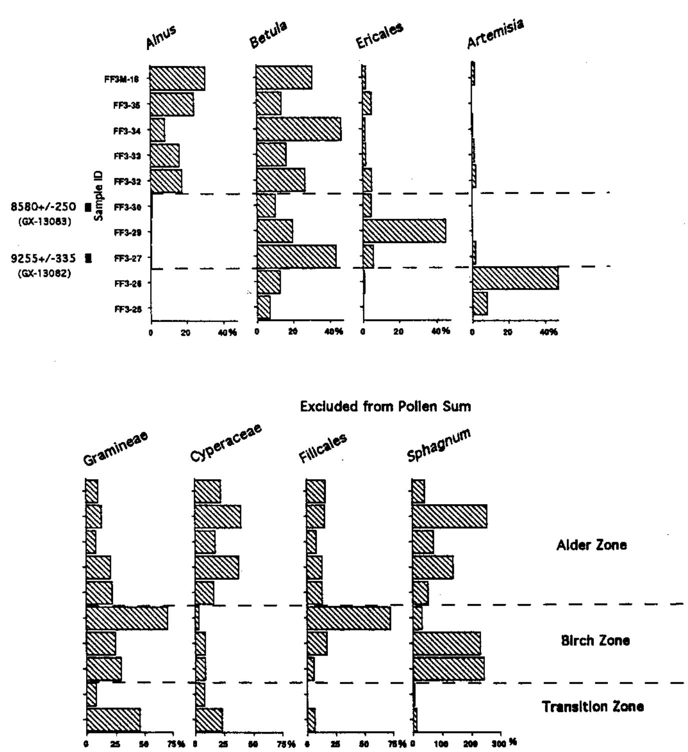

FIG. 2. Percentage pollen diagram Flounder Flat 3 section, southwest Alaska (reduced data set). Pollen sum excludes spores.

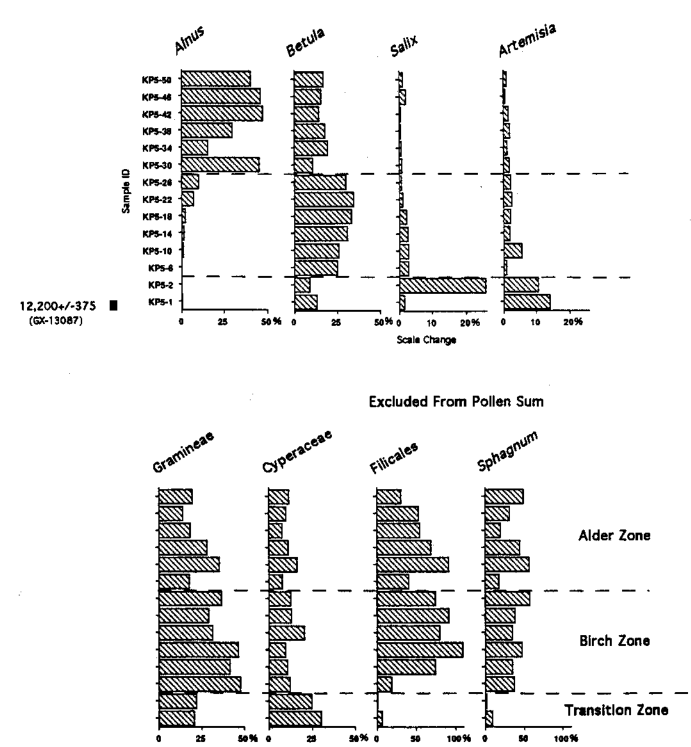

FIG. 3. Percentage pollen diagram, Kvichak Peninsula 5 section, southwest Alaska (reduced data set). Pollen sum excludes spores.

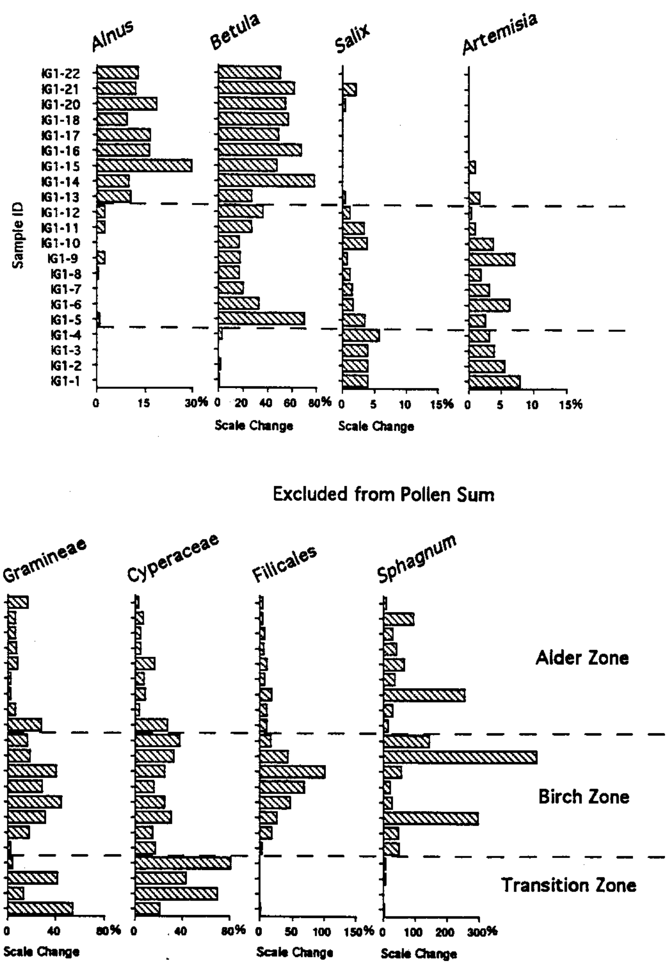

FIG. 4. Percentage pollen diagram, Igushik 1 section, southwest Alaska (reduced data set). Pollen sum excludes spores.

