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Plant Macrofossils Associated with an Early Holocene Beaver Dam in Interior Alaska

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ABSTRACT. Dynamic climate changes and expansion of new biomes characterize the late Pleistocene–early Holocene of eastern Beringia. Analysis of plant macrofossils from an early Holocene (ca. 9300 ^{14}C yrs BP) beaver dam in central Alaska provides insight into the local environment and vegetation. The plant macrofossil assemblage comprises remains of trees and shrubs, graminoids, and forbs, including *Betula* sp., *Carex* sp., *Rubus* sp., *Eleocharis* sp., *Scirpus* sp., *Potamogeton* sp., *Najas flexilis* and *Typha latifolia*, indicative of standing water of a beaver pond. Bryophytes from the beaver dam include *Warnstorfia* spp. and *Drepanocladus aduncus*, suggesting shallow, stagnant, or slow-moving water. The presence of *Najas flexilis*, *Typha latifolia*, and modern beaver (*Castor canadensis*) suggest that central Alaska had a warmer climate during the early Holocene.

Key words: Alaska, plant macrofossils, beaver, Holocene, *Typha latifolia*, paleoenvironment, post-glacial vegetation

RÉSUMÉ. Changements climatiques dynamiques et expansion de nouveaux biomes caractérisent la période du Pléistocène supérieur et de l'Holocène inférieur de la Béringie de l'Est. L'analyse des macrofossiles de plantes provenant d'une digue de castor du centre de l'Alaska datant de l'Holocène inférieur (env. 9300 ^{14}C années BP) donne des indices sur l'environnement et la végétation de la région. L'assemblage de macrofossiles de plantes est composé d'arbres et d'arbustes, de graminoïdes et d'herbes non graminéennes, dont *Betula* sp., *Carex* sp., *Rubus* sp., *Eleocharis* sp., *Scirpus* sp., *Potamogeton* sp., *Najas flexilis* et *Typha latifolia*, ce qui signale la présence d'eau stagnante dans un étang de castor. Parmi les bryophytes de la digue de castor, notons *Warnstorfia* spp. et *Drepanocladus aduncus*, ce qui laisse supposer la présence d'eau peu profonde stagnante ou se déplaçant lentement. Par ailleurs, la présence de *Najas flexilis*, *Typha latifolia* et du castor contemporain (*Castor canadensis*) laissent croire que le climat du centre de l'Alaska était plus chaud pendant l'Holocène inférieur.

Mots clés : Alaska, macrofossiles de plantes, castor, Holocène, *Typha latifolia*, paléoenvironnement, végétation post-glaciaire

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INTRODUCTION

Dynamic changes in the east Beringian landscape and its biota during the late Pleistocene–early Holocene transition included increased solar insolation (Bartlein et al., 1992; Kaufman et al., 2004), the expansion of new biomes (Bigelow and Powers, 2001; Brubaker et al., 2005; Edwards et al., 2005), the extinction of large mammals (Guthrie, 2006), and the arrival of humans (Yesner, 2001). Vegetation of this time has been reconstructed primarily through pollen analysis of lacustrine sediments (Ager, 1975, 1983; Anderson and Brubaker, 1994; Edwards and Barker, 1994; Bigelow and Edwards, 2001). Pollen, however, has disadvantages as a proxy for vegetation, which include limitations in taxonomic resolution and regional and local integration of pollen, as well as low pollen productivity and input in treeless environments (Birks, 1980; Birks and Birks, 2000). Plant macrofossils are more representative of the local vegetation than pollen and can commonly be identified to species level. Moreover, individual macrofossils can be radiocarbon-dated by accelerator mass spectrometry (AMS), confirming the local presence of a particular taxon at a specific time. Previous studies in Beringia that included plant macrofossil analyses have yielded valuable records of local vegetation (e.g., Carlson and Finney, 2004; Edwards et al., 2005).

Plant macrofossils can be recovered from a variety of materials and sediment contexts. Unlike pollen, however, plant macrofossils are neither abundant nor widely dispersed; therefore, sediments from large lakes generally yield few macrofossils. Small ponds are more likely to yield a suite of plant macroremains that are representative of the local vegetation. In boreal areas, beaver ponds provide such a depositional setting. The ponds are created when modern beavers (*Castor canadensis* L.) dam small streams using wood from surrounding vegetation. Beaver ponds gradually infill with sediment containing plant macrofossils and wood from the dam that can be radiocarbon dated (Rains, 1987). Here we report a macrofossil record from an early Holocene beaver pond in central

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Alaska, which provides insight into the early post-glacial vegetation of the area.

STUDY LOCATION AND SETTING

The beaver pond is seen as an organic collection of beaver-chewed wood and sandy silt near the top of a ca. 50 m high bluff of loess on the east bank of the Yukon River in central Alaska, approximately 2 km downstream from the Dalton Highway bridge (Fig. 1). Most of the Yukon River in this part of Alaska is braided, but at this site, the river flows in a single channel within a relatively narrow floodplain confined by bedrock slopes. Discontinuous permafrost occurs throughout the area, and modern ice wedges are exposed by landslides near the bluff (Froese et al., 2005).

The climate of the region is subarctic and continental. Temperatures at Fort Yukon, approximately 170 km east of the site, range from 30˚C in the summer to -60˚C in the winter. The July mean temperature is about 15˚C, and the annual mean is -4˚C. Annual precipitation is 170 mm at Fort Yukon (NCDC 1949–2000 for Fort Yukon, Western Regional Climate Center, 2007).

Boreal forest of white spruce (*Picea glauca*) and black spruce (*Picea mariana*), grows on uplands and the floodplain of the Yukon River (Viereck et al., 1992). Low willow (*Salix planifolia*), thinleaf alder (*Alnus tenuifolia*), and sedges (*Carex* spp.) are also present on the floodplain. Forbs, especially sage (*Artemisia frigida*) and grasses, including *Festuca altaica*, occur on south-facing bluffs in interior Alaska. Upland spruce forest includes stands of balsam poplar (*Populus balsamifera*) and paper birch (*Betula papyrifera*). Willow (*Salix* spp.), alder (*Alnus*), and quaking aspen (*Populus tremuloides*) grow on well-drained soils in these uplands (Viereck et al., 1992, 1993). *Sphagnum* spp. are common in wet lowland areas. Common mosses on forest floors are *Hylocomium splendens*, *Rhytidium rugosum*, and *Pleurozium schreberi* (Viereck et al., 1992).

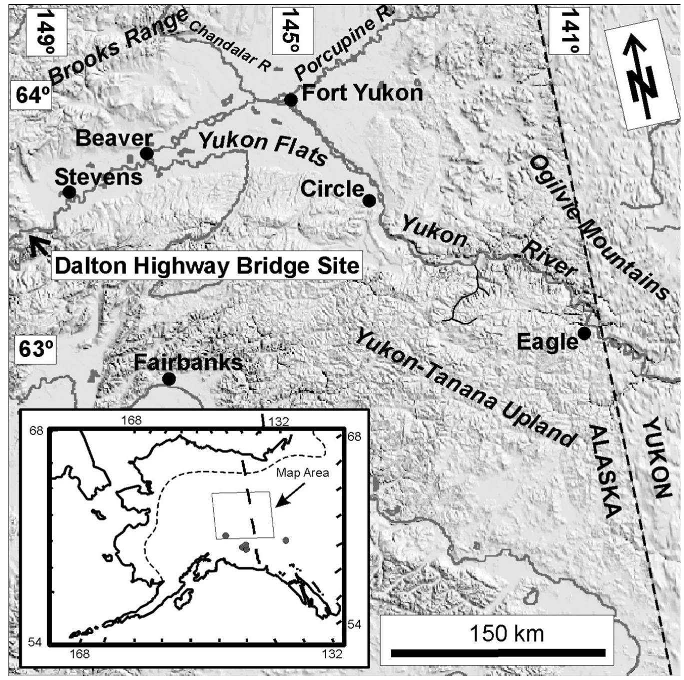

FIG. 1. Location of the Dalton Highway bridge site in central Alaska. The dashed line on the inset map indicates the modern northern limit of *Castor canadensis* (after Jenkins and Busher, 1979); dots on the insert map are occurrences of living *Typha latifolia* (after Porsild and Cody, 1980).

METHODS

Fieldwork was conducted in August 2002 and June 2005. The section was photographed, including the beaver-chewed wood near the top of the bluff. Samples were collected and a stratigraphic description was prepared (Fig. 2). Each sample consisted of about 500 ml of sediment, collected using a trowel from a clean exposed section. Samples were placed in sealed plastic bags to prevent contamination and sample degradation. Plant macrofossil results are reported for the 2005 samples, though some moss taxa are reported from the 2002 samples.

Samples were analyzed in the Paleoenvironmental Laboratory at the Royal Alberta Museum. Vascular plant macrofossils were identified by S.C. Robinson and A.B. Beaudoin, and bryophytes, by J. Doubt. Samples of 50 ml were measured by water displacement for consistency and comparisons and sieved on a 90 µm mesh screen to remove finer sediment. Material coarser than 90 µm was screened through 2 µm, 1.18 µm, 500 µm, 250 µm, and 90 µm meshes and sorted into mosses, roots, bark, leaf fragments, wood, bones, and seeds using a binocular dissecting microscope at 12× magnification. In this paper, the term "seeds" is used in a broad sense and includes achenes, nutlets, and samaras. The general condition of the plant macrofossils and the abundance of each group were noted. Abundance was estimated from coverage on a Petri dish and rated from one to five, with one being a trace and five being abundant. Seeds and bryophytes were identified to the lowest taxonomic level possible, with the aid of literature (Nyholm, 1954; Berggren, 1969; Lawton, 1971; Montgomery, 1977; Steere, 1978; Porsild and Cody, 1980; Crum and Anderson, 1981; Levesque et al., 1988; Warner, 1990; Clifford, 1991; Smith, 1993; Cody, 1996; Hurd et al., 1998) and reference collections in the Paleoenvironmental Laboratory and the Herbarium at the Royal Alberta Museum. Wood was identified by R.J. Mott.

RESULTS

Stratigraphy

The beaver dam is 2–3 m below the top of the bluff, approximately 50 m above river level (Fig. 2). The presence of the dam is not indicative of changes to the Yukon

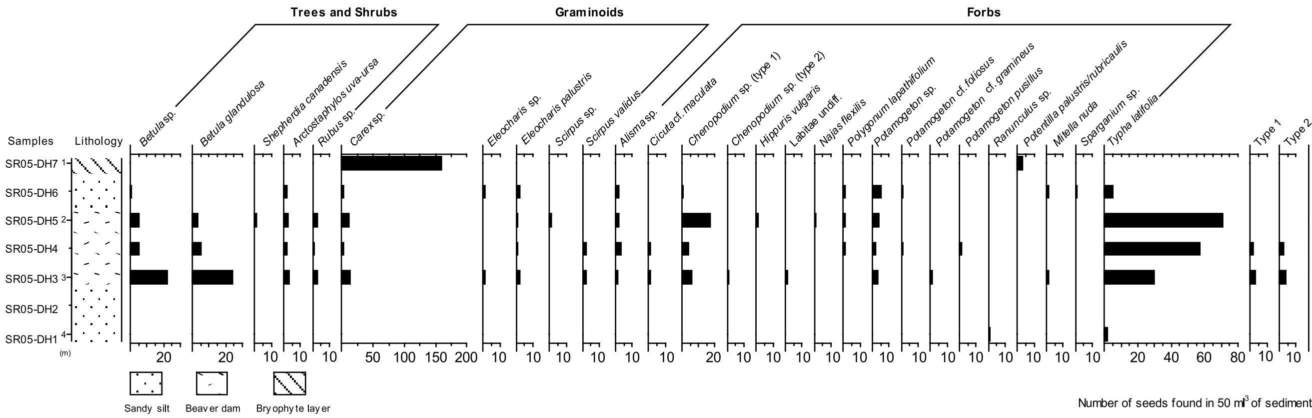

FIG. 2. Stratigraphy, chronology, and plant macrofossil assemblage at the Dalton Highway bridge site with sample numbers.

River, but rather was likely a result of damming of a small stream, probably fed by thaw lakes and ponds, on the upland landscape. The dam itself is about 1 m in depth and contains abundant, densely packed beaver-chewed wood fragments (Fig. 3) lying flat within a sandy silt matrix. It is underlain by 1 m of sandy silt, which contains gastropods, some twigs, and discontinuous fibrous organic beds, overlying massive inorganic sandy-silt (loess) of much greater age. Overlying the beaver dam is 1 m of crudely stratified sandy silt containing some wood. The sandy silt is overlain by a bryophyte-rich organic layer 0.3 m thick, which in turn is overlain by sandy silt, to the top of the bluff. The latter sandy silt is interpreted as primary loess which accumulated following drainage of the pond.

Radiocarbon Ages

Three samples of beaver-chewed wood from the lower, middle, and upper parts of the beaver dam were radiocarbon-dated (Table 1 and Fig. 2). The lower sample (*Populus* sp.) yielded an age of 9280 ± 90 yrs BP (GSC-6701); the middle sample (*Populus* sp.), 9290 ± 90 yrs BP (GSC-6703); and the upper sample (*Salix* sp.), 9280 ± 90 yrs BP (GSC-6705). Calibration of these conventional ages using Oxcal v 3.10 (Bronk Ramsey, 2005) gives an age range of 10 580 – 10 290 cal. yrs BP (2 sigma). Comparison with other dated sites in eastern Beringia (Table 1) indicates that the beaver dam at the Dalton Highway bridge site is one of the earliest Holocene occurrences of beaver in the region.

PLANT MACROFOSSILS

The plant macrofossil assemblage (Table 2 and Fig. 2) represents 16 emergent and aquatic forbs, 4 graminoids, 5 shrubs, and 19 mosses. No arboreal taxa are recorded in the assemblage, other than the wood in the beaver dam itself. The wood includes willow (*Salix*) and poplar (*Populus*), which must have been living adjacent to the site.

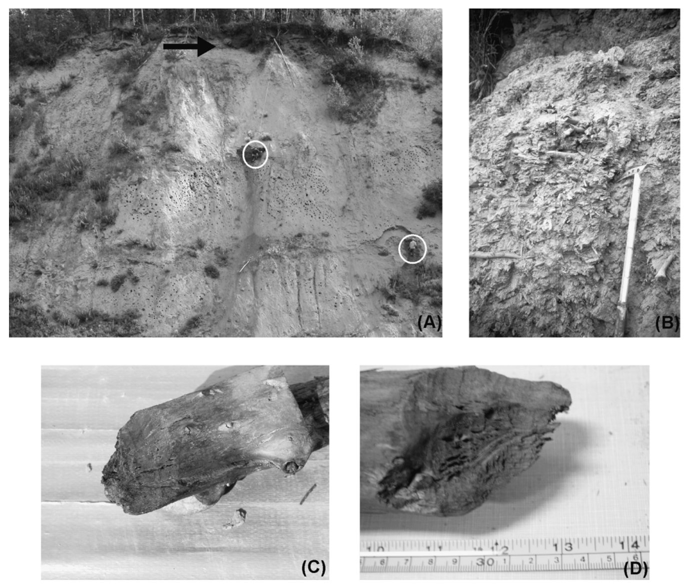

FIG. 3. (A) Study site with location of beaver dam (arrow) near top of bluff, ca. 50 m above river level. Note people for scale (circles). (B) Beaver dam with abundant chewed wood and twigs. Ice axe is 80 cm long. (C) and (D) are close-up photos of beaver-chewed wood.

Seeds

Abundances of seeds vary vertically through the beaver dam and bounding sediments. Samples SR05-DH1 and SR05-DH2 contain only one achene from *Ranunculus* sp. and *Typha latifolia* seeds. Macrofossil abundance is much greater within the beaver dam. SR05-DH3, the lowest of the beaver dam samples, contains remains of shrubs, forbs, and graminoids. Shrubs are dominated by *Betula* sp. and *Betula glandulosa*; *Arctostaphylos uva-ursi* and *Rubus* sp. are also present. Cyperaceae include *Carex* spp. and *Eleocharis palustris*. *Typha latifolia* is common and *Potamogeton* sp. is present. Sample SR05-DH4, from the middle of the dam, contains emergent and aquatic macrofossils, including *Typha latifolia*, *Potamogeton* cf. *foliosus*, *Potamogeton pusillus*, and *Polygonum lapathifolium*. The upper beaver dam sample, SR05-DH5, contains the most abundant *Typha latifolia* achenes in the sequence and increased numbers of

TABLE 1. Radiocarbon ages of beaver fossils and beaver-chewed wood in Alaska, Yukon, and the Northwest Territories. Evidence of beaver remains or chewed wood is adapted from Harington (2003).

Location	Dated Material	Age (^{14}C yrs BP)	Reference
West of Mackenzie River, NWT	Beaver-gnawed wood	> 38600 (GSC-120)	Morlan (1999)
Hungry Creek, Bonnet Plume Basin, Yukon	Beaver-gnawed wood (*Picea* sp. or *Salix* sp.)	36900 ± 300 (GSC-2422)	Hughes et al. (1981)
5 km SE of Sabine Point, Yukon	Beaver-gnawed wood (*Populus*)	9940 ± 90 (GSC-2022)	Lowdon & Blake (1979)
Dome Creek, Fairbanks, Alaska	Sticks in beaver dam, not chewed (*Populus*, *Salix*)	9650 ± 140 (Beta 69,379)	Péwé et al. (1997)
Near Arctic Red River, NWT	Beaver-cut sticks from organic sediments	9500 ± 90 (GSC-1814)	Harington (1978); Lowdon & Blake (1979)
Fairbanks Creek, Fairbanks, Alaska	Beaver-chewed wood (a) *Populus*, (b) *Salix*	(a) 9350 ± 80 (Beta 58,408); (b) 13600 ± 600 (1952 solid carbon date L117I)	Péwé et al. (1997)
Washington Creek, Alaska	Beaver-cut wood from dam	9330 ± 300 (W-2160)	Harington (1978)
		9280 ± 90 (GSC-6701)	This paper
Dalton Highway bridge, Alaska	Beaver-chewed wood (*Populus*, *Salix*)	9280 ± 90 (GSC-6705)	This paper
		9290 ± 90 (GSC-6703)	This paper
Upper Eva Creek, Fairbanks, Alaska	Beaver-chewed sticks in beaver dam (*Picea*)	8940 ± 80 (Beta 46,215)	Péwé et al. (1997)
Dome Creek, Fairbanks, Alaska	Beaver-chewed log (*Populus*)	8800 ± 70 (Beta 50,685)	Péwé et al. (1997)
Upper Eva Creek, Fairbanks, Alaska	Beaver-chewed sticks in beaver dam (*Salix*)	8780 ± 100 (Beta 48,788)	Péwé et al. (1997)
Mouth of Old Wound, Alaska	Log from beaver dam (*Betula* or *Populus*)	8480 ± 300 (W-2596)	Hopkins et al. (1981)
Mud Creek, near Candle, Alaska	Beaver-chewed wood (*Betula*)	8080 ± 300 (W-2808)	Hopkins et al. (1981)
Dawson Cut, Fairbanks, Alaska	Log of a beaver dam (*Picea*)	7280 ± 80 (Beta 50,683)	Péwé et al. (1997)
Acasta Lake, NWT	Fossil remains of beaver	7000 (suggested from charcoal)	Harington (1978)
Sullivan Creek, Hot Springs District, Alaska	Beaver-chewed log (*Betula* or *Populus*)	6820 ± 200 (W-733)	Hopkins et al. (1981)
Sullivan Pitt (Tofty Placer District), Alaska	Logs extracted from a mass of beaver-gnawed wood	6730 ± 260 (W-1108)	Harington (1978)
Sheep Creek, Fairbanks, Alaska	Beaver-chewed wood (*Populus*)	6100 ± 80 (Beta 52,700)	Péwé et al. (1997)

Chenopodium sp. (type 1) seeds. It includes remains of several shrubs, graminoids, and forbs, including first occurrences of *Najas flexilis*, *Hippuris vulgaris*, and *Shepherdia canadensis*. Sample SR05-DH6, from the sandy silt overlying the beaver dam, records a substantial decrease in the number of seeds, especially those of *Typha latifolia*, *Chenopodium* sp., *Betula* sp., and *Betula glandulosa*. The highest sample, SR05-DH7, which is from the bryophyte layer, contains no shrub macrofossils, and forbs are represented by only three *Potentilla palustris/rubricaulis* seeds. The major wetland species are absent, but *Carex* sp. seeds are abundant.

Mosses

Emergent wetland species associated with shallow, stagnant, or slow-moving water, including *Warnstorfia* spp. and *Drepanocladus aduncus*, dominate the moss fraction of macrofossils in all samples collected in 2005 (Table 3). Species associated with moist and dry terrestrial sites are less frequent, and occur only in some samples. In contrast, upland species dominated some 2002 samples. The apparent discrepancy between 2002 and 2005 samples probably reflects the local response of moss species to microhabitat variability or the local incorporation of upland moss species as beaver dam caulk.

Samples SR05-DH1 and SR05-DH2, from below the beaver dam, contain few moss fragments and those are *Warnstorfia* sp. (Tables 3 and 4). Samples SR05-DH3 and SR05-DH4 (the lower and middle beaver dam samples) have 11 and 10 species of mosses, respectively, and include non-aquatic species such as *Amblystegium serpens*, *Ceratodon purpureus*, *Dicranum undulatum*, *Hylocomium splendens*, *Leptobryum pyriforme*, and *Rhytidium rugosum*. *Hylocomium splendens* and *R. rugosum* dominate the 2002 sample from this level. Most moss species from samples SR05-DH5 and SR05-DH6 are emergent wetland species, such as *Calliergon* spp., *Drepanocladus aduncus*, and *Warnstorfia* spp. (Table 3). The number of species is lower in those samples than in samples SR05-DH3 and SR05-DH4. Moss macrofossils are most abundant in sample SR05-DH7, although only five species, all wetland emergents, are represented (Table 3). *Scorpidium scorpioides*, which is found in nutrient-rich pools and shores (Crum and Anderson, 1981), dominates the moss assemblage at this level.

Abundance

The abundance chart (Table 4) shows that macrofossil groups differ through time. The most notable differences are between the three beaver dam samples (SR05-DH3, SR05-DH4, and SR05-DH5) and the samples underlying (SR05-DH1 and SR05-DH2) and overlying (SR05-DH6 and SR05-DH7). The underlying samples contain small amounts of wood, bark, stem, and mosses. Nearly all groups are present in the three beaver dam samples, with bark and wood being most abundant. The overlying samples show a reduction of most groups except for stem parts and mosses, which are both abundant.

DISCUSSION

Early Holocene Vegetation in Interior Alaska

The plant macrofossil data (Figs. 2 and 4) provide a detailed record of the local vegetation and the evolution of a beaver dam and pond in interior Alaska for a brief

TABLE 2. Plant macrofossils from the Dalton Highway bridge site. Habitat descriptions and plant nomenclature follow Cody (1996) except as noted.

Taxa	Common Name	Macrofossil Type	Numbers	%	Habitat Description
Trees and Shrubs:					
Betula sp.	Birch	Samaras	33	6.20	Acidic rocks, woodland muskegs, peat bogs
Betula glandulosa	Dwarf birch	Samaras	32	6.01	Bogs
Shepherdia canadensis	Buffaloberry	Achenes	1	0.19	Dry calcareous open woods, banks
Arctostaphylos uva-ursi	Kinnikinnick	Seeds	9.5	1.78	Exposed rocks, riverbanks, eskers, sandplains
Rubus sp.	Raspberry	Nutlets	7	1.32	Moderately dry open forests, riverbanks
Graminoids:					
Carex sp.	Sedge	Achenes	190	35.68	Wet calcareous or acidic soils, meadows, riverbanks, ponds
Eleocharis sp.	Spikerush	Achenes	2	0.38	Calcareous sandy ponds, riverbanks
Eleocharis palustris	Common spikerush	Achenes	6	1.13	Sheltered margins of lake/ponds
Scirpus sp.	Bulrush	Achenes	1	0.19	Wet marshes, lake shores
Scirpus validus	Softstem bulrush	Achenes	4	0.75	Sheltered lake shores, water up to 1 m deep
Forbs:					
Alisma sp.[1]	Water plantain	Achenes	8	1.50	Marshy places, edges of sloughs
Cicuta cf. *maculata*	Spotted water hemlock	Fruits	2	0.38	Marshy lake shores, stream banks
Chenopodium sp. (type 1)	Goosefoot	Seeds	28	5.26	Moist saline areas, clearings
Chenopodium sp. (type 2)	Goosefoot	Seeds	1	0.19	
Hippuris vulgaris	Common mare's-tail	Fruits	1	0.19	Shallow ponds, lakes
Labiatae undiff.	Mint	Nutlets	1	0.19	
Najas flexilis[1]	Nodding water-nymph	Seeds	1	0.19	Shallow fresh and brackish waters
Polygonum lapathifolium	Curlytop knotweed	Achenes	3	0.56	Wet lake shores
Potamogeton sp.	Pondweed	Achenes	14	2.63	Edge of shallow ponds, meadows, lakeshores, banks
Potamogeton cf. *foliosus*	Leafy pondweed	Achenes	2	0.38	Shallow still waters
Potamogeton cf. *gramineus*	Variable-leaf pondweed	Achenes	1	0.19	Still waters, 0.5–3 m deep
Potamogeton pusillus[1]	Small pondweed	Achenes	1	0.19	Quiet waters up to 2 m deep
Ranunculus sp.	Buttercup	Achenes	1	0.19	Calcareous shallow ponds
Potentilla palustris	Purple marshlocks	Achenes	3	0.56	Wet marshes, bogs
Mitella nuda	Naked miterwort	Seeds	2	0.38	Cold boreal forest
Sparganium sp.	Bur-reed	Achenes	1	0.19	Shallow ponds, bog pools, lakes
Typha latifolia	Common cattail	Achenes	165	30.99	Wet moist places
Unknowns:					
Type 1			5	0.94	
Type 2			7	1.32	
Total			**532.5**	**100**	

[1] Habitat description and nomenclature follow Montgomery, 1977.

interval in the early Holocene. Modern analogues indicate that the lowest samples (SR05-DH1–SR05-DH6) record a pond with emergent forbs growing at its edges. Sedges and shrub birch were present near the pond. SR05-DH7 records the establishment of a sedge community on the drained or infilled pond, indicating a typical terrestrialization sequence (Beaudoin et al., 1996). The dominance of aquatic/emergent mosses in sample SR05-DH7 indicates that despite the declining moisture suggested by the vascular plant remains, standing water persisted at this time.

The bryophyte macrofossils reveal aspects of local vegetation additional to those revealed by the vascular plant macrofossils. Bryophyte richness correlates with boreal microhabitat diversity (e.g., Vitt et al., 1995, 2003; Crites and Dale, 1998; Gignac and Dale, 2005). Thus, the small number of species in the lowermost and uppermost samples suggests that the site was homogeneous and wet, with little topographic relief. The ecological preferences of moss species in samples SR05-DH1 and SR05-DH2 support conclusions, drawn from vascular plant remains, that the site was influenced by still or slow-moving water. Mid-sequence samples (SR05-DH3 and SR05-DH4) have more diverse moss assemblages, suggesting an increase in moss microhabitats. Several possible explanations exist for the occurrence of upland species in these samples. For example, the local microhabitat heterogeneity of the dam itself may have supported a greater number of species. Alternatively, the dam may have acted as a sieve for water draining through it, trapping fragments of upland species that were transported by floodwater or other means from the pond banks, or upland species may have been introduced as caulk material by beavers.

Although the plant macrofossil and bryophyte data are in general agreement, there is an inconsistency. In the uppermost sample (SR05-DH7), abundance of the emergent basiphile *Scorpidium scorpioides* suggests nutrient enrichment and water saturation, while vascular plant macrofossils in this same sample, particularly *Carex* sp., suggest acidic and increasingly dry soil conditions.

TABLE 3. Bryophytes from the Dalton Highway bridge site, showing presence of each species in the 2005 samples (+) and additions from the 2002 samples (*). Identification, habitat description, and plant nomenclature follow Nyholm (1954), Lawton (1971), Steere (1978), Crum and Anderson (1981), and Smith (1993).

	SR05-Samples								
Moss Taxa	DH1	DH2	DH3	DH4	DH5	DH6	DH7	Preferred Habitat	
Amblystegium serpens			+	+		+		Terrestrial wet-dry	Trees, wood, rock, soil, humus
Barbula convoluta				+*				Terrestrial wet-dry	Soil, rock
Brachythecium starkei			+					Terrestrial mesic-dry	Trees, wood, rock, soil, humus
Brachythecium sp.				+*	+				
Bryum sp.				+*	+	+			
Calliergon giganteum			+	+*	+*	+	+	Aquatic emergent or submerged	Peat, humus
Calliergon richardsonii			+			+	+	Aquatic emergent or submerged	Peat, humus
Calliergon stramineum					+	+		Aquatic emergent	Peat, humus
Ceratodon purpureus			+					Terrestrial wet-dry	Wood, rock, soil, humus
Dicranum acutifolium			+*					Terrestrial mesic-dry	Wood, rock, soil, humus
Dicranum undulatum			+*					Terrestrial wet-mesic	Wood, peat, humus
Drepanocladus aduncus			+	+		+	+	Emergent or submerged	Soil, peat, humus
Hylocomium splendens		+	+		+*			Terrestrial wet-mesic	Wood, rock, soil, humus
Hypnum pratense						+		Terrestrial wet	Soil, peat, humus
Leptobryum pyriforme				+*				Terrestrial wet-mesic	Wood, rock, soil, humus
Mniaceae				+	+				
Plagiomnium ellipticum								Terrestrial wet	Peat, humus
Rhytidium rugosum			+					Terrestrial dry	Rock, soil
Scorpidium scorpioides							+	Aquatic submerged or floating	Peat, humus
Warnstorfia sp.	+	+	+	+	+	+	+	Aquatic emergent or submerged	Peat, humus

It is surprising that *Populus* seeds or catkin bracts were not found in the assemblage because poplar wood is present in the beaver dam and poplar pollen is a component of other interior records (Ager, 1975, 1982; Cwynar, 1982; Edwards et al., 1985; Anderson et al., 1988, 1990; Hu et al., 1993; Brubaker et al., 2001). However, the absence of poplar seeds despite the presence of poplar wood has been noted elsewhere (e.g., Beaudoin et al., 1996).

The spread of spruce (*Picea*) after the Last Glacial Maximum is a topic of interest in Beringian studies. Samples from the Dalton Highway bridge site do not contain spruce macrofossils, suggesting that spruce was not present in the vicinity ca. 9300 ^{14}C yrs BP., though spruce wood is not generally sought by beaver. Pollen records suggest that spruce appeared on a regional scale in central Alaska 9000–8500 ^{14}C yrs BP (Brubaker et al., 1983; Anderson et al., 1990; Edwards and Barker, 1994) although Hu et al. (1993) and Ager and Brubaker (1985) suggest a slightly earlier appearance at ca. 9500 ^{14}C yrs BP.

The presence of cattail (*Typha latifolia*) and nodding water-nymph (*Najas flexilis*) in our record could have implications for early Holocene climate. The modern northern limit of cattail is near our site, and near Fairbanks in central Alaska (Fig. 1) and near Mayo in central Yukon (Porsild and Cody, 1980). Edwards and McDowell (1991) confirm that *Typha latifolia* is near its northern limit in the Fairbanks area. *Najas flexilis* in Alaska is less understood, but has a modern distribution similar to that of *Typha latifolia*. The *Typha latifolia* and *Najas flexilis* seeds at our site are well preserved and are unlikely to have been transported to the site from more southerly locations. This finding indicates that both species were at the northernmost range of their distributions in the early Holocene and suggests that the climate could have been warmer than it is today, which is consistent with findings of other studies in the region (e.g., Kaufman et al., 2004).

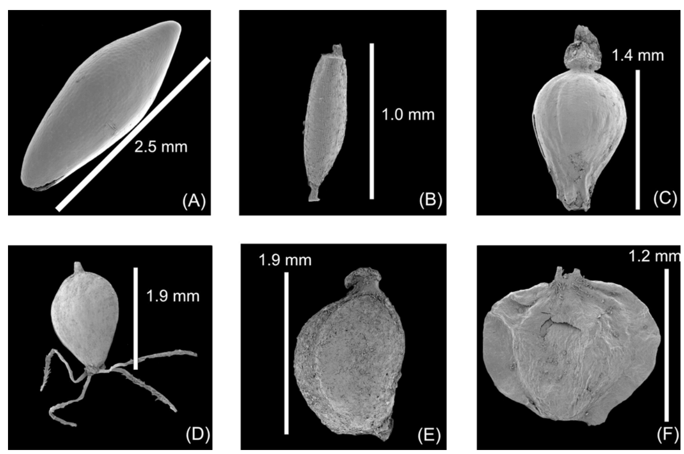

FIG. 4. Selected SEM images of plant macrofossils found in the assemblage. (A) *Najas flexilis*, (B) *Typha latifolia*, (C) *Eleocharis palustris*, (D) *Scirpus validus*, (E) *Potamogeton* sp., and (F) *Betula glandulosa*.

The Implications of the Presence of Early Holocene Beaver in Central Alaska

No reliably dated beaver remains dating to the last glaciation have yet been found in the Yukon or in Alaska. A single finite age of 13600 ± 600 ^{14}C yr BP on beaver-chewed wood from the early 1950s is discordant with a

TABLE 4. Plant macrofossil abundances.[1]

Sample & Fraction	Mosses	Roots/ Organics	Bark	Leaf Fragments	Large Wood	Small Wood	Seed Covers	Seeds	Bones	Stem Parts	Insect Remains
SR05-DH7 > 2 mm	5	×	1	×	×	×	×	×	×	5	×
SR05-DH7 > 1.18 mm	5	×	×	×	×	×	×	3	×	5	×
SR05-DH6 > 2 mm	2	×	2	×	2	×	×	×	×	3	×
SR05-DH6 > 1.18 mm	2	×	2	1	3	1	×	1	×	5	×
SR05-DH5 > 2 mm	3	2	4	1	5	2	2	1	×	3	1
SR05-DH5 > 1.18 mm	3	×	3	1	4	2	1	1	×	3	1
SR05-DH4 > 2 mm	3	2	4	1	5	1	1	1	×	4	1
SR05-DH4 > 1.18 mm	2	×	3	1	3	1	1	1	×	3	1
SR05-DH3 > 2 mm	3	3	5	2	5	1	3	1	×	4	1
SR05-DH3 > 1.18 mm	2	1	3	1	3	1	1	2	×	3	1
SR05-DH2 > 2 mm	×	1	×	×	1	1	×	×	×	2	×
SR05-DH2 > 1.18 mm	1	1	1	×	1	2	×	×	×	2	1
SR05-DH1 > 2 mm	1	×	1	×	2	2	×	×	1	2	×
SR05-DH1 > 1.18 mm	1	1	2	×	2	2	×	×	×	2	×

[1] × = absent, 1 = trace, 2 = present, 3 = common, 4 = frequent, 5 = abundant. Ratings based on abundance of macrofossils in Petri dish. Seed covers are mainly from *Carex* sp. perigynia.

more recent associated age of 9350 ± 80 ^{14}C yr BP (Péwé et al., 1997; Table 1) and must be considered suspect. The absence of beaver during the last glaciation may have been due to a lack of trees in the region or a cold and arid climate unsuitable for beaver habitation. Evidence for late Pleistocene beaver prior to the last glaciation is limited to a single finite radiocarbon age on beaver-chewed wood of 36 900 ± 300 ^{14}C yrs BP, which may be associated with the mid-Wisconsinan interstadial (Hughes et al., 1981). However, associated pollen and insect fossils suggest conditions similar to those at present and may indicate that the assemblage is of last interglacial age (Mathews and Telka, 1997). In short, evidence for beaver during the mid-Wisconsinan is not abundant in the Yukon or in Alaska.

Beaver-chewed wood is associated with last interglacial deposits in the Yukon and in Alaska (Harington, 1978; Matheus et al., 2003). Fossils of giant beaver (*Castoroides*) thought to be of last interglacial age have been found in the Old Crow region, northern Yukon, where they may have coexisted with modern beaver (Harington, 1978). No giant beaver fossils within the range of radiocarbon dating are known from the Yukon or Alaska (Harington, 2003). Given this background, we assume that the beaver-chewed wood at our site was cut by modern beaver. The dam at the Dalton site is composed mainly of willow, poplar, and aspen wood, which indicates that the climate had become sufficiently warm to allow tree growth prior to dam construction. These taxa are the preferred diet of modern beaver (Hakala, 1952; Murray, 1961) and probably aided their migration into Alaska from southern refugia.

The beaver dam and plant macrofossil data at the Dalton site record local vegetation and landscape changes during the last glacial-interglacial transition. Eolian processes, recorded by sandsheet accumulation, were dominant along the Yukon River immediately to the east during the latest Pleistocene, as recently as 10 200 ^{14}C yrs BP (Froese et al., 2005). We suggest that the beaver dam was formed through blocking of local drainage associated with interconnecting thaw ponds on the upland site. This change during the early Holocene is likely linked to regional changes in temperature and moisture availability (Abbott et al., 2000; Mann et al., 2002) and to regional degradation of permafrost, as recorded in adjacent interior Yukon at this time (Burn et al., 1986). The Dalton site provides evidence for one of the earliest occurrences of beaver in Alaska at ca. 9300 ^{14}C yrs BP. Collectively, the presence of the beaver dam on this upland site and the presence of *Typha latifolia* and *Najas flexilis* at or beyond their northern limits suggest that conditions were as warm or warmer than modern conditions, with greater availability of water on the landscape than during the late Pleistocene, when eolian processes were dominant.

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REFERENCES

ABBOTT, M.B., FINNEY, B.P., EDWARDS, M.E., and KELTS, K.R. 2000. Lake-level reconstructions and paleohydrology of Birch Lake, central Alaska, based on seismic reflection profiles and core transects. Quaternary Research 53:154–166.

AGER, T.A. 1975. Late Quaternary environmental history of the Tanana Valley, Alaska. Institute of Polar Studies Report 54. Columbus, Ohio: The Ohio State University Research Foundation. 117 p.

———. 1982. Vegetational history of western Alaska during the Wisconsin 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. 75–93.

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

AGER, T.A., and BRUBAKER, L. 1985. Quaternary palynology and vegetational history of Alaska. In: Bryant, V.M., Jr., and Holloway, R.G., eds. Pollen records of late-Quaternary North American sediments. Dallas, Texas: American Association of Stratigraphic Palynologists (AASP) Foundation. 353–384.

ANDERSON, P.M., and BRUBAKER, L.B. 1994. Vegetation history of northcentral Alaska: A mapped summary of late-Quaternary pollen data. Quaternary Science Reviews 13:71–92.

ANDERSON, P.M., REANIER, R.E., and BRUBAKER, L.B. 1988. Late Quaternary vegetational history of the Black River Region in northeastern Alaska. Canadian Journal of Earth Sciences 25:84–94.

———. 1990. A 14,000-year pollen record from Sithylemenkat Lake, north-central Alaska. Quaternary Research 33:400–404.

BARTLEIN, P.J., ANDERSON, P.M., EDWARDS, M.E., and McDOWELL, P.F. 1992. A framework for interpreting paleoclimatic variations in eastern Beringia. Quaternary International 10–12:73–83.

BEAUDOIN, A.B., WRIGHT, M., and RONAGHAN, B. 1996. Late Quaternary landscape history and archaeology in the 'ice-free corridor': Some recent results from Alberta. Quaternary International 32:113–126.

BERGGREN, G. 1969. Atlas of seeds and small fruits of northwest European plant species with morphological descriptions. Part 2: Cyperaceae. Stockholm: Swedish Natural Science Research Council. 68 p.

BIGELOW, N.H., and EDWARDS, M.E. 2001. A 14,000 yr paleoenvironmental record from Windmill Lake, central Alaska: Lateglacial and Holocene vegetation in the Alaska Range. Quaternary Science Reviews 20:203–215.

BIGELOW, N.H., and POWERS, W.M.R. 2001. Climate, vegetation, and archaeology 14,000–9,000 cal yr B.P. Arctic Anthropology 38:171–195.

BIRKS, H.H. 1980. Plant macrofossils in Quaternary lake sediments. Archiv für Hydrobiologie 15:1–60.

BIRKS, H.H., and BIRKS, H.J.B. 2000. Future uses of pollen analysis must include plant macrofossils. Journal of Biogeography 27:31–35.

BRONK RAMSEY, C. 2005. OxCal Program v 3.10. Oxford: University of Oxford Radiocarbon Accelerator Unit. http://www.rlaha.ox.ac.uk/oxcal/oxcal.htm.

BRUBAKER, L.B., GARFINKEL, H.L., and EDWARDS, M.E. 1983. A late Wisconsin and Holocene vegetation history from the central Brooks Range: Implications for Alaskan paleoecology. Quaternary Research 20:194–214.

BRUBAKER, L.B., ANDERSON, P.M., and HU, F.S. 2001. Vegetation ecotone dynamics in southwest Alaska during the late Quaternary. Quaternary Science Reviews 20:175–188.

BRUBAKER, L.B., ANDERSON, P.M., EDWARDS, M.E., and LOZHKIN, A.V. 2005. Beringia as a glacial refugium for boreal trees and shrubs: New perspectives from mapped pollen data. Journal of Biogeography 32:833–848.

BURN, C.R., MICHEL, F.A., and SMITH, M.W. 1986. Stratigraphic, isotopic, and mineralogical evidence for an early Holocene thaw unconformity at Mayo, Yukon Territory. Canadian Journal of Earth Sciences 23:794–803.

CARLSON, L.J., and FINNEY, B.P. 2004. A 13,000-year history of vegetation and environmental change at Jan Lake, east-central Alaska. The Holocene 14:818–827.

CLIFFORD, H.F. 1991. Aquatic invertebrates of Alberta. Edmonton: The University of Alberta Press. 538 p.

CODY, W.J. 1996. Flora of the Yukon Territory. Ottawa, Ontario: NRC Research Press. 643 p.

CRITES, S., and DALE, M.R.T. 1998. Diversity and abundance of bryophytes, lichens, and fungi in relation to woody substrate and successional stage in aspen mixedwood boreal forests. Canadian Journal of Botany 76:641–651.

CRUM, H., and ANDERSON, L. 1981. Mosses of Eastern North America, Vol. 1. New York: Columbia University. 328 p.

CWYNAR, L.C. 1982. A late-Quaternary vegetation history from Hanging Lake, northern Yukon. Ecological Monographs 52:1–24.

EDWARDS, M.E., and BARKER, E.D. 1994. Climate and vegetation in northeastern Alaska 18,000 yr B.P.–present. Palaeogeography, Palaeoclimatology, Palaeoecology 109: 127–135.

EDWARDS, M.E., and McDOWELL, P.F. 1991. Interglacial deposits at Birch Creek, northeast interior Alaska. Quaternary Research 35:41–52.

EDWARDS, M.E., ANDERSON, H.L., GARFINKEL, H.L., and BRUBAKER, L.B. 1985. Late Wisconsin and Holocene vegetation of the Upper Koyukuk Region, Brooks Range, Alaska. Canadian Journal of Botany 63:616–626.

EDWARDS, M.E., BRUBAKER, L.B., LOZHKIN, A.V., and ANDERSON, P.M. 2005. Structurally novel biomes: A response to past warming in Beringia. Ecology 86:1696–1703.

FROESE, D.G., SMITH, D.G., and CLEMENT, D.T. 2005. Characterizing large river history with shallow geophysics: Middle Yukon River, Yukon Territory and Alaska. Geomorphology 67:391–406.

GIGNAC, L.D., and DALE, M.R.T. 2005. Effects of fragment size and habitat heterogeneity on cryptogam diversity in the low-boreal forest of western Canada. The Bryologist 108:50–66.

GUTHRIE, R.D. 2006. New carbon dates link climate change with human colonization and Pleistocene extinctions. Nature 441: 207–209.

HAKALA, J.B. 1952. The life history and general ecology of the beaver in interior Alaska. MS thesis, College University of Alaska, Anchorage, Alaska. 189 p.

HARINGTON, C.R. 1978. Quaternary vertebrate faunas of Canada and Alaska and their suggested chronological sequence. Syllogeus 15. Ottawa, Ontario: National Museums of Canada, Natural Museum of Natural Sciences. 105 p.

———. 2003. Annotated bibliography of Quaternary vertebrates of northern North America, with radiocarbon dates. Toronto, Ontario: University of Toronto Press. 539 p.

HOPKINS, D.M., SMITH, P.A., and MATTHEWS, J.V., Jr.1981. Dated wood from Alaska and the Yukon: Implications for forest refugia in Beringia. Quaternary Research 15:217–249.

HU, F.S., BRUBAKER, L.B., and ANDERSON, P.M. 1993. A 12,000 year record of vegetation change and soil development from Wien Lake, central Alaska. Canadian Journal of Botany 71:1133–1142.

HUGHES, O.L., HARINGTON, C.R., JANSSENS, J.A.P., MATTHEWS, J.V., Jr., MORLAN, R.E., RUTTER, N.W., and SCHWEGER, C.E. 1981. Upper Pleistocene stratigraphy, paleoecology, and archaeology of the northern Yukon interior, Eastern Beringia: I. Bonnet Plume Basin. Arctic 34(4): 329–365.

HURD, E.G., SHAW, N.L., MASTROGIUSEPPE, J., SMITHMAN, L.C., and GOODRICH, S. 1998. Field guide to intermountain sedges. General Technical Report RMRS-GTR-10. Ogden, Utah: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. 282 p.

JENKINS, S.H., and BUSHER, P.E. 1979. *Castor canadensis*. Mammalian Species 120:1–9.

KAUFMAN, D.S., AGER, T.A., ANDERSON, N.J., ANDERSON, P.M., ANDREWS, J.T., BARTLEIN, P.J., BRUBAKER, L.B., COATES, L.L., CWYNAR, L.C., DUVALL, M.L., DYKE, A.S., EDWARDS, M.E., EISNER, W.R., GAJEWSKI, K., GEIRSDÓTTIR, A., HU, F.S., JENNINGS, A.E., KAPLAN, M.R., KERWIN, M.W., LOZHKIN, A.V., MACDONALD, G.M., MILLER, G.H., MOCK, C.J., OSWALD, W.W., OTTO-BLIESNER, B.L., PORINCHU, D.F., RÜHLAND, K., SMOL, J.P., STEIG, E.J., and WOLFE, B.B. 2004. Holocene thermal maximum in the western Arctic (0–180˚W). Quaternary Science Reviews 23:529–560.

LAWTON, E. 1971. Moss flora of the Pacific Northwest. Miyazaki, Japan: The Hattori Botanical Laboratory. 362 p. + 195 ill.

LÉVESQUE, P.E.M., DINEL, H., and LAROUCHE, A. 1988. Guide to the identification of plant macrofossils in Canadian peatlands. Ottawa, Ontario: Land Resource Research Centre. 65 p.

LOWDON, J.A., and BLAKE, W., Jr. 1979. Geological Survey of Canada radiocarbon dates XIX. Geological Survey of Canada Paper 79-7:1–58.

MANN, D.H., PETEET, D.M., REANIER, R.E., and KUNZ, M.L. 2002. Responses of an Arctic landscape to Lateglacial and early Holocene climatic change: The importance of moisture. Quaternary Science Reviews 21:997–1021.

MATHEUS, P., BEGÉT, J., MASON, O., and GELVIN-REYMILLER, C. 2003. Late Pliocene to late Pleistocene environments preserved at the Palisades Site, central Yukon River, Alaska. Quaternary Research 60:33–43.

MATTHEWS, J.V., Jr., and TELKA, A. 1997. Insect fossils from the Yukon. In: Danks, H.V., and Downes, J.A., eds. Insects of the Yukon. Ottawa: Biological Survey of Canada (Terrestrial Arthropods). 911–962.

MONTGOMERY, F.H. 1977. Seeds and fruits of plants of eastern Canada and northeastern United States. Toronto, Ontario: University of Toronto. 232 p.

MORLAN, R.E. 1999. Canadian Archaeological Radiocarbon Database. www.canadianarchaeology.com/radiocarbon/card/card.htm.

MURRAY, D.F. 1961. Some factors affecting the production and harvest of beaver in the upper Tanana River, Alaska. MS thesis, College University of Alaska, Anchorage, Alaska. 103 p.

NYHOLM, E. 1954. Illustrated moss flora of Fennoscandia II. Musci. Botanical Society of Lund, ed. Malmö, Sweden: CWK Gleerup. 799 p.

PÉWÉ, T.L., BERGER, G.W., WESTGATE, J.A., BROWN, P.M., and LEAVITT, S.W. 1997. Eva interglaciation forest bed, unglaciated east-central Alaska: Global warming 125,000 years ago. Geological Society of America Special Paper 319. 54 p.

PORSILD, A.E., and CODY, W.J. 1980. Vascular plants of continental Northwest Territories, Canada. Ottawa, Ontario: National Museum of Natural Sciences. 667 p.

RAINS, B. 1987. Holocene alluvial sediments and a radiocarbon-dated relict beaver dam, Whitemud Creek, Edmonton, Alberta. The Canadian Geographer 31:272–277.

SMITH, A.J.E. 1993. The moss flora of Britain and Ireland. Cambridge: Cambridge University Press. 706 p.

STEERE, W.C. 1978. The mosses of Arctic Alaska. Bryophytorum Bibliotheca 14. Hirschberg, Germany: J. Cramer. 508 p.

VIERECK, L.A., DYRNESS, C.T., BATTEN, A.R., and WENZLICK, K.J. 1992. The Alaska vegetation classification. General Technical Report PNW-GTR-286. Portland, Oregon: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. 278 p.

VIERECK, L.A., DYRNESS, C.T., and FOOTE, M.J. 1993. An overview of the vegetation of the floodplain ecosystem of the Tanana River, interior Alaska. Canadian Journal of Forest Research 23:889–898.

VITT, D.H., LI, Y., and BELLAND, R.J. 1995. Patterns of bryophyte diversity in peatlands of continental western Canada. The Bryologist 98:218–227.

VITT, D.H., HALSEY, L.A., BRAY, J., and KINSER, A. 2003. Patterns of bryophyte richness in a complex boreal landscape: Identifying key habitats at McClelland Lake Wetland. The Bryologist 106:372–382.

WARNER, B.G. 1990. Methods in Quaternary ecology. St. John's, Newfoundland: Geological Association of Canada. 170 p.

WESTERN REGIONAL CLIMATE CENTER. 2007. Fort Yukon online climate data for 1938–1990. National Climate Data Center, National Oceanic and Atmospheric Administration. http://www.wrcc.dri.edu/cgi-bin/cliMAIN.pl?ak3175.

YESNER, D.R. 2001. Human dispersal into interior Alaska: Antecedent conditions, mode of colonization, and adaptations. Quaternary Science Reviews 20:315–327.