

New Spruce (*Picea* spp.) Macrofossils from Yukon Territory: Implications for Late Pleistocene Refugia in Eastern Beringia

G.D. ZAZULA,^{1,2} A.M. TELKA,³ C.R. HARINGTON,⁴ C.E. SCHWEGER⁵ and R.W. MATHEWES¹

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ABSTRACT. New radiocarbon-dated plant macrofossils provide evidence for black spruce (*Picea mariana*) and white spruce (*Picea glauca*) within the unglaciated Yukon Territory at the onset of glacial conditions during the Marine Isotope Stage 3/2 transition, between about 26 000 and 24 500 ¹⁴C yr BP. These data indicate that spruce trees were able to reproduce sexually and grow to maturity within a glacial environment characterized by widespread steppe-tundra vegetation, loess aggradation, and ice-wedge formation. These trees may have been restricted to rare valley-bottom habitats that provided adequate shelter and moisture similar to those at the present latitudinal tree line. Previously published hypotheses suggest that low *Picea* frequencies in regional Beringian pollen data point to the local persistence of spruce trees through the last glaciation. Although our data provide evidence for local spruce trees at the onset of the last glaciation, the available macrofossil record is inconclusive regarding the survival of spruce through the Last Glacial Maximum in Eastern Beringia. These new plant macrofossil data require palynologists to re-examine the relationship between *Picea* pollen frequency and local trees and highlight the importance of integrated pollen- and macrofossil-based paleoecological reconstructions.

Key words: spruce, refugia, Beringia, Yukon Territory, macrofossils, paleoecology

RÉSUMÉ. De nouveaux macrofossiles de plantes datés au C14 attestent de la présence d'épinette noire (*Picea mariana*) et d'épinette blanche (*Picea glauca*) dans le territoire non glaciaire du Yukon au début des conditions glaciaires, pendant la transition Marine Isotope Stage 3/2, et s'étendant entre environ 26 000 et 24 500 années avant le présent, daté au C14. Selon ces données, les épinettes étaient capables de se reproduire par voie sexuée et de croître jusqu'à maturité dans un milieu glaciaire caractérisé par une végétation à forte densité de steppe et de toundra, par l'aggradation de loess et par une formation de glace fossile. Il se peut que ces arbres se limitaient à de rares habitats au fond de vallées, habitats qui leur procuraient un abri adéquat et un degré d'humidité similaires à ceux qui existent dans la limite actuelle transversale de végétation des arbres. D'après des hypothèses déjà publiées, la faible fréquence de *Picea* dans les données régionales de pollen bérégien laissent supposer la persistance locale des épinettes pendant la dernière glaciation. Bien que nos données fournissent la preuve de l'existence d'épinettes locales au début de la dernière glaciation, les données macrofossiles disponibles ne sont pas concluantes en ce qui a trait à la survie de l'épinette pendant le dernier maximum glaciaire dans la Bérégie de l'Est. Ces nouvelles données macrofossiles de plantes impliquent que les palynologues doivent réexaminer la relation entre la fréquence du pollen de *Picea* et les arbres locaux, et font ressortir l'importance des reconstructions paléoécologiques intégrées du pollen et des macrofossiles.

Mots clés : épinette, refuge, Bérégie, territoire du Yukon, macrofossiles, paléoécologie

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INTRODUCTION

The question of whether spruce trees (*Picea* spp.) survived the Marine Isotope Stage (MIS) 2 glacial interval (ca. 25 000 to 10 000 ¹⁴C yr BP) in Eastern Beringia (unglaciated Alaska and Northwest Canada) has provoked much inquiry and discussion (Hopkins, 1970; Hopkins et al., 1982; Anderson and Brubaker, 1994; Brubaker et al., 2005). White spruce (*P. glauca* (Moench) Voss s.l.) and black spruce (*P. mariana* (Mill.) B.S.P.) are the dominant conifer

trees in the present boreal forest of northern North America (Payette et al., 2001) and were during Pleistocene interglacial periods (e.g., the Last Interglacial, MIS 5) of Eastern Beringia (Schweger, 2002). Paleoecological data for Eastern Beringia during MIS 2 have revealed pollen assemblages dominated by graminoids (grass and sedge), sage (*Artemisia*), and herbs, with limited arboreal taxa, suggesting that open herb-tundra vegetation dominated regional vegetation during the cold, dry glacial interval (Anderson and Brubaker, 1994; Bigelow et al., 2003).

¹ Department of Biological Sciences, Simon Fraser University, Burnaby, British Columbia V5A 1S6, Canada

² Corresponding author: gdzazula@sfu.ca

³ PALEOTEC Services, 1–574 Somerset Street W, Ottawa, Ontario K1R 5K2, Canada

⁴ Canadian Museum of Nature, P.O. Box 3443, Ottawa, Ontario K1P 6P4, Canada

⁵ Department of Anthropology, 13–15 HM Tory Building, University of Alberta, Edmonton, Alberta T6G 2H4, Canada

Plant macrofossil studies have begun to resolve the local floristic and ecological details of this reconstruction, revealing diverse tundra and steppe communities (Goetcheus and Birks, 2001; Zazula et al., 2003a, 2005, 2006). The apparent lack of spruce or other tree macrofossils between 30 000 and 10 000 yr BP (Hopkins et al., 1981) and the low frequency of spruce pollen (generally < 5%) have led some to suggest that Eastern Beringia was a treeless landscape during the last glaciation (Ritchie, 1984; Anderson and Brubaker, 1994). Low-frequency spruce pollen from Eastern Beringian sites is often dismissed as having been transported long distances from forested areas in more southerly latitudes or reworked from older interglacial deposits. Thus, many have assumed that spruce only re-entered Eastern Beringia by migrating northwestward during post-glacial times (Ritchie, 1984; Ritchie and MacDonald, 1986). However, the most recent review of this topic (Brubaker et al., 2005) examined mapped pollen data from sites across northeast Asia, Alaska, and Yukon, which they interpreted as evidence for the persistence of spruce in local cryptic refugia in Eastern Beringia throughout MIS 2.

This paper presents new Accelerator Mass Spectrometry (AMS) radiocarbon-dated plant and insect macrofossils from terrestrial deposits in west-central and northern Yukon Territory (Fig. 1), which indicate that both black and white spruce trees were locally present during the onset of glacial conditions between about 26 000 and 24 500 ^{14}C yr BP (Table 1). These data are important for reconstructing the paleoenvironments of Eastern Beringia because macrofossils indicate that spruce trees were able to live within glacial environments characterized by widespread steppe-tundra vegetation, loess aggradation, and ice-wedge formation. These macrofossil data are important for the interpretation of Late Pleistocene pollen records, since interpretation of low spruce-pollen frequencies has been ambiguous for the identification of local spruce.

STUDY SITES

The plant macrofossils analyzed were recovered from a variety of settings across Yukon Territory (Fig. 1). Sites include exposures along Last Chance Creek and Quartz Creek in the Klondike goldfields of west-central Yukon (Fig. 1 inset), where ice-rich loess sediments preserve a wealth of paleoecological remains (Harrington and Eggleston-Stott, 1996; Harrington, 2003; Zazula et al., 2003a, b, 2005). We also obtained macrofossils from alluvial sediments at the Bluefish Exposure, 30 km southwest of Old Crow, in northern Yukon Territory (Zazula et al., 2006). Our study sites are all within the present-day boreal forest. Radiocarbon dates are presented in ^{14}C years before present (yr BP) unless otherwise indicated. Calibrated ages (cal. yr BP) mentioned follow those presented in the source publications.

In the boreal forest of present-day Yukon Territory, vegetation and substrate characteristics vary considerably

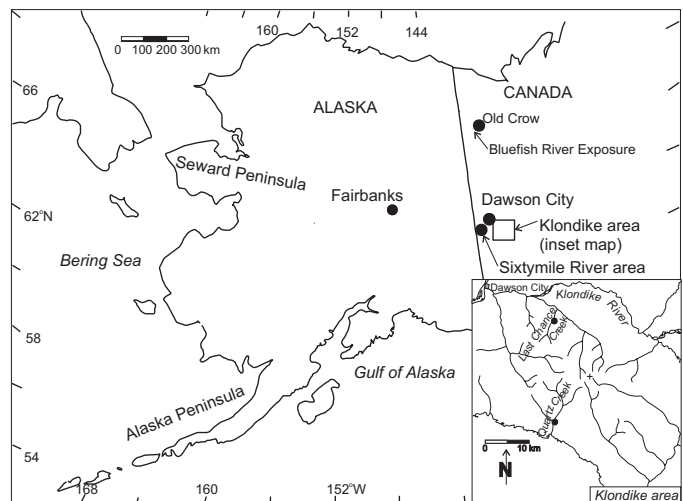


FIG. 1. Map of study area from Yukon Territory and Eastern Beringia, with inset showing the Klondike region.

with topography, aspect, and local moisture. In general, north- and northeast-facing sites and other habitats with poor drainage and shallow permafrost are typically occupied by black spruce stands with an insulating ground cover dominated by moss, sedges, and ericaceous shrubs. Sites with southerly aspect and better drainage, where permafrost is absent or lies far below the surface, are occupied by open white spruce stands, often with trembling aspen (*Populus tremuloides*) and a variety of shrubs and forbs. Thus, within the Subarctic boreal forest, a variety of plant community types commonly form a patchwork of vegetation cover, depending on local environmental variables. The local tree line is found near 1100 m asl in central Yukon, and about 600 m asl near Old Crow to the north. The factors that determine latitudinal tree line are complex and include length of growing season, growing season temperatures, wind, snow cover, and soil nutrients (Larsen, 1989). In Alaska, the northern tree line is usually defined as the limit of white spruce along the south slope of the Brooks Range, though black spruce may be present in some areas (Viereck, 1979). In general, for Alaska and Yukon Territory, the latitudinal tree line ecotone where spruce forest gives way to tundra occurs north of the July daily mean isotherm of 12°C (Thompson et al., 1999; Muhs et al., 2001).

RESULTS

Klondike Goldfields, West-Central Yukon Territory

Two fossil arctic ground squirrel (*Spermophilus parryii*) middens recovered from north-facing, ice-rich silt exposures with massive ice-wedges below Dawson tephra (ca. 25 300 ^{14}C yr BP; Froese et al., 2002, 2006) at Quartz Creek yielded complete spruce needles. Within the Klondike region, Dawson tephra provides a widespread stratigraphic marker for the onset of glacial conditions during early MIS 2. Fossil middens

TABLE 1. Late Pleistocene radiocarbon dates obtained from spruce macrofossils and other samples that provide supporting evidence for Late Pleistocene spruce trees.

Age ^{14}C yr BP	Lab No.	Context	Dated material	Sites in Yukon	Reference
25 870 \pm 190	Beta-210521	squirrel midden with <i>Picea</i>	<i>Polemonium</i> fruits	Quartz Creek	this paper
25 800 \pm 240	Beta-210522	squirrel midden with <i>Picea</i>	Grass leaves	Quartz Creek	this paper
26 280 \pm 210	Beta-67407	horse carcass with <i>Picea</i>	Horse bone	Last Chance Creek	Harington and Eggleston-Stott, 1996
26 080 \pm 300	Beta-13870	<i>Picea</i> stump	<i>Picea</i> stump	Sixtymile	Harington, 1989, 1997; Matthews et al., 1989
25 700 \pm 400	Beta-171748	valley bottom peat	<i>Carex</i> achenes	Last Chance Creek	Zazula et al., 2003b
24 530 \pm 180	Beta-193791	Two <i>Picea</i> needle fragments	Two <i>Picea</i> needle fragments	Bluefish River	this paper; Zazula et al., 2006
18 460 \pm 350	TO-7745	American mastodon (<i>Mammot americanum</i>)	Mastodon tooth	Goldrun Creek	Storer, 2002
24 980 \pm 1300	Beta-16163	American mastodon (<i>Mammot americanum</i>)	Mastodon tooth	Sixtymile	Harington, 1997
29 600 \pm 300	TO-292	seeds in association with single <i>Picea</i> needle	<i>Corispermum</i> seeds	Mayo Indian Village	Matthews et al., 1990
38 100 \pm 1330	GSC-4554	organic remains with abundant <i>Picea</i>	Bulk organic	Mayo Indian Village	Matthews et al., 1990

consist of frozen accumulations of fossil grassy nest material and cached seeds within hibernacula (Harington, 1997; Zazula et al., 2005). These fossil midden records provide excellent data on local vegetation since arctic ground squirrels typically forage within a limited radius from their burrows (Batzli and Sobaski, 1980).

The first midden (GZ.05.34; Fig. 2) was recovered from an exposure 3 m below Dawson tephra. *Polemonium* fruits (capsules) from the midden yielded an AMS ^{14}C date of 25 870 \pm 190 ^{14}C yr BP (Beta-210521). A complete *Picea* needle (Fig. 3a) was recovered within a macrofossil assemblage dominated by graminoid foliage, along with seeds or fruits or both of *Elymus*, *Festuca*, *Poa*, *Kobresia myosuroides*, *Bistorta vivipara*, *Anemone patens* var. *multifida*, *Silene taimyrensis*, *Draba* sp., *Potentilla*, and *Polemonium*. The poor preservation of this spruce needle precluded successful cross-sectioning to identify the species. The second midden (GZ.05.44) was recovered approximately 10 m downstream from midden GZ.05.34, and 2 m below Dawson tephra. Graminoid foliage from the midden (Beta-210522) yielded an AMS ^{14}C date of 25 800 \pm 240 ^{14}C yr BP. Two complete *Picea* needles (Fig. 3b) were recovered from within a plant macrofossil assemblage dominated by dry-land steppe-tundra graminoids and herbs, including *Elymus*, *Festuca*, *Poa*, *Kobresia myosuroides*, *Artemisia frigida*, *Bistorta vivipara*, *Silene taimyrensis*, *Draba* sp., *Potentilla*, *Phlox hoodii*, *Plantago* cf. *canescens*, and *Bupleurum americanum*. Three separate cross sections along the apex, middle, and base of the fossil needle from midden GZ.05.44 (Fig. 3d) reveal two resin ducts, identifying the specimen as *P. mariana*. According to Weng and Jackson (2000), *Picea glauca* needles have discontinuous resin ducts (typically with a single resin duct revealed in cross section), while *P. mariana* always has two continuous resin ducts. Although we did not obtain radiocarbon dates directly on the *Picea* needles, the inability of arctic ground squirrels to burrow into frozen sediments suggests it is highly improbable that needles from the middens could be reworked from older deposits. These two middens are unique in that they are the

only ones out of 48 individual middens from the Klondike dated between 29 450 \pm 320 ^{14}C yr BP (Beta-202418) and 23 990 \pm 130 ^{14}C yr BP (Beta-161238) that contain spruce macrofossils (Zazula, 2006).

Rare *Picea* needles and cone scales (Fig. 3c, e, h) were recovered from intestinal contents of a partially mummified horse (*Equus lambei*) carcass and surrounding silt matrix from Last Chance Creek dated to 26 280 \pm 210 ^{14}C yr BP (Beta-67407) (Harington and Eggleston-Stott, 1996). The macrofossil assemblage is dominated by tundra and steppe herbs, including *Poa*, *Chenopodium*, *Cerastium*, *Silene*, *Potentilla*, *Papaver*, *Androsace septentrionalis*, *Plantago* and *Artemisia* (Harington, 2002; A.M. Telka and C.R. Harington, unpubl. data). Other arboreal remains include *Betula* (tree type) and *Alnus* fruits. Since an abundance of silt was found within the stomach, we suggest that spruce needles may have washed into the horse's mouth after it died, and their presence is probably not the result of browsing. The ingestion by mired Pleistocene mammals of mud and other organic inclusions from their surroundings has also been noted for Pleistocene mammal fossils elsewhere (Harington et al., 1993). Cross sections of a needle recovered from the horse stomach revealed a four-angle shape with a single resin duct (Fig. 3e), identifying the specimen as *Picea glauca* (Durrell, 1916; Weng and Jackson, 2000).

Bluefish Exposure, Northern Yukon Territory

At the Bluefish River Exposure (Zazula et al., 2006), two *Picea* needle fragments yielded an AMS ^{14}C age of 24 530 \pm 180 ^{14}C yr BP (Beta-193791). Previous work at the site had revealed a plant macrofossil assemblage dominated by steppe and tundra herbs (including *Artemisia frigida*, several Poaceae and diverse forbs) deposited during the Last Glacial Maximum (LGM) (Zazula et al., 2003a, 2006). This ^{14}C date on spruce needles is older than other dates from the deposit and indicates that reworking of older material occurred within the sediments. Nine AMS ^{14}C ages obtained on terrestrial herbaceous macrofossils (e.g., Poaceae caryopses, *Artemisia* flowers,

Phlox capsules) indicate the deposit was formed between ca. 18 880 and 16 400 ^{14}C yr BP (Zazula et al., 2006). Other evidence for reworking of older material from the site is provided by an age greater than 44 450 ^{14}C yr BP (Beta-193790) on *Picea* wood from the same horizon that yielded the dated needle fragments and an age of $20\,800 \pm 200$ ^{14}C yr BP (GSC-3946; Blake, 1987) obtained from associated bulk sediments. The new AMS ^{14}C age on spruce needle fragments confirms the presence of spruce during the transition from MIS 3 to MIS 2 in northern Yukon Territory.

Insects

Fossil insects from our study sites support plant macrofossil evidence for local spruce trees. The weevil *Pissodes* sp. was recovered in association with the fossil horse carcass at Last Chance Creek (Fig. 3i). Species of *Pissodes* inhabit boreal and boreal-montane forests, where they feed upon host spruce trees (both black and white spruce) and sometimes pine (Anderson, 1997). The ground beetle *Pterostichus adstrictus*, commonly found at present in northern coniferous forest, was recovered from valley bottom peat dating to $25\,700 \pm 400$ ^{14}C yr BP (Beta-171748; Zazula et al., 2003b) at Last Chance Creek (Fig. 3j). But unlike *Pissodes* this ground beetle prefers more open country including lush meadows of grasses and herbs (Ball and Currie, 1997). *Pterostichus adstrictus* is not found above tree line in “true tundra,” but does occur on coastal tundra with a habitat range that extends into the Aleutian Islands (Lindroth, 1961–69). Specimens of the fly *Xylophagus* sp. were recovered from a few study sites including the Last Chance Creek horse carcass (Fig. 3f, g), valley bottom peat at Last Chance Creek (Zazula et al., 2003b), and alluvial sediments at the Bluefish Exposure (Zazula et al., 2006). Adult *Xylophagus* are often collected on herbaceous vegetation along wooded river ravines and in woodlands. Immature forms live in rotting logs or under bark of coniferous and deciduous trees (Webb, 1979).

ADDITIONAL EVIDENCE FOR SPRUCE IN YUKON DURING MIS 2 AND MIS 3

The history of spruce trees in Eastern Beringia during the Middle Wisconsinan interstadial (MIS 3 = ca. 65 000–25 000 yr BP) is complicated by chronological uncertainties and limited sites (Anderson and Lozhkin, 2001). MIS 3 climates are generally considered warmer than those of MIS 2 (Begét, 1990), and paleoecological data suggest that open spruce forests became established in Yukon Territory and interior Alaska, but did not reach their modern latitudinal or longitudinal limits (Anderson and Lozhkin, 2001). This vegetation may be best described as a forest-tundra mosaic and not the dense boreal forest that typifies the interior regions of Alaska and Yukon today. Spruce probably formed open stands in sheltered valley-bottom settings within regional tundra-type vegetation



FIG. 2. Fossil arctic ground squirrel midden (GZ.05.34) from Quartz Creek site.

that was more widespread. Anderson and Lozhkin (2001) suggest that some pollen sequences record forest-tundra vegetation being replaced by herb-willow or herb-graminoid tundra by about 30 000 yr BP.

Macrofossils obtained from alluvial sediments dated around $29\,600 \pm 300$ ^{14}C yr BP (TO-292) at the Mayo Indian Village (MIV) site along the Stewart River in central Yukon Territory are dominated by diverse tundra herbs, including *Corispermum hyssopifolium*, *Bupleurum americanum*, *Potentilla*, *Dryas*, *Papaver*, several Caryophyllaceae, and shrubs (*Salix*, *Betula glandulosa*), suggesting a cold and dry tundra environment (Matthews et al., 1990). The single spruce needle reported from this assemblage was originally interpreted as being reworked even though there are consistently low frequencies of spruce pollen (ca. 5%–10%). Spruce macrofossils and pollen are more abundant in a sample dated to $38\,100 \pm 1330$ ^{14}C yr BP (GSC-4554) from an exposure upstream of the main MIV site. These data suggest climatic deterioration following forested conditions at about 38 000 ^{14}C yr BP, culminating in the depression of the tree line by at least 850 m below present at 29 600 ^{14}C yr BP, when some spruce trees may have been isolated in small groves in sheltered localities (Matthews et al., 1990).

Along the Sixtymile River in west-central Yukon Territory, several well-preserved spruce stumps up to 120 cm in circumference and 36 cm in diameter were found in growth position at the base of ice-rich silt sediments overlying gold-bearing gravel (Fig. 4). An age of $26\,080 \pm 300$ ^{14}C yr BP (Beta-13870; Harington, 1989, 1997; Matthews et al., 1989) on one specimen (30 cm in diameter) indicates that mature spruce trees (presumably *Picea glauca*, judging from the size) inhabited the region near the onset of glacial conditions during the transition from MIS 3 to MIS 2. This is the youngest Late Pleistocene spruce macrofossil age previously published from Eastern Beringia, yet it is absent from prior discussions of tree refugia (e.g., Brubaker et al., 2005).

A pollen record from “Antifreeze Pond” in the Snag-Klutlan region of southwest Yukon Territory provides

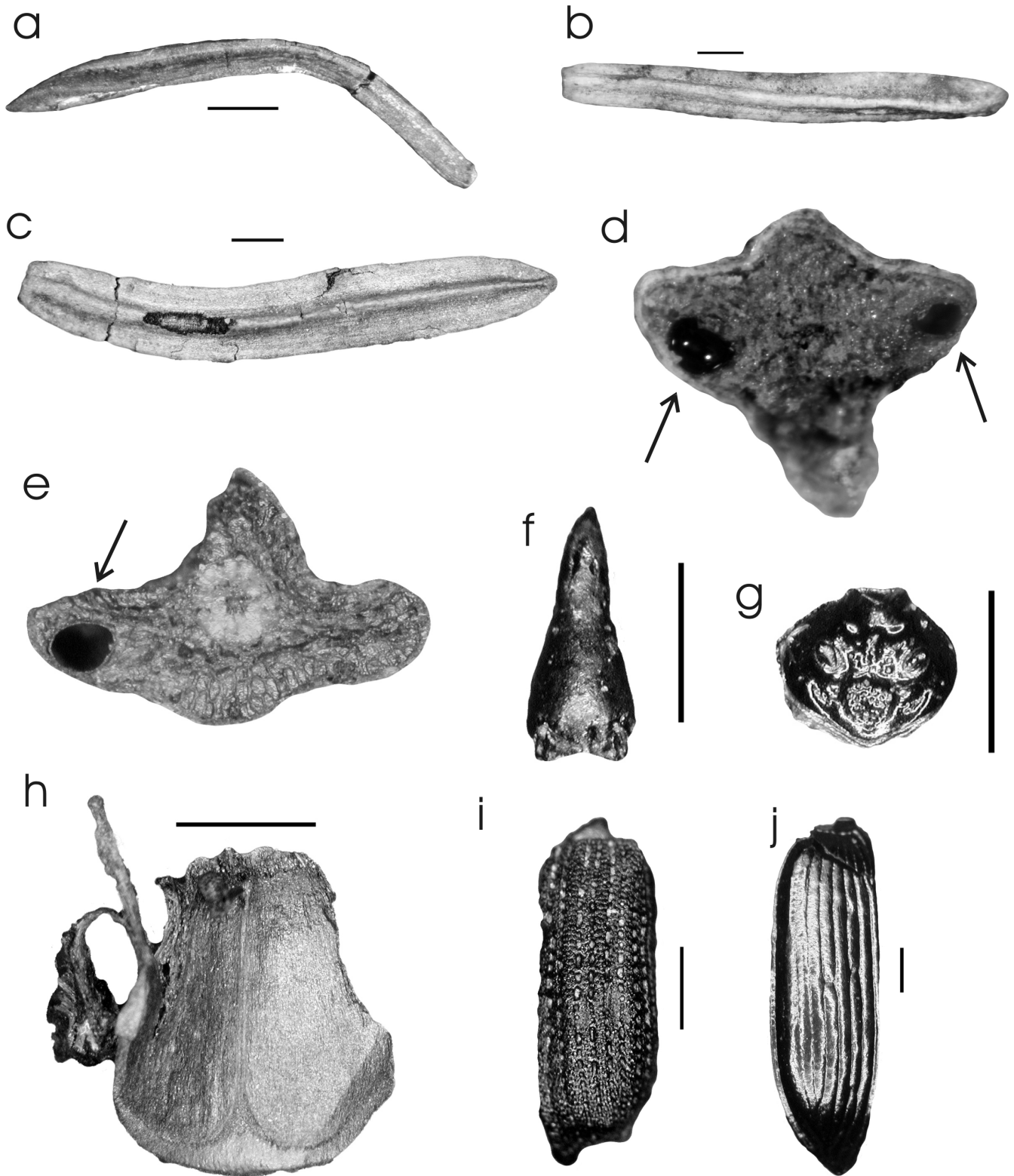


FIG. 3. Selected spruce and insect macrofossils recovered from our study sites in Yukon Territory. Scale bars = 1 mm except where otherwise noted. a) *Picea* needle from Quartz Creek midden (GZ.05.34); b) *Picea* needle from Quartz Creek midden (GZ.05.44); c) *Picea* needle from Last Chance Creek horse stomach; d) cross section of *Picea* needle from midden GZ.05.44, arrows point to two resin ducts, indicating the specimen represents *P. mariana*; e) cross section of *Picea* needle from Last Chance Creek horse stomach, arrow points to single resin duct, indicating the specimen represents *P. glauca*; f) *Xylophagus* larva head capsule from Last Chance Creek horse stomach; g) *Xylophagus* larva caudal plate from Last Chance Creek horse stomach; h) *Picea* cone scale from Last Chance Creek horse stomach (scale bar = 4 mm); i) *Pissodes* sp. elytron from Last Chance Creek horse pelt; j) *Pterostichus adstrictus* elytron from Last Chance Creek valley bottom peat.

evidence for Late Pleistocene and Holocene vegetation changes (Vermaire, 2005). In the basal part of this lacustrine

record, considered to represent the late Middle Wisconsinan interstadial (ca. > 30 000 yr BP), herbaceous taxa dominate



FIG. 4. Rooted in situ spruce stumps at exposure in Sixtymile River valley with ice-rich silt in background. Photo by C.R. Harington, 4 September 1985. This photo was taken at the same exposure, about one year after the $26\,080 \pm 300$ ^{14}C yr BP year old spruce stump sample (Beta-13870) was collected.

the pollen assemblage. However, rare *Picea* needles and associated *Picea* stomates indicate that scattered spruce trees persisted locally in the herb-dominated vegetation. Trees were present even though spruce pollen frequency is consistently less than 10% and most often under 5% during this interval (Vermaire, 2005). Unfortunately, chronological and stratigraphic problems at Antifreeze Pond do not permit precise timing of paleoecological changes during MIS 3 and MIS 2.

Supporting evidence for the local presence of spruce in the central Yukon during the last glaciation is provided by fossil remains of the American mastodon (*Mammuth americanum*). American mastodons were browsing specialists and are known to have eaten spruce, since their gastrointestinal and fecal samples have yielded needles and twigs (Laub et al., 1994; Ponomarenko and Telka, 2003). Furthermore, their fossil remains are often recovered in association with paleoecological evidence for open spruce forests (Peterson et al., 1983; Harington et al., 1993). Thus, mastodon fossils dating to $24\,980 \pm 1300$ ^{14}C yr BP (Beta-16163, Harington, 1997) from Sixtymile and $18\,460 \pm 350$ ^{14}C yr BP (TO-7745; Storer, 2002) at Gold Run Creek in the Klondike may in fact provide supporting paleoecological data for the presence of spruce in Eastern Beringia during MIS 2.

Late-Glacial and Post-Glacial Spruce

The widespread post-glacial establishment of spruce is recorded in pollen and macrofossil records from across Eastern Beringia. Low frequencies of spruce pollen (usually < 2%) are present in some central Alaskan lake records (e.g., Harding and Wonder lakes) during the late glacial 11 000 cal. yr BP, though chronological uncertainties and artifacts of data analysis suggest that spruce trees may not actually have been present (Bigelow and Powers, 2001). The local arrival of spruce in central Alaskan lakes (e.g., Ten Mile Lake, Harding Lake, Birch Lake, Dune Lake) is

signified by increased *Picea* pollen (up to 10%) by around 10 000 cal. yr BP (Bigelow and Powers, 2001; Carlson and Finney, 2004). Combined pollen and stomate evidence confirms the local presence of spruce trees by about 10 000 cal. yr BP at Jan Lake in east-central Alaska (Carlson and Finney, 2004) and by 9500 cal. yr BP at Antifreeze Pond in west-central Yukon (Vermaire, 2005). The earliest dated Holocene *Picea* macrofossils from Eastern Beringia are from the Canyon Creek locality, where a single cone of white spruce (*Picea glauca*) was recovered from a paleosol dated to 9460 ± 155 ^{14}C yr BP (I-8291; Weber et al., 1981) and from Tangle Lakes, where white spruce cones are associated with a marked rise in spruce pollen at 9100 ± 80 ^{14}C yr BP (UCLA-1858; Schweger, 1981).

DISCUSSION

Our data represent the youngest AMS radiocarbon-dated Pleistocene spruce macrofossils from Eastern Beringia found thus far. These and other supporting data indicate that scattered spruce trees occupied west-central and northern Yukon Territory within widespread steppe-tundra vegetation at the transition from MIS 3 to MIS 2, between about 26 000 and 24 500 ^{14}C yr BP. This time interval coincides with the onset of cold, arid glacial conditions when stratigraphic records across Yukon Territory document the aggradation of abundant loess and features such as ice-wedges (Cinq-Mars and Morlan, 1999; Froese et al., 2002; Zazula et al., 2003a, b). Given what is known about the climatological limits on the northern tree line (Thompson et al., 1999; Muhs et al., 2001), the lack of zonal forests in central and northern Yukon Territory suggests that July mean air temperatures at about 25 000 ^{14}C yr BP could not have been more than about 10–12°C. At present, July mean air temperatures at Dawson City, Yukon, are 15.6°C, suggesting paleotemperature depression by at least 5.6–3.6°C during the transition from MIS 3 to MIS 2. These estimates agree with Mutual Climate Range (MCR) reconstructions based on insect fauna from the Klondike, which suggest that paleotemperatures in the region at the time of Dawson tephra deposition were depressed by around 5.6–6.6°C (Zazula et al., in press). These paleotemperature estimates are typical for MIS 2 in Eastern Beringia (Elias, 2000) and suggest that our spruce macrofossil record reflects trees that lived under typical full-glacial climates characterized by aridity and colder air temperatures than at present. Moisture requirements for trees may have restricted spruce to sheltered, well-watered habitats such as valley bottom stream courses and persistent snowbanks.

However, our plant macrofossil data are ambiguous to whether spruce trees survived in this region beyond 24 500 ^{14}C yr BP and into the LGM (ca. 18 000 ^{14}C yr BP) of MIS 2. The lack of dated spruce macrofossil remains from Eastern Beringia between about 24 500 ^{14}C yr BP and 9500 ^{14}C yr BP suggests two possible explanations: 1) that

spruce was absent in Eastern Beringia during the LGM, or 2) that spruce persisted there throughout the LGM, although we lack macrofossils dating to this interval.

1. Absence of Spruce in Eastern Beringia during the LGM

The ca. 16000-year-long gap in the spruce macrofossil record of Eastern Beringia suggests that spruce may have been extirpated during the peak LGM in Eastern Beringia. The period of the gap included the full emergence of the Bering Land Bridge, widespread advance of continental ice-sheets, and significant reduction of regional atmospheric moisture sources in the interior of Alaska-Yukon (Hopkins et al., 1982; Elias, 2000; Brigham-Grette, 2001; Guthrie, 2001). Pronounced aridity and decreased temperatures after 24500 ^{14}C yr BP may have made Eastern Beringia inhospitable for spruce trees, since soil moisture availability is a key factor in the survival of spruce at the latitudinal tree line (Payette et al., 2001; Brubaker et al., 2005). This scenario suggests that our new data may record the last occurrences of spruce before they were extirpated from Eastern Beringia during the LGM and thus, they support previous reconstructions (e.g., Hopkins et al., 1981; Ritchie, 1984; Ritchie and Macdonald, 1986) which proposed that trees did not survive the last glaciation in this region.

2. Persistence of Spruce in Eastern Beringia during the LGM

Although there is still no macrofossil evidence for spruce between ca. 24500 and 9500 ^{14}C yr BP, our macrofossil record confirms that spruce trees could inhabit suitable microsites within a glacial steppe-tundra ecosystem. This evidence lends support to previous pollen-based hypotheses that suggest trees could survive in Eastern Beringia through the LGM. Payette et al. (2002) and Brubaker et al. (2005) suggest that limited LGM spruce pollen (typically < 2%) is best explained by cryptic refugia rather than by poorly defined long-distance sources or reworking of older (interstadial or interglacial) deposits. Furthermore, Payette et al. (2002) and Brubaker et al. (2005) suggest that the dramatic increase in spruce pollen frequency during the early Holocene is best explained by expansion from local LGM spruce refugia as opposed to unrealistically high rates of migration from southern refugia. The single dated American mastodon tooth at 18460 ± 350 ^{14}C yr BP from the Klondike provides additional support for the presence of LGM spruce.

Problematic Identification of Cryptic Refugia

As Brubaker et al. (2005) suggest, cryptic refugia are difficult to identify in the paleoecological record. If spruce inhabited only rare habitats, the likelihood that spruce would appear in macrofossil assemblages may be low. For example, spruce macrofossils are absent from valley-bottom peat dating to 25700 ± 400 ^{14}C yr BP (Beta-

171748) at Last Chance Creek (Zazula et al., 2003b) and under Dawson tephra at Quartz Creek (Zazula, 2006) even though contemporaneous data presented in this paper indicate that spruce trees were present in both watersheds at that time. Also, in situ riparian vegetation buried by Dawson tephra at nearby Goldbottom Creek in the Klondike lacks spruce macrofossils (Froese et al., 2006; Zazula, 2006; Zazula et al., in press). Thus, since the recovery of glacial-aged spruce macrofossils in terrestrial deposits may be fortuitous, they should be looked for in a variety of depositional contexts.

The lack of LGM spruce macrofossils may also reflect a lack of correlative terrestrial deposits. The only other reported macrofossils from this interval come from the now-submerged Bering Land Bridge (Elias et al., 1997) and from buried in situ vegetation on the Seward Peninsula (Goetcheus and Birks, 2001). To our knowledge, no terrestrial deposits with macrofossil assemblages dating to the peak LGM in the interior of Alaska or Yukon have been reported. If spruce did survive through MIS 2 in Eastern Beringia, deposits that contain spruce macrofossils may be absent, or they may have yet to be discovered.

Central to the problem of identifying refugia without plant macrofossils is how to interpret the low *Picea* pollen frequencies. In general, full-glacial pollen assemblages from across Eastern Beringia record low (< 5%) *Picea* pollen frequency, and some palynologists adhere to a 10% *Picea* pollen threshold for local trees (Anderson and Brubaker, 1986; Bigelow and Powers, 2001). *Picea* pollen frequency lower than 2% is recorded in sediments associated with Dawson tephra at Goldbottom Creek in the Klondike, even though our data indicate spruce trees were present in the adjacent Quartz and Last Chance creek valleys (Zazula, 2006). A similar situation occurs at Antifreeze Pond, with stomates and macrofossils indicating local spruce, but low (< 5%) pollen frequencies suggesting otherwise (Vermaire, 2005). Macrofossil evidence for local spruce trees recovered from sites with low *Picea* pollen frequencies requires palynologists to reconsider how to interpret pollen records with regard to glacial refugia.

Spruce at its Environmental Limits

Our macrofossil evidence for spruce within zonal steppe-tundra vegetation raises questions about the autoecology and physiology of spruce near the onset of the last glaciation. Cross sections of spruce needles indicate that our macrofossil record includes both black and white spruce trees. Much of the work on spruce at its present-day environmental limits has been conducted in the Eastern Arctic, where black spruce forms the latitudinal tree line (Laberger et al., 2000, 2001; Payette et al., 2001; Gamache and Payette, 2004). In these areas, trees are confined to wind-protected, well-watered or seepage areas, while exposed uplands have tundra vegetation. A common growth form in these tree line environments is stunted black spruce clones (krummholz) that rarely exceed 30 cm in

height. Danby (2003) also indicates that white spruce (*Picea glauca*) at the altitudinal tree line in southwest Yukon Territory layer vegetatively and produce stunted growth forms. In Alaska, where black spruce and white spruce are found together at the northern tree line, black spruce is typically in limited distribution, with layered growth forms. White spruce most often occurs as single trees, though layering occasionally occurs (Viereck, 1979). However, not all trees at the latitudinal tree line are krummholz, as demonstrated in areas such as the Firth River Basin on the Yukon North Slope, where open mature spruce woodlands occupy south-facing slopes and certain low terrace edges within zonal tundra (Larsen, 1989).

The analogy of stunted spruce trees or those that reproduce vegetatively may not be good analogues for our spruce macrofossil record. The presence of spruce cone scales associated with the Last Chance Creek horse and large (36 cm in diameter) spruce stumps indicate that reproductively viable, full-stature trees were able to adapt to glacial conditions and form scattered stands between about 26 000 and 24 500 ¹⁴C yr BP. However, the vegetation suggested by our macrofossil data may have been physiognomically similar to Arctic tree-line vegetations, with tundra-covered uplands and trees in the valley bottoms and on some steep slopes (Larsen, 1989; Laberge et al., 2000, 2001; Payette et al., 2001; Gamache and Payette, 2004). The redistribution of sparse snowfall into valley-bottom drifts may have been important for spruce survival during the late Pleistocene, since such protected sites may have prevented the desiccation of foliage and provided moisture later into the growing season (Payette et al., 1996; Epstein et al., 2004). Autoecological preferences suggest that our Pleistocene black spruce may have favored the wettest lowland sites with permafrost, while white spruce may have occupied more mesic sites. These habitat differences inferred from the presence of both black and white spruce trees at our sites support previous discussions on the importance of ecological mosaics in glacial Beringia (Hopkins et al., 1982; Zazula et al., 2005, 2006).

CONCLUSIONS

New radiocarbon-dated plant macrofossils place spruce trees in central and northern Yukon until at least 24 500 ¹⁴C yr BP. This was a time when steppe-tundra formed zonal vegetation on well-drained loessal soils and climates were significantly colder than modern ones and typical of full-glacial conditions (Froese et al., 2002; Zazula et al., 2003a, b, in press; Sanborn et al., 2006; Zazula, 2006). Macrofossil data indicate that rare black and white spruce trees, some of which were able to reproduce sexually and grow to maturity, could survive in suitable habitats within the glacial steppe-tundra ecosystem at the transition from MIS 3 to MIS 2. However, the available macrofossil data are inconclusive on whether spruce actually did survive through the LGM to form populations from which trees expanded

during the Early Holocene. Although some aspects of the regional pollen data may suggest the persistence of local spruce through MIS 2 (Payette et al., 2002; Brubaker et al., 2005), the recovery and dating of LGM spruce macrofossils is the only way to make definitive claims about the existence of glacial tree refugia.

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