TABLE 1. Minor pollen and spore taxa, postglacial assemblages, southwest Alaska

Caryophyllaceae	*Pedicularis*
Chenopodiaceae	*Pinus*
Compositae-Liguliflorae	*Plantago*
Compositae-Tubuliflorae	*Polemonium*
Cruciferae	*Potentilla*
Ephedra torreyana type	Ranunculaceae
Epilobium	Rosaceae
Equisetum	*Rubus chamaemorus*
Geranium	*Rumex*
Geum	Saxifragaceae
Leguminosae	*Thalictrum*
Lycopodium annotinum	*Typha/Sparganium* type
Lycopodium selago	Umbelliferae
Oxyria	*Valeriana*

Samples FF3-25 and FF3-26 were collected from a compact humified peat that caps a massive loess unit at Flounder Flat (Fig. 5). The sediments from this section record diminished eolian deposition probably associated with deglaciation and progressive revegetation of the landscape. FF3-25, the basal sample, is dominated by Gramineae (45.7%) and Cyperaceae (23.4%) pollen, but it is also characterized by moderate percentages of *Betula* (7%) and *Artemisia* (8%) and a diverse non-arboreal pollen flora, including Umbelliferae (parsley family), *Polemonium* (Jacob's ladder), and *Lycopodium annotinum* (stiff club moss) (Fig. 2). FF3-26 is characterized by high *Artemisia* values (47%), and birch has risen to 12.6%. No *Alnus*, *Picea*, or *Pinus* (pine) pollen were recorded in these samples.

The KP5 section (Lea, 1989:Fig. 5.13) records deposition in a thaw-lake basin that developed on last glacial eolian sediments. Sample KP5-1 (Fig. 3) yielded a radiocarbon age of 12 200 ± 375 BP (GX-13087) and indicates the end of eolian deposition. Peat formation at this time records the beginning of the postglacial interval. The basal pollen spectra (KP5-1 and KP5-2) also record the transitional phase from late-glacial to postglacial environments (Fig. 3). Both samples record *Betula* percentages high enough (9-13%) to indicate the presence of birch shrubs in the region, but Gramineae (20.8%) and *Artemisia* (14%) also are important in sample KP5-1, while *Salix* (25.7%), Gramineae (22%), and *Artemisia* (10.5%) are important components of KP5-2. *Alnus*, *Picea*, and *Pinus* are either absent or present in very low values.

Four samples (IG1-1, IG1-2, IG1-3, and IG1-4) represent the transition period at the Igushik 1 section (Lea, 1989: Fig. 3.4). The pollen spectra (Fig. 4) are dominated by Gramineae (4-54%) and Cyperaceae (21-81%), with no *Alnus* and little *Betula*, *Picea*, or *Pinus*. Non-arboreal taxa, especially *Polemonium*, *Rumex* (dock), Cruciferae (mustard family), and Ranunculaceae (buttercup family), are important at this time.

2) Birch Zone: Pollen samples that record conditions associated with the Birch Zone include FF3-27, 3-29, and 3-30 (Fig. 2), FF1-36, KP5-6 through KP5-26 (Fig. 3), and IG1-5 through IG1-12 (Fig. 4). These samples are dominated by *Betula* (*ca.* 30%) and Gramineae (25-40%) percentages, with significant amounts of Cyperaceae (7-25%), Ericales (3-18%), Filicales (2-186%), and *Sphagnum* (also variable, 20-477%). These data record the establishment of a diverse, mesic, birch shrub tundra; the large values for non-arboreal taxa focus on the importance of tundra vegetation in this coastal region. *Alnus* values are very low, suggesting that alder was not present in the regional vegetation. Radiocarbon dates and pollen analyses from a stratigraphic section on the Kvichak Peninsula indicate that birch arrived in the Bristol Bay region between 12 700 and 7600 yr BP (Ager, 1982). A date of 9255 ± 335 BP (GX-13082) on slightly humified peat with shrub wood from sample FF3-27 (Fig. 2) indicates that birch shrubland was established in the Nushagak lowland by this time.

3) Alder Zone: Peaty deposits that accumulated during the Alder Zone contain pollen spectra characterized by *Alnus* (10-50%), *Betula* (10-78%), Gramineae (*ca.* 15-20%), Cyperaceae (*ca.* 10-30%), Filicales (5-95%), and *Sphagnum* (10-250%) (FF3M-18 through FF3-35, KP5-30 through KP5-50, and IG1-3 through IG1-22) (Figs. 2-4) and form a continuous sequence with deposits that formed during the Birch Zone. This assemblage represents the arrival of alder shrubs in the region and the time when the coastal tundra of southwest Alaska assumed much of its present character. These pollen spectra are comparable to the modern polster samples from the region (Elias and Short, 1992:Fig. 5). In western Alaska, the Alder Zone began about 6000-7000 yr BP. However, in the Bristol Bay region alder is an important component of the pollen spectra by about 7600 yr BP (Ager, 1982). Peaty sediments (FF3-30) that underlie deposits associated with the Alder Zone yielded a radiocarbon date of 8580 ± 250 BP (GX-13083), indicating the spread of alder sometime after this time.

TABLE 2. Combined fossil arthropod faunal list, postglacial assemblages, southwest Alaskan sites, in minimum number of individuals per sample

Taxon	Sample* A	B	C	D	E	F	G	H	I	J	K	L
Coleoptera												
Carabidae												
Nebria sp.	1	—	1	—	—	—	—	—	—	—	—	—
Diacheila polita Fald.	3	2	1	—	3	6	—	1	—	—	1	1
Elaphrus lapponicus Gyll.	1	—	—	—	—	—	—	—	—	—	—	—
Elaphrus sp.	—	—	—	—	—	—	—	—	—	1	—	—
Dyschirius integer LeC.	1	1	—	—	—	—	—	—	—	—	—	—
Dyschirius sp.	—	—	—	1	—	—	—	—	—	—	—	—
Patrobus fovecollis Eschz.	1	—	1	—	2	—	—	—	—	—	—	—
Patrobus septentrionis Dej.	—	—	—	—	—	—	—	—	—	—	1	—
Trechus apicalis Mots.	13	4	3	18	1	14	—	—	—	2	8	11
Bembidion (Plataphodes) sp.	—	—	—	—	—	—	—	—	—	—	1	—
Bembidion spp.	2	2	1	2	1	—	—	1	—	1	—	—
Pterostichus agonus Horn	—	1	—	—	—	—	—	—	—	—	1	—
Pterostichus (Cryobius) arcticola Chd.	—	4	—	—	—	—	—	—	—	—	—	—
Pterostichus (Cryobius) caribou Ball	1	—	—	—	—	—	—	1	—	—	—	—
Pterostichus circulosus Ball	—	—	—	—	—	—	—	—	—	3	—	—
Pterostichus (Cryobius) kotzebuei Ball	—	—	—	—	—	—	—	—	—	1	—	—
Pterostichus (Cryobius) nivalis Sahlb.	—	—	1	—	—	—	1	—	1	—	—	1
Pterostichus (Cryobius) parasimilis Ball	—	—	—	—	1	—	—	—	—	—	—	—
Pterostichus (Cryobius) pinguedineus Eschz.	—	—	—	1	1	—	—	—	—	—	—	—
Pterostichus (Cryobius) similis Kby.	4	—	—	1	2	—	—	—	—	—	—	—
Pterostichus (Cryobius) tareumiut Ball	—	—	—	—	1	—	—	—	—	—	—	—
Pterostichus (Cryobius) spp.	7	2	1	5	9	6	2	14	2	4	3	2
Agonum gratiosum Mannh.	—	—	—	—	1	—	—	—	—	2	—	—
Agonum picicornoides Lth.	—	1	—	—	—	—	—	—	—	—	—	—
Agonum (Melanagonum) sp.	—	—	1	—	—	—	—	—	—	—	—	—
Agonum spp.	—	1	1	—	—	—	—	1	1	2	—	1
Dytiscidae												
Hydroporus spp.	—	—	—	—	—	—	—	1	8	83	1	6
Agabus wasastjernae (Sahlb.)	—	—	—	—	—	—	—	—	—	—	—	3
Agabus spp.	—	—	—	—	—	—	—	—	2	1	—	1
Ilybius discedens Sharp	—	—	—	—	—	—	—	1	—	—	—	—
Ilybius sp.	—	—	—	—	—	—	—	—	1	1	—	—
Rhantus sp.	—	—	—	—	—	—	—	1	—	—	—	—
Hydrophilidae												
Hydrobius fuscipes L.	—	—	—	—	—	—	—	—	—	—	—	1
Cercyon sp.	4	1	3	—	2	—	—	—	—	—	—	1
Helophorus sp.	—	—	—	—	—	—	—	—	—	—	—	1
Gen. et sp. indet.	—	—	—	4	—	—	—	1	—	—	—	—
Limnebiidae												
Ochthebius sp.	—	—	—	2	1	—	—	—	—	—	—	—
Staphylinidae												
Arpedium or *Eucnecosum* spp.	24	11	11	74	176	15	12	—	1	8	10	17
Olophrum consimile (Gyll.)	1	—	—	3	8	—	—	—	—	1	2	1
Olophrum latum Mäkl.	—	—	—	3	6	—	—	28	—	—	—	—
Olophrum rotundicolle (Sahlb.)	2	1	—	1	18	6	5	—	—	3	10	3
Olophrum spp.	—	1	2	12	42	8	5	57	1	11	15	7
Acidota crenata (Fab.)	1	1	—	1	—	—	—	—	—	1	—	—
Acidota quadrata (Zett.)	—	—	—	1	—	—	—	2	1	2	—	1
Holoboreaphilus nordenskioeldi (Mäkl.)	1	—	—	—	—	—	—	—	—	—	—	—
Pycnoglypta nr. *lurida* (Gyll.)	—	—	—	—	3	—	—	—	—	—	—	—
Stenus austini Csy.	—	—	—	—	—	—	—	—	—	—	1	1
Stenus dissentiens Csy.	—	—	—	—	—	—	—	—	—	—	2	—
Stenus hyperboreus Sahlb.	—	—	—	—	—	—	—	—	—	—	—	1
Stenus immarginatus Mäkl.	—	—	—	—	—	—	—	—	—	2	—	—
Stenus intrusus Csy.	—	—	—	—	—	—	—	—	1	9	—	—
Stenus kamtschaticus Mots.	—	—	—	—	—	—	—	—	1	—	—	—
Stenus mammops Csy.	—	—	—	—	—	—	—	—	1	8	1	1
Stenus melanarius Steph.	—	—	—	—	—	—	—	—	1	2	—	—
Stenus cf. *scabiosus* Csy.	—	—	—	—	—	—	—	—	—	—	1	—
Stenus spp.	—	—	1	1	1	1	—	14	—	—	—	—
Lathrobium spp.	6	14	8	1	8	1	1	13	3	10	1	1
Oxytelini gen. et sp. indet.	—	—	—	—	—	—	—	—	—	1	—	—
Philonthus spp.	—	2	1	1	2	—	—	—	—	—	—	—
Quedius aenescens Mäkl.	—	—	—	—	1	—	—	—	—	—	—	—
Quedius fellmani (Zett.)	—	—	—	—	1	—	—	—	—	—	3	1

(continued)

TABLE 2. (Continued)

Taxon	Sample* A	B	C	D	E	F	G	H	I	J	K	L
Quedius fulvicollis (Steph.)	6	2	—	1	1	—	—	—	—	—	—	—
Quedius pediculus (Nordm.)	—	—	1	—	—	—	—	—	—	—	—	—
Quedius (*s. str.*) sp.	—	—	—	—	3	—	—	—	—	—	—	—
Quedius spp.	7	5	3	10	—	1	—	—	—	—	—	3
Lordithon sp.	—	—	—	—	5	—	—	—	—	—	—	—
Mycetoporus sp.	4	—	—	1	—	—	—	—	—	—	—	—
Tachinus brevipennis (Sahlb.)	—	—	—	—	3	—	—	1	—	—	—	—
Tachinus sp.	—	—	—	2	—	—	—	—	—	—	—	—
Tachyporus borealis Campbl.	1	—	—	—	—	—	—	1	—	2	—	—
Tachyporus canadensis Campbl.	6	—	—	5	4	1	4	—	—	—	—	—
Tachyporus nimbicola Campbl.	—	—	—	—	—	—	—	—	—	—	—	1
Tachyporus rulomus Blckwldr.	—	1	—	—	—	—	—	10	—	—	—	—
Tachyporus spp.	1	—	—	—	—	1	1	1	—	—	—	—
Gymnusa (Variegata) sp.	1	—	—	—	2	2	—	1	1	—	—	1
Aleocharinae gen. et sp. indet.	—	3	2	2	—	1	2	4	—	2	—	1
Silphidae												
Thanatophilus trituberculatus Kby.	1	—	—	—	1	—	—	—	—	—	1	—
Leiodidae												
Leiodes sp.	—	—	—	—	—	—	—	—	—	1	—	—
Scarabaeidae												
Aegialia sp.	—	—	—	—	—	—	—	—	1	—	—	—
Helodidae												
Cyphon sp.	—	—	—	—	—	—	—	—	—	—	—	1
Cantharidae												
Podabrus sp.	—	1	—	—	—	—	—	—	—	—	—	—
Lampyridae												
Ellychnia capitosa Fendr.	—	—	—	—	1	—	—	—	—	—	—	—
Cryptophagidae												
Anchicera kamtschatica Mots.	—	—	—	—	—	—	—	3	—	—	—	—
Coccinellidae												
Gen. et sp. indet.	—	—	—	—	—	—	—	1	—	—	—	—
Cerambycidae												
Prionus sp.	—	—	—	—	1	—	—	—	—	—	—	—
Chrysomelidae												
Plateumaris (Pusilla) sp.	—	—	1	—	—	—	—	—	—	—	—	—
Donacia sp.	—	—	—	—	—	—	—	—	—	1	—	—
Altica sp.	—	—	—	—	—	—	—	—	—	1	—	—
Crepidodera sp.	1	1	1	—	—	—	—	—	—	—	—	—
Gen. et sp. indet.	—	1	—	—	—	—	—	1	—	—	—	—
Curculionidae												
Apion spp.	3	3	1	—	7	—	—	—	—	—	—	—
Lepyrus gemellus Kby.	1	—	—	—	—	—	—	—	—	—	—	—
Dorytomus cf. *leucophyllus* (Mots.)	—	—	—	—	—	—	—	—	—	1	—	—
Notaris aethiops Fab.	—	—	—	2	—	—	—	—	—	2	—	—
Gen. et sp. indet.	2	—	1	3	2	—	—	—	1	1	—	—
Scolytidae												
Phloeotribus lecontei Schedl	—	—	—	—	—	—	—	—	—	—	—	1
Polygraphus rufipennis Kby.	—	—	—	—	—	—	—	—	—	—	—	1
Hemiptera												
Cicadellidae												
Gen. et sp. indet.	—	1	—	—	—	—	1	—	—	—	—	—
Trichoptera												
Limnephilidae												
Homophylax crotchi or *H. andax*	—	—	—	—	5	1	2	—	—	3	5	—
Grensia praeterita (Walker)	—	—	—	—	—	—	—	7	—	—	—	—
Limnephilus sp.	—	—	—	—	—	—	—	3	—	—	—	—
Phryganaeidae												
Agrypnia pagetana Curtis	—	—	—	—	—	—	—	5	—	—	—	—
Oligotricha lapponica (Hagen)	—	—	—	—	—	—	—	—	—	1	—	—

(continued)

TABLE 2. (Concluded)

Taxon	A	B	C	D	E	F	G	H	I	J	K	L
						Sample*						
Lepidoptera												
Microlepidoptera												
Gen. et sp. indet.	—	1	—	—	—	—	—	—	—	—	—	—
Hymenoptera												
Chalcidoidea												
Gen. et sp. indet.	—	1	1	—	—	—	1	3	—	—	—	—
Arachnida												
Acari												
Oribatei												
Gen. et sp. indet.	—	1	15	4	8	2	9	50	—	—	—	—
Crustacea												
Cladoera												
Daphnia sp.	—	—	—	—	—	—	—	1	—	—	—	—

*Samples: A – 83FF, 3-M-9; B – 83FF, 3-M-10; C – 83FF, 3-M-11; D – 83FF, 3-M-12; E – 83FF, 3-M-13; F – 83FF, 3-M-16; G – 83FF, 3-M-18; H – Kvichak 1-9; I – 83CW 212A; J – 83CW 212B; K – 83CW 148B; L – 83CW 230C.

Picea pollen was not recovered in postglacial-age pollen samples from the Flounder Flat site, and it was rare (< 1%) in the Kvichak and Igushik samples. *Pinus* pollen was consistently recorded in small values (< 3%). *Picea* pollen is also rare in modern polsters, despite the proximity of spruce forest to the north. Because the dominant summer wind patterns in the region are from the south, spruce pollen is underrepresented in the regional pollen rain. *Pinus* pollen grains, however, are especially suited to long-distance transport. Modern sources for pine pollen may include *P. contorta* (lodgepole pine) in southeastern Alaska (Hultén, 1968:59; Viereck and Little, 1972:Maps 2a and 2b), 1200 km to the east, and *Pinus*

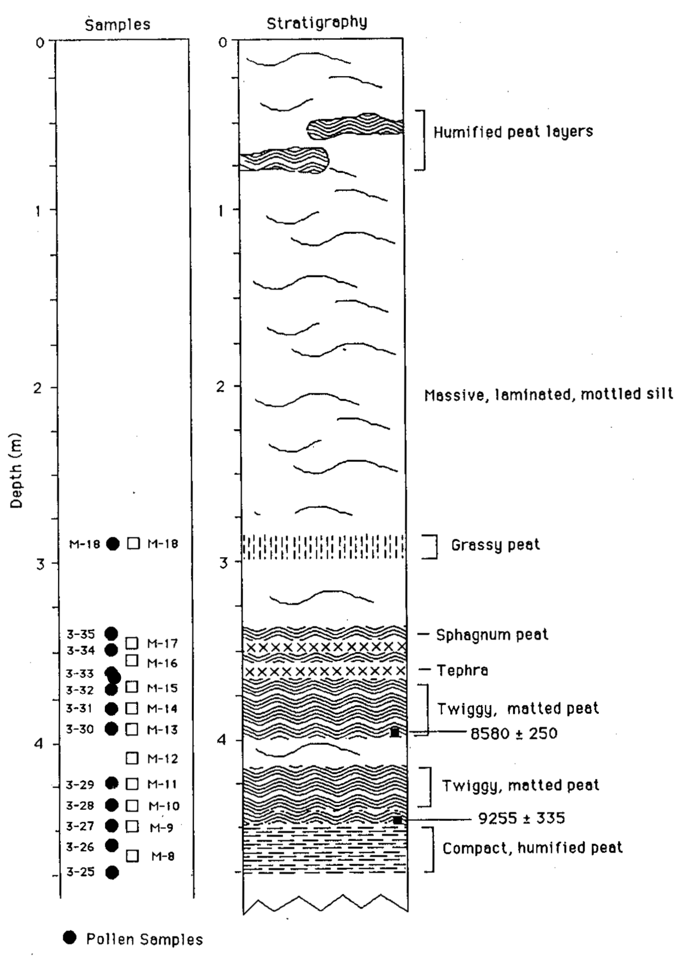

FIG. 5. Stratigraphic section, Flounder Flat section 3, showing locations of pollen, insect and radiocarbon samples.

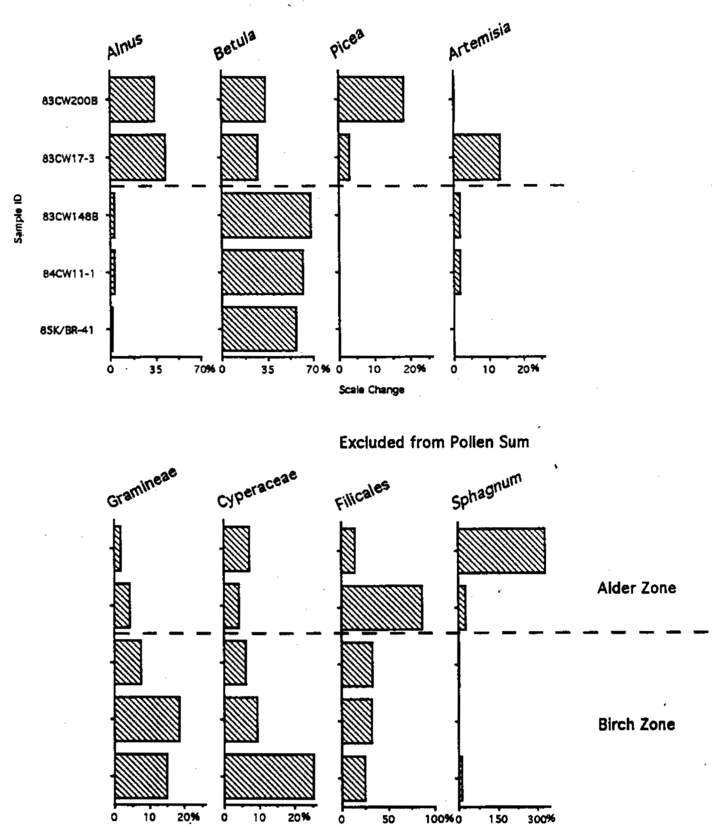

FIG. 6. Percentage pollen diagram, Interior Lowland Region sites, southwest Alaska (reduced data set). Pollen sum excludes spores.

pumila (dwarf Siberian pine) that forms the tree limit with birch on Kamchatka Peninsula.

Interior Lowland Region: Five pollen samples were collected from peaty sediments at several localities in the Holitna –upper Kuskokwim lowland region (Waythomas, 1990: Fig. 2-18) (Fig. 1). None of the samples has been dated; however, they can be arranged in a relative age sequence based on their stratigraphic position with respect to deposits of known age beneath them. The peaty deposits record the regional transition from the Birch to Alder zones (Fig. 6).

Samples 83CW148B (Holokuk Mountain) and 84CW11-1 (Lower Holitna) from the Holitna lowland and sample 85K/BR-41 (Kuskokwim/Big River) from the upper Kuskowkim lowland can be assigned to the Birch Zone. *Betula* percentages range from 56 to 68%, and Gramineae, Cyperaceae, and Filicales also are important. *Betula* shrubs probably populated much of the river valleys, and herbaceous plants such as sedges, grasses, and assorted forbs continued to be important in the drier interfluves.

Significant amounts of *Picea* pollen (18%) are found in only one sample, 83CW200B, from Chineekluk Creek (Fig. 1). *Alnus* (34.3%), *Betula* (33.6%), and *Sphagnum* (336.3%) also are significant. Spruce woodland was present as scattered stands along rivers. *Picea* began to invade the eastern edge of southwest Alaska about 5500 yr BP (Ager, 1983), thus providing a maximum age for this sample.

Maximum *Alnus* percentages (42.6%) are registered in one sample, 83CW17-3, recovered from a cirque above the present altitudinal tree line on the north side of Kioluk Mountain (Fig. 1). Also important are *Betula* (27.2%), Filicales (86.8%), *Lycopodium annotinum* (30%), and *Sphagnum* (27.2%). This pollen spectrum suggests a mesic environment with alder shrubs and a rich understory of moss, ferns, and fern allies and compares well to modern polsters from the same region (Elias and Short, 1992:Fig. 5).

Insect Data

Twelve samples have been analyzed for fossil insects; these include seven from the Flounder Flat 3 section (Fig. 5), one from the Kvichak Peninsula 5 section, and four from the Holitna lowland (Fig. 1). The postglacial arthropod faunas comprise 106 identified taxa in 24 families and seven orders of insects, arachnids, and crustaceans (Table 2). Of these, 58 taxa (55%) have been identified to species. The faunas are dominated by mesic and, in some assemblages, hygrophilous species. Xeric taxa are absent in all but the oldest (late-glacial age) assemblage.

Discussion of Selected Species: Most of the ground beetles (Carabidae) in the postglacial assemblages from southwest Alaska are indicative of mesic tundra habitats. *Diacheila polita* (Fig. 7A) usually inhabits peaty soil on open tundra or the margins of sedge-lined ponds, but it also is found in dry habitats with shrub birch (Lindroth, 1961). *Pterostichus circulosus* and *P. agonus* (Fig. 7C) are likewise indicative of mesic to moist habitats. *P. circulosus* has been collected from wet muds and sedge marshes in interior Alaska and the northern foothills of the Brooks Range (Lindroth, 1966). *P. agonus* is more widely distributed in southeastern Siberia and in the arctic and subarctic regions of North America west of Hudson Bay (Lindroth, 1966). It lives on moist tundra.

Patrobus foveocollis (Fig. 7B) is associated with deciduous leaf litter, including shrub alders, but is not found beyond the northern tree line (Lindroth, 1961). Whereas most of the *Cryobius* group of the genus *Pterostichus* live in mesic tundra habitats (e.g., *P. brevicornis*, *P. caribou*, *P. kotzebuei*, and *P. tareumiut* [Fig. 7D]), *P. nivalis* is associated with dry tundra, as is *P. parasimilis* (Lindroth, 1966). Truly xeric-adapted species, such as the ground beetles *Amara alpina* and *Harpalus amputatus* or the weevil *Lepidophorus lineaticollis*, are not present. These taxa are well preserved and abundant in late Quaternary insect assemblages from interior regions of Alaska and the Yukon Territory (Matthews, 1968, 1975; Matthews *et al.*, 1990), but are found only in last glacial-age sediments in southwest Alaska (Elias, 1992).

The water beetles include predaceous diving beetles (Dytiscidae) and water scavenger beetles (Hydrophilidae), as well as beetles in several families (Limnebiidae, Staphylinidae, Helodidae, and Chrysomelidae) that are indicative of semiaquatic or riparian environments (Table 2). In addition, several species of caddisfly (Trichoptera) larvae were identified; these are all aquatic. This part of the fossil fauna provides substantial information about postglacial aquatic environments. The dytiscid *Ilybius discedens* (Fig. 7E) is restricted to cold waters of *Sphagnum* bogs and moss mats in sedge marshes. Today its distribution is transcontinental in the boreal zone of North America, ranging as far north as Nome, Alaska (Larson, 1975). *Agabus wasastjernae* also lives in small, peat-choked pools and sedge fens. It ranges from the low Arctic south through the boreo-montane regions of eastern and central North America (D.J. Larson, Memorial University of Newfoundland, pers. comm. 1990). Species of the aquatic leaf beetle *Plateumaris* (*Pusilla*) (Chrysomelidae group) are also associated with bog and fen environments, feeding on *Carex*, *Eleocharis*, and *Scirpus* (I. Askevold, University of Manitoba, pers. comm. 1985).

The postglacial assemblages contain a characteristic caddisfly larval fauna, different from late glacial assemblages (Lea *et al.*, 1991; Elias, unpubl. data). The *Homophylax* specimens (Fig. 8A) probably belong to the species *H. crotchi* or *H. andax*. This genus is restricted to the western montane regions of North America, from Alaska to California (Wiggins, 1977). Most larvae have been collected from small, cold streams on mountain slopes. *Oligotricha lapponica* (Fig. 8D) is principally a boreal Palearctic species. In North America, it has been collected only in western Alaska. In Europe and Asia it is found in slow-flowing streams or ponds (Botosaneanu and Malicky, 1978). Caddis larvae identified from older assemblages, including specimens from the Boutellier interstadial, *ca.* 30-70 000 yr BP (Lea *et al.*, 1991), are dominated by the limnephilid *Grensia praeterita* (Fig. 8B,C), which today inhabits arctic tundra lakes and ponds in the Canadian Northwest Territories and Alaska. *G. praeterita* is distinctly northern in distribution and is probably a good indicator of arctic tundra landscapes.

The rove beetles (Staphylinidae) include mesic tundra species (*Olophrum latum*, *Holoboreaphilus nordenskioeldi*) and numerous taxa associated with damp leaf litter and mosses (*Acidota quadrata*, *Olophrum consimile*, *O. rotundicolle*, *Boreaphilus henningianus*, *Quedius aenescens*, *Q. fellmani* [Fig. 7J], *Q. pediculus*, *Tachyporus canadensis* [Fig. 7K], and *T. rulomus*). *Pycnoglypta lurida* is also found in these habitats. The fossil specimens from southwest Alaska (Fig. 7F) belong to an undescribed species similar to *P. lurida*. Modern specimens of this undescribed *Pycnoglypta* species have been collected thus far only in northern Alaska, and although the ecological

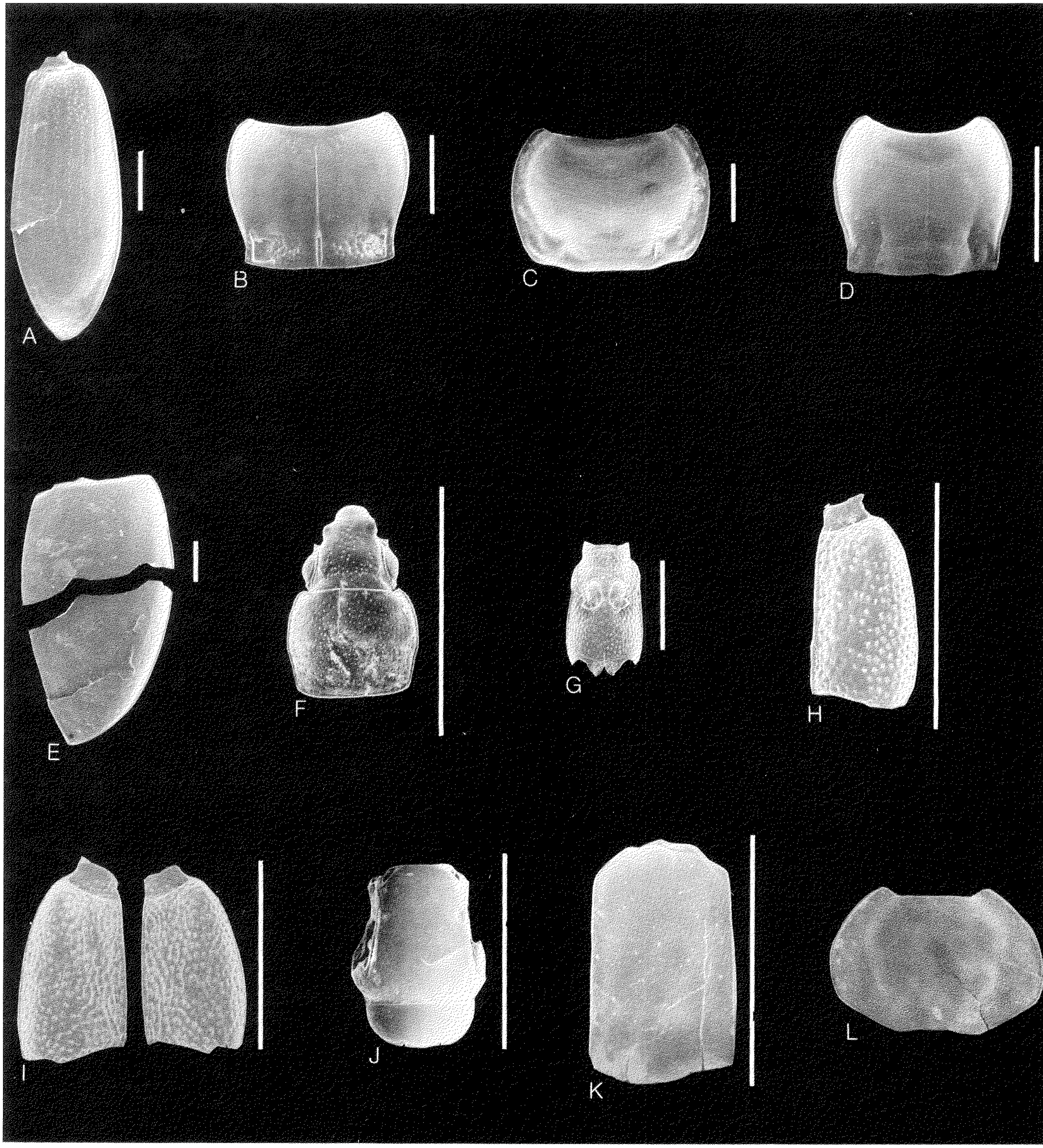

FIG. 7. Scanning electron micrographs of insect fossils from southwest Alaska: A) Right elytron of *Diacheila polita*. B) Pronotum of *Patrobus foveocollis*. C) Pronotum of *Pterostichus agonus*. D) Pronotum of *Pterostichus tareumiut*. E) Right elytron of *Ilybius discedens*. F) Head and pronotum of *Pycnoglypta* nr. *lurida*. G) Head of *Stenus kamtschaticus*. H) Right elytron of *Stenus immarginatus*. I) Left and right elytra of *Stenus austini*. J) Head of *Quedius fellmani*. K) ? elytron of *Tachyporus canadensis*. L) Pronotum of *Thanatophilus trituberculatus*.

requirements of this species have not been studied, they are probably similar to *P. lurida* (J.M. Campbell, Biosystematics Research Centre, Ottawa, pers. comm. 1985).

Acidota crenata and *Tachyporus borealis* are boreal species. *A. crenata* is associated with mosses and sedges in bogs and wet meadows in the boreal zone (Campbell, 1982). *T. borealis* is frequently found in coniferous leaf litter, often at the edges of streams, ponds, and lakes (Campbell, 1979).

The several species of the rove beetle *Stenus* (Fig. 7G,H,I) that were identified are all riparian beetles found along the

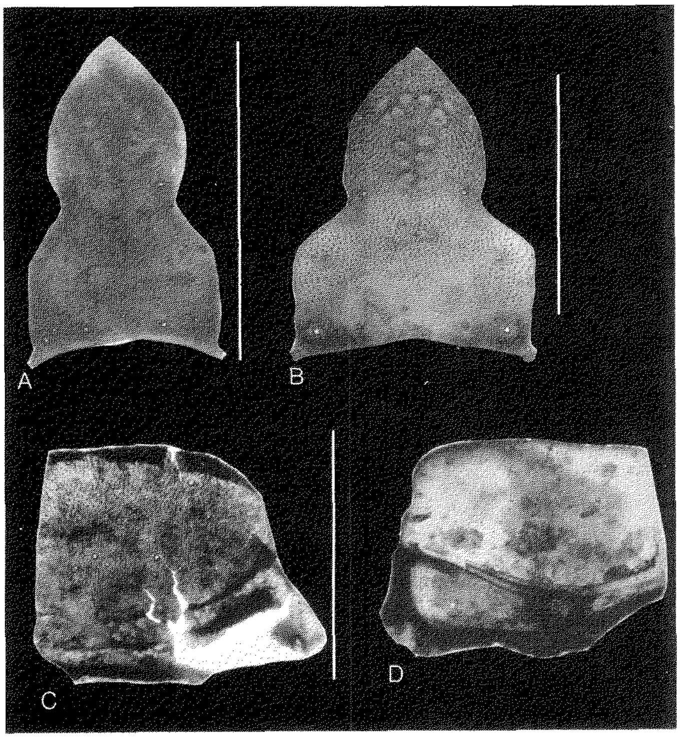

FIG. 8. Light microscope photographs of caddisfly larvae from southwest Alaska: A) Frontoclypeus of *Homophylax*. B) Frontoclypeus of *Grensia praeterita*. C) Pronotum of *Grensia praeterita*. D) Pronotum of *Oligotricha lapponica*.

margins of both standing and running water. Fossil *Stenus* fauna from southwest Alaska is remarkably abundant and diverse and indicates the persistence of fluvial and limnic habitats throughout much of the late Quaternary.

The carrion beetle, *Thanatophilus trituberculatus* (Fig. 7L), was found in several fossil assemblages. This beetle is found throughout the boreo-arctic regions west of Hudson Bay. Adult beetles are most often found beneath carrion and debris along lakeshores and riversides (Anderson and Peck, 1985).

Weevils (Curculionidae) from the postglacial assemblages include *Lepyrus gemellus*, a willow-feeding beetle found today in northern regions west of Hudson Bay, and *Dorytomus leucophyllus*, a species of northwestern North America that also feeds on willows (described under a synonym, *D. longulus* LeC., in O'Brien, 1970). *Notaris aethiops* is a Holarctic, boreo-arctic, and alpine species that lives in semi-aquatic habitats and feeds on *Sparganium* (bur-reed).

Two species of bark beetle (Scolytidae) were identified from mid-postglacial assemblages from the Holokuk River site on the north side of the Kioluk Mountains (Fig. 1). *Phloeotribus lecontei* and *Polygraphus rufipennis* attack spruce as well as other conifers not found in most of Alaska but within the extended range of the beetle (Wood, 1982).

PALEOENVIRONMENTAL INTERPRETATION

During the last glaciation, *ca.* 25-12 000 yr BP (equivalent to the Duvanny Yar interval of Hopkins, 1982), the vegetation of unglaciated Alaska was herbaceous tundra, dominated by Cyperaceae, Gramineae, *Salix*, *Artemisia*, and various herbs (Ager, 1983:Table 9-1; Ager and Brubaker, 1985:Fig. 5) (the Herb Zone of Livingstone, 1955, 1957). These herbaceous communities are variously interpreted (i.e., the "steppe-tundra problem" [Cwynar and Ritchie, 1980; Hopkins *et al.*, 1982]), but in all cases herbaceous tundra was abruptly replaced by birch shrub tundra (Birch Zone) as early as 14 500 to 13 700 yr BP. This transition was likely caused by a climatic change to warmer, moister summers and perhaps deeper winter snows (Ager, 1983). The high percentage of fern spores in samples assigned to the Birch Zone supports the interpretation of expanding mesic habitats within the region. Ager (1982) notes that ferns, which had been restricted by the arid full-glacial climate, quickly spread into expanded mesic habitats in sheltered sites in ravines, hollows, and rocky crevices.

In southwest Alaska, the cessation of eolian deposition and the establishment of a diverse, mesic birch shrub tundra indicate the transition from cold, dry, full glacial conditions to warmer, moister postglacial (Birch Zone) conditions. Two radiocarbon dates from the southern Nushagak lowland place the Birch Zone between 12 200 and 9200 yr BP. Insect assemblages, although small, are dominated by *Tachinus brevipennis*, an indicator of cold, dry environments; these were replaced by mesic tundra (*Cryobius*)–dominated faunas during the Birch Zone in southwest Alaska. Figure 9 summarizes these events at Flounder Flat section 3. The postglacial insect assemblages from southwest Alaska are characterized by abundant mesic and hygrophilous species and by a lack of

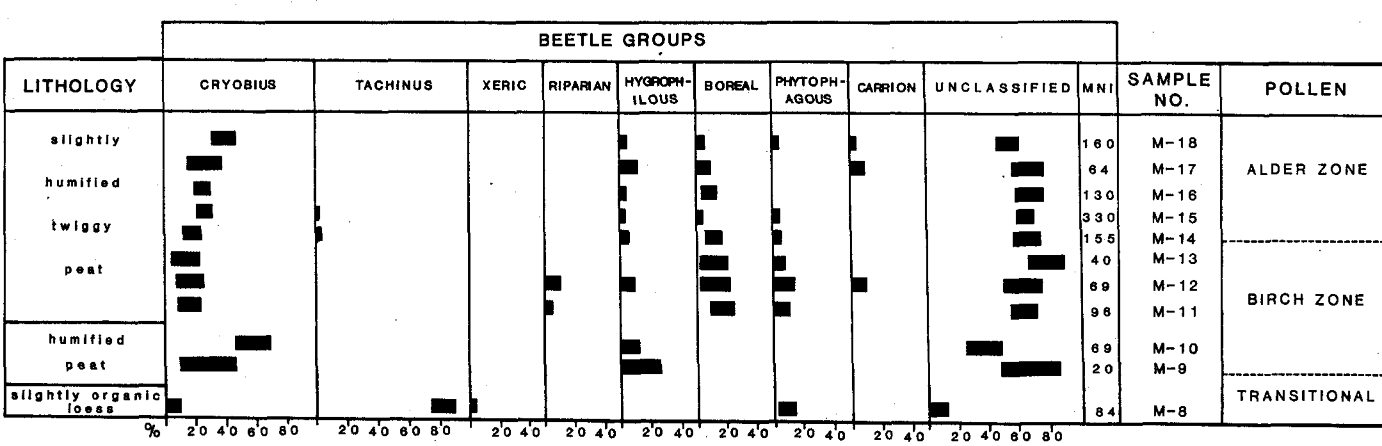

FIG. 9. Percentage composition of insect ecological categories, combined with stratigraphy and pollen zones, Flounder Flat 3, southwest Alaska. Bars represent 95% confidence intervals.

xeric species. This is in sharp contrast to the insect assemblages identified from the interior of eastern Beringia, where species indicative of mesic and wet environments are rare and xeric species often dominate (Matthews, 1968, 1975, 1983). The degree of continentality of interior climates during postglacial times must have been much greater than those in southwest Alaska. Postglacial transgression of the Nushagak Bay coastline brought maritime climatic conditions to southwest Alaska, a change that greatly influenced the composition of vegetation and insect assemblages.

In stratigraphic sequences from the Nushagak lowland, insect faunas that indicate periglacial conditions at the end of the last glacial interval are rapidly replaced by many relatively thermophilous species (e.g., "boreal" category of Fig. 9). These data are consistent with the postglacial amelioration of regional climate interpreted from fossil pollen studies in other parts of Alaska (Ager, 1982, 1983; Ager and Brubaker, 1985). While these thermophilous insects are associated with the boreal zone today, they are not obligatory tree dwellers or tree feeders. Rather, they occupy open-ground habitats (meadows, bogs, and fens) within the boreal forest. This suggests that while climatic conditions were sufficient to support the growth of conifers, the trees themselves had not yet reinvaded southwest Alaska (Ager, 1982, 1983).

The insect assemblages we studied show little change between the Birch and Alder zones (Fig. 9). Mesic tundra flora persisted regionally and continued warm conditions supported the open-ground, boreal-zone faunas that became established in the early Birch Zone. This faunal continuity suggests that the transition from Birch Zone to Alder Zone, which probably postdates 8500 yr BP in southwest Alaska, was influenced by ecological succession of plant communities rather than by changes in climate.

The chronology of alder and conifer establishment in Alaska during the postglacial has been summarized by several workers (Ager, 1983; Ager and Brubaker, 1985; Lamb and Edwards, 1988). Spruce was probably present in northeastern interior Alaska by 9000-8000 yr BP. In some parts of the North Alaska Range foothills, *Picea glauca* was established as early as 9100 yr BP, but in other valleys, *Alnus* and *Picea* arrived about 7500 yr BP (Ager, 1983; Ager and Brubaker, 1985). In southern Alaska, *Alnus* appears in the pollen spectrum by about 9500 yr BP, and in southwest and northwest Alaska, the arrival of alder dates around 7500 yr BP (Ager, 1982). By 6000 yr BP, boreal forest with *Picea glauca* and *P. mariana* was established in the Alaskan interior (Brubaker *et al.*, 1983; Lamb and Edwards, 1988), but spruce did not reach far-western Alaska until *ca.* 5000-4000 yr BP (Ager, 1982; Anderson, 1985).

In the mid-postglacial, conifers invaded the Holitna lowland. In the Nushagak lowland, there is no pollen or insect evidence to indicate coniferous forest in the region at any time in the postglacial, despite the proximity of spruce forest to the north. Southwest Alaska appears to be the last region of eastern Beringia to be recolonized by spruce forest during the postglacial. Lamb and Edwards (1988) conclude that Alaska appears to be unique among arctic regions in recording late postglacial extensions of the tree line.

The discrepancy between the early postglacial establishment of insects indicative of climatic conditions warm enough to support the growth of coniferous forest (*ca.* 12 000 yr BP) and the arrival of coniferous forest in the mid-postglacial suggests that forest establishment lagged behind climatic amelioration by as much as 7000 yr. Parallel studies of Quaternary insects and plants from various regions have demonstrated that plant migration lags behind insect migration for the glacial-postglacial transition in Great Britain (Coope, 1977), eastern North America (Morgan and Morgan, 1980), the Rocky Mountains (Elias, 1985), and the Chihuahuan Desert (Elias and Van Devender, 1990).

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