Vegetation buried under Dawson tephra (25,300 ^{14}C years BP) and locally diverse late Pleistocene paleoenvironments of Goldbottom Creek, Yukon, Canada

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Abstract

Paleoecological research at Goldbottom Creek in the Klondike region of Yukon Territory (NW Canada) documents an in situ riparian grassy meadow that was buried during the winter or early spring by Dawson tephra, near the onset of Marine Isotope Stage (MIS) 2, ca. 25,300 ^{14}C years BP. Analyses of vascular plant macrofossils, bryophytes, pollen, insects and paleosols from the riparian meadow contrast with evidence for well-drained, upland steppe–tundra habitats obtained from fossil arctic ground squirrel middens within the same valley. The mesic valley bottom vegetation consisted of grasses (*Deschampsia caespitosa*, *Alopecurus*), sedges (*Carex*), horsetail (*Equisetum* cf. *palustre*), diverse bryophytes and few forbs. Upland habitats with dry loessal soils along the valley slopes contained graminoids (*Elymus*, *Festuca*, *Kobresia myosuroides*), sage (*Artemisia frigida*) and diverse steppe and tundra forbs (*Phlox hoodii*, *Plantago* cf. *canescens*, *Anemone patens* var. *multifida*, *Bistorta vivipara*, *Draba*). These paleoecological data highlight the effect of topographic position and moisture on substrates and their control on local-scale habitat variability. This study represents the first recorded in situ riparian surface from the unglaciated Pleistocene refugium of Beringia and provides well-documented evidence for local habitat heterogeneity and ecosystem structure within the mammoth–steppe biome. Other radiocarbon dated paleoecological data from our study sites indicate that full-glacial steppe–tundra habitats in west-central Yukon Territory were established during the later stages of the MIS 3 interstadial, by 29,000 ^{14}C years BP. The diverse data obtained through integration of multiple paleoecological methods

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at the site demonstrate the efficacy of interdisciplinary research in furthering our understanding of Beringian glacial environments.

1. Introduction

Tephra are well-defined stratigraphic markers and may entomb and preserve exceptional, intact biotic communities in sedimentary deposits. However, there are few examples of in situ Pleistocene fossil ecosystems preserved by volcanic ash, even though tephra are abundant and well-documented within terrestrial sediments of many regions. For example, Eastern Beringia, the unglaciated Pleistocene refugium of Alaska and Yukon Territory, is within the fallout zone of at least 70 Pleistocene eruptions from the volcanoes in Aleutian arc—Alaska Peninsula and Wrangell–St. Elias Mountains (Begét, 2001). However, until now the only documented in situ vegetation preserved under tephra in this region is an 18,000 ^{14}C years BP vegetated surface on the Seward Peninsula, where an upland tundra community is buried beneath tephra derived from a local maar (Goetcheus and Birks, 2001). Buried fossil surfaces under tephra provide a detailed record of the actual composition and structure of a past ecosystem at a single place and time.

In this paper, we provide a multi-proxy record of riparian vegetation preserved beneath late-Pleistocene tephra in the Klondike region of west-central Yukon Territory, Canada. Paleoecological reconstruction based on in situ vegetation is especially important for Eastern Beringia where decades of previous research have yet to resolve many significant details of terrestrial ecosystems during the last glaciation (e.g., Cwynar and Ritchie, 1980; Hopkins et al., 1982; Schweger, 1982; Guthrie, 1990; Colinvaux, 1996; Elias et al., 1997; Bigelow et al., 2003). Most of what we know about regional Beringian ecosystems during the Marine Isotope Stage (MIS) 2 glacial interval is based on the analysis of fossil pollen (Anderson and Brubaker, 1994; Bigelow et al., 2003) and vertebrate assemblages (Guthrie, 1990; Harington, 2003). Although different interpretations of these data have been controversial (Hopkins et al., 1982; Guthrie, 1990; Colinvaux, 1996), paleoenvironmental reconstruction of Beringia suggests an open landscape covered by graminoid and herbaceous tundra/steppe

vegetation which supported the diverse, now-extinct "mammoth–fauna". However, these data lack the spatial or taxonomic resolution to make unambiguous conclusions about meso- and local-scale ecosystem composition or variability. Most previous reconstructions of habitat variability are speculative, such as Schweger's (1982) "mosaic hypothesis". This hypothesis suggests that Beringian paleoenvironments consisted of a variety of tundra, steppe and meadow habitats that were distributed with respect to variables such as moisture availability, aspect and topographic position. Other models are based on extrapolation of data from different sites. For example, habitat variability related to topography and local moisture availability is highlighted by plant macrofossils from upland vegetation buried by tephra on the Seward Peninsula, Alaska (Goetcheus and Birks, 2001) and lowland peat recovered from the now-submerged Bering Land Bridge (Elias et al., 1997). Since these data were recovered from very different contexts, spanning distinct temporal ranges, little can be said about how various habitat types contributed to local-scale ecosystem structure and function. Knowledge of local habitat heterogeneity is important for understanding mammal foraging on the mammoth–steppe since the spatial patterning of forage may influence where and when particular herbivores utilize different habitats.

Here we present multi-proxy paleoecological results from four sites exposed along Goldbottom Creek (Figs. 1 and 2), including the analysis of a vegetated land surface buried by Dawson tephra at ca. 25,300 ^{14}C years BP (Froese et al., 2002, 2006). Data from our sites include Accelerator Mass Spectrometry (AMS) ^{14}C dates, fossil arctic ground squirrel middens, vascular plant macrofossils, bryophytes, fossil insects, paleosols, and pollen. This paper builds upon the stratigraphy, chronology and preliminary paleoecological interpretations from the site reported by Froese et al. (2006). These data provide a unique opportunity to further our understanding of how late Pleistocene ecosystems were structured at the local scale through comparison of paleoecological data from lowland and upland habitats.
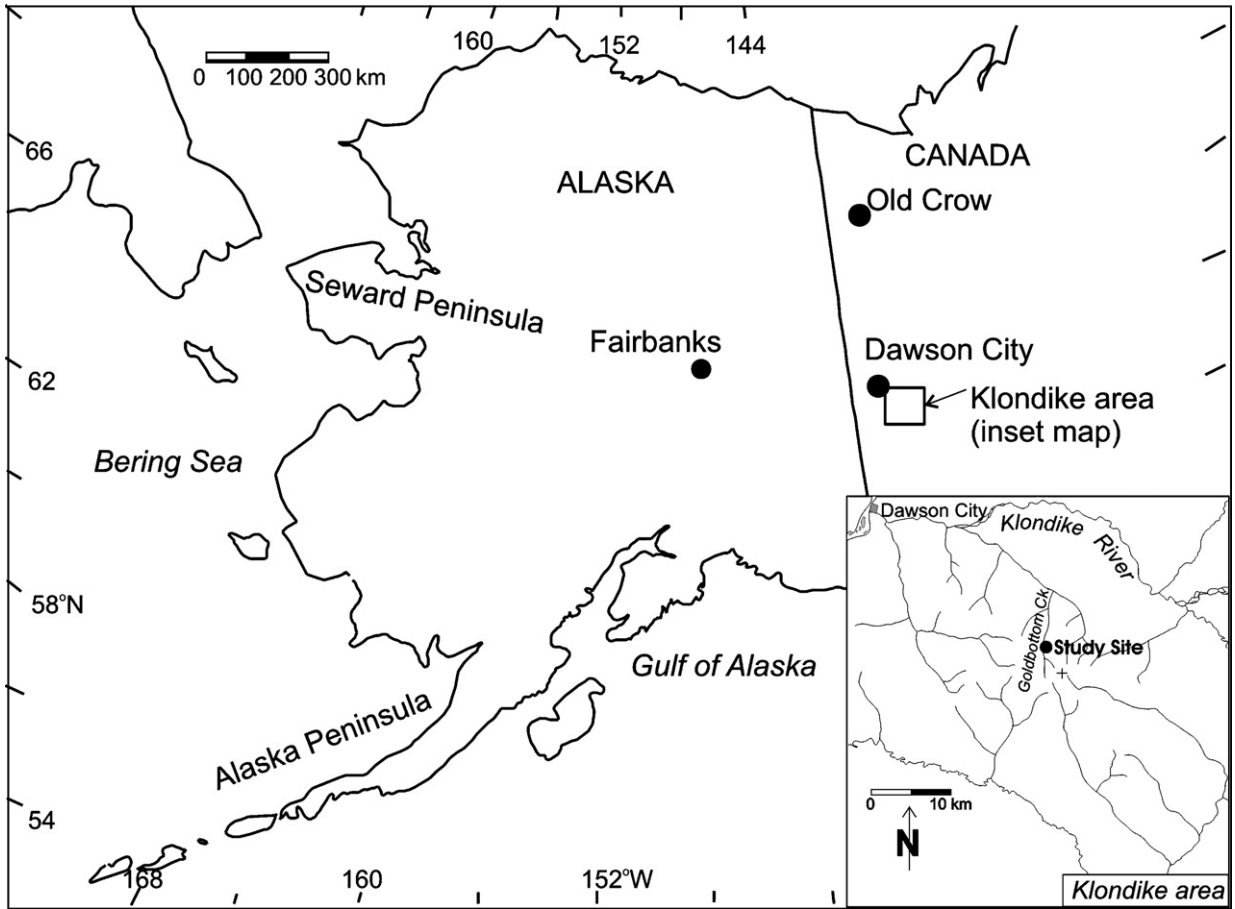
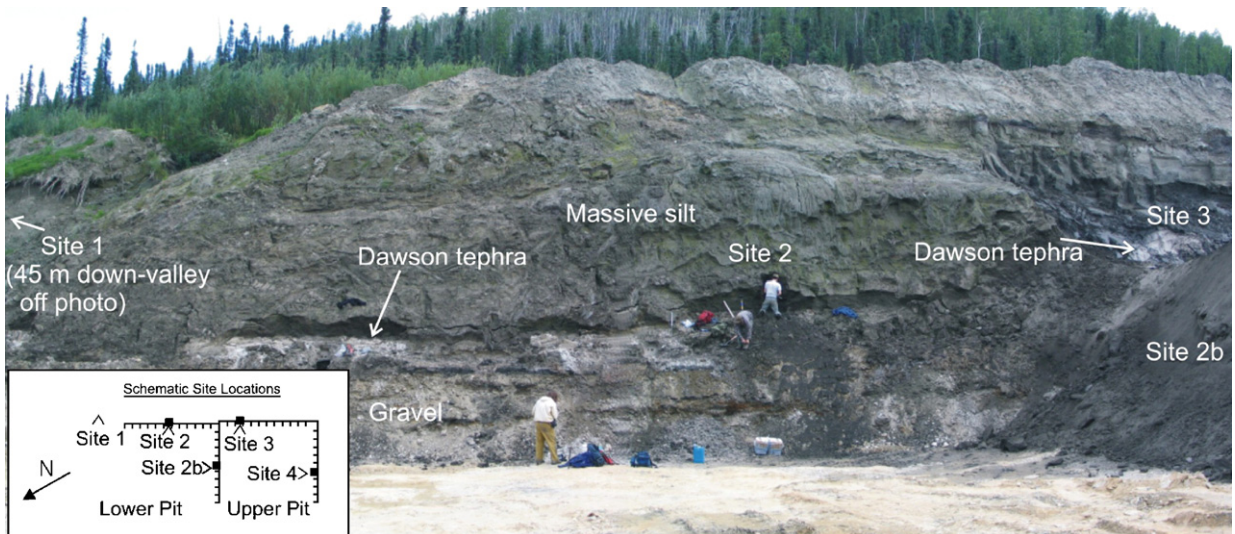Fig. 1. Map of eastern Beringia with Klondike area and study site inset.

Fig. 2. Positions of study sites with Dawson tephra at Goldbottom Creek.

2. Klondike Goldfields, west-central Yukon Territory, Canada

The Klondike goldfields consist of ca. 2000 km^2 of unglaciated terrain within the Klondike Plateau, an uplifted early to mid Cenozoic erosional surface dissected by streams with V-shaped valleys radiating from rounded domes. The valleys have undergone several cycles of erosion and subsequent filling by clastic sediments, forming terraces along the valley sides (Tempelman-Kluit, 1980). The floor of the Klondike River is currently about 370 m asl, and the summits of the domes reach about 1100 m. Multiple glacial advances approached the Klondike area during the late Cenozoic, though the area escaped direct glaciation (Froese et al., 2000). Placer gold mining in the Klondike valleys has produced numerous exposures of Pleistocene ice-rich loess-derived silt or "muck" that contain exceptional paleoenvironmental records (Fraser and Burn, 1997; Froese et al., 2002; Harington, 2003; Zazula et al., 2003a,b, 2005; Sanborn et al., 2006).

Topography and aspect of the numerous, narrow V-shaped Klondike valleys strongly affect present-day distribution of vegetation and permafrost (Yukon Ecoregions Working Group, 2004). The Klondike region lies within the northern boreal forest and zone of extensive discontinuous permafrost. Permafrost in the area is considered "warm" (ca. −2 °C) and up to 60 m thick, but perennial frozen ground is largely absent from south-facing slopes and beneath deciduous forests that include aspen (*Populus tremuloides*). Black spruce (*Picea mariana*) dominates forests on north-facing slopes with poorly drained soils (Turbic Cryosols), thick accumulations of surface organic matter and shallow active layers (∼30–40 cm below surface). These forests have an understory of willow (*Salix* spp.), ericaceous shrubs (*Ledum decumbens*, *Arctostaphylos alpinus*, *Vaccinium vitis-idaea*) and thick (∼10–15 cm) bryophyte ground cover (e.g., *Hylocomium splendens*, *Sphagnum* spp.). Black spruce forests contrasts sharply with the open aspen and white spruce (*Picea glauca*) forests on south-facing slopes that have an understory of willows (*Salix* spp.), soap berry (*Shepherdia canadensis*), bearberry (*Arctostaphylos uva-ursi*), and arctic lupine (*Lupinus arcticus*) and a restricted presence of bryophytes. These drier sites typically have Brunisolic soils with relatively thin surface organic horizons and lack permafrost. Present local treeline is near the summit of King Solomon dome (∼1100 m asl) where shrub birch (*Betula glandulosa*), lingon berry (*V. vitis-idaea*), blueberry (*Vaccinium uliginosum*), crowberry (*Empetrum nigrum*), bryophytes and lichen dominate shallow lithic soils composed of weathered bedrock and colluvium.

3. Methods

Exposures at the Goldbottom Creek site (63°56′N, 138°58′W) 30 km southeast of Dawson City (Fig. 1) were examined during May and July 2004 and July 2005. Placer gold mining at the site has produced a series of mining cuts ranging from 25 to 50 m in length, exposing 2–3 m of gold-bearing fluvial gravel overlain by up to 5 m of ice-rich "muck" (Fig. 2). Samples were collected from several sites for paleoecological analyses. Site stratigraphy was documented by D. Froese, A. Reyes and G. Zazula in the field. Site descriptions follow Froese et al. (2006). In particular, six 25 cm × 30 cm intact portions of the buried vegetation were sampled at Site 2 at 6 m intervals across a 40 m laterally continuous exposure (Site 2).

Bulk samples for plant macrofossil analyses were soaked in water to disperse sediment and screened through a 250 μm brass sieve. The screened residue was scanned while suspended in water in Petri dishes using a dissecting microscope. Vascular plant macrofossils were identified by G. Zazula with the aid of plant herbarium reference material. Nomenclature and habitat information follow Cody (2000) and the *Flora of North America* (Flora of North America Editorial Committee, 1993+).

Some vascular paleobotanical remains were isolated, dried and submitted to the Christian-Albrechts Universität and Beta Analytic Ltd. to obtain Accelerator Mass Spectrometry (AMS) ^{14}C ages that were converted to calendar years using the closest calendar years available from the dataset of Hughen et al. (2004).

Subsamples of bryophyte macrofossils plus detrital material were suspended in water and scanned in Petri dishes for identifiable fragments by C. La Farge. The bryophytes were isolated, mounted on permanent slides, identified and deposited in the Cryptogamic Herbarium, University of Alberta. Inferred paleoecological reconstruction used contemporary floristic data for species identified (Nyholm, 1954–1969; Steere, 1978; Janssens, 1983). Classification of the bryophytes followed Buck and Goffinet (2000).

Fossil insects were analyzed by S. Elias and S. Kuzmina and paleotemperature estimates based on these assemblages were made using the Mutual Climatic Range (MCR) method (Atkinson et al., 1986). For the MCR analysis, a climate envelope for each predatory and scavenging species in the fossil assemblage was determined based on the mean July and January

temperatures of all the North American locations where the species presently occur. The 25-km gridded North American climate database (Bartlein et al., 1994) was used to pair climate parameters with the modern beetle collection sites, using the grid location corresponding to each collecting site. Analysis is focused on predators and scavengers, as these groups are assumed to show the most rapid response to climate change.

Paleosols were described in the field by P. Sanborn and S. Smith, using standard Canadian terminology and soil horizon nomenclature (Soil Classification Working Group, 1998). Thin sections (30 μm thick) were prepared for selected horizons from intact samples that were impregnated with epoxy resin. Soil analyses were performed by the Agriculture and Agri-Food Canada laboratory using methods described by McKeague (1978) unless noted otherwise (i.e. particle size analysis by the pipette method with pretreatments to remove organic matter and carbonates, total C and N (LECO CNS-2000 analyzer), $CaCO_3$ equivalent by the gravimetric method, and oxalate-extractable Fe and Al.

Subsamples of the paleosols and buried vegetation (Sites 1, 2b and 4) were processed to isolate fossil pollen by C. Schweger. Pollen extraction from sediments followed standard methods of NaOH, HF, and acetolysis treatments. Pollen residue was mounted in silicone oil, and pollen grains were examined and identified. Pollen sums include all identifiable taxa. Indeterminate pollen grains were calculated outside the identified pollen sum.

4. Site descriptions

4.1. Site 1

Site 1 is on the northern (downstream) end of the exposure ∼5 m above the projected gravel-silt contact which is covered at this locale (Figs. 2 and 3a,b). Dawson tephra is preserved as a thin bed (up to 35 cm thick) at least 5 m across within massive silt with rare graminoid rootlets. A thin (∼2 cm thick) discontinuous and weakly developed paleosol (GZ.04.49) directly underlies the tephra. The silts underlying and overlying
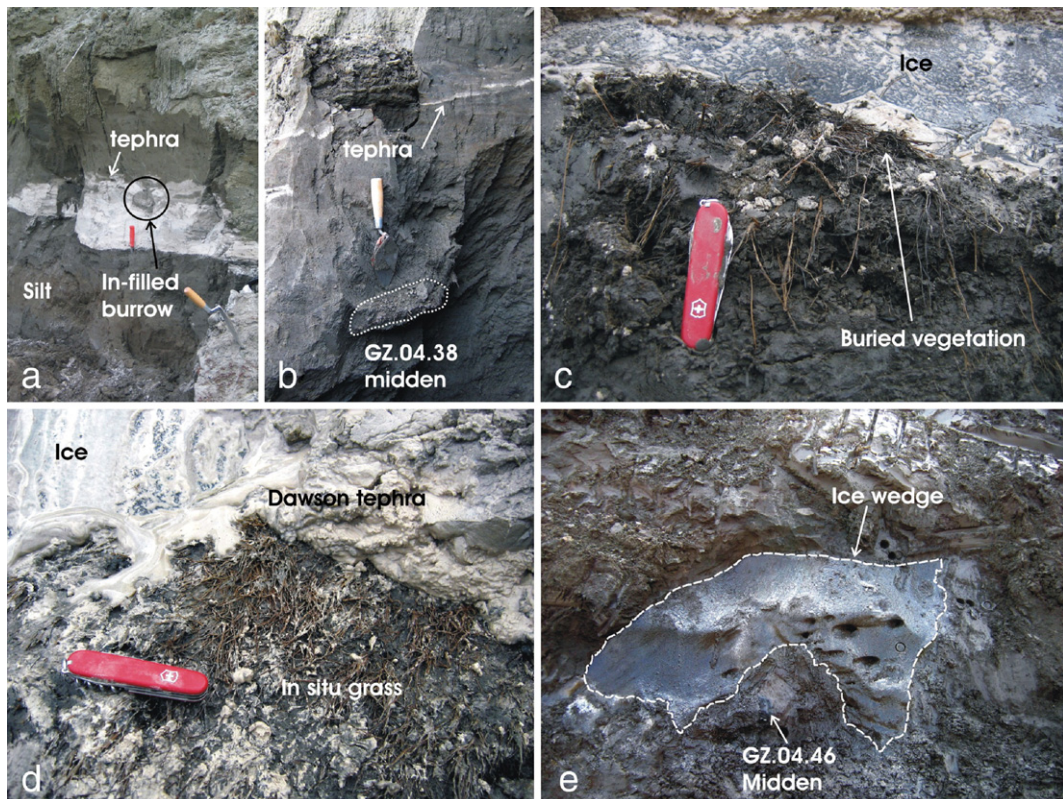
Fig. 3. Photographs of Dawson tephra, buried vegetation, and middens. (a) Site 1 with in-filled arctic ground squirrel burrow within bed of Dawson tephra (knife handle is 11 cm long); (b) arctic ground squirrel midden (GZ.04.38) below Dawson tephra at Site 1; (c) in situ grassy vegetation at site 2 showing abundance of roots; (d) in situ riparian grassy vegetation at Site 2 buried by Dawson tephra (knife handle is 9 cm long); (e) ice wedge and arctic ground squirrel midden (GZ.04.46) at Site 4.

the tephra were frozen at depth, but are ice-poor, representing dry permafrost. Further downstream, Dawson tephra is crosscut by an ice-wedge that has largely melted. Six fossil arctic ground squirrel middens (GZ.04.37, GZ.04.38, GZ.04.47, GZ.05.24, GZ.05.25, and GZ.05.26) were collected in close stratigraphic association with the tephra and at least one large (15 cm) burrow trace was observed (Fig. 3a).

4.2. Site 2

Site 2 is 45 m south of Site 1 in the middle of the lower pit and is where the thickest occurrence of Dawson tephra (up to 80 cm) was established (Fig. 2). This remarkable exposure consists of a fossil vegetated surface buried by Dawson tephra (Fig. 3c,d). The tephra and vegetation can be traced for 40 m along the main valley margin exposure and for 30 m along the adjoining south-facing mining cut that is perpendicular to the main valley orientation (Site 2b). At some localities, ice beds are present between the tephra and underlying vegetation, interpreted as a paleo-surface icing (i.e. Aufeis), which are presently common in the region during spring (Froese et al., 2006). The fossil vegetation directly overlies silt and local creek gravel.

4.3. Site 3

Site 3 is in the upper pit where the base of Dawson tephra is 3.9 m above the base of the tephra at Site 2 (Fig. 2). Dawson tephra (12–30 cm thick) overlies beds of massive ice-rich silt, wavy-horizonally-layered ice free of tephra, and flat-lying to elongate detrital organic remains (Froese et al., 2006). A large bulk sample (GZ.04.44) of the detrital organic beds was collected for macrofossil analyses.

4.4. Site 4

Site 4 is exposed within the central part of the valley at the south-end of the upper pit (Figs. 2 and 3e). The exposure of frozen silt revealed a small ice wedge complex whose upper surface was truncated by an

organic-rich silt horizon that makes up an apparent paleosol (Fig. 3e). A fossil arctic ground squirrel seed/ fruit cache (GZ.04.46) was recovered beneath the ice-wedge. Although Dawson tephra was not exposed when the site was described, the ice-wedge and fossil cache were determined to be stratigraphically below the tephra based on the projected elevation of the tephra from the other sites. This supposition is supported by AMS radiocarbon dates (see below).

5. Results

5.1. Radiocarbon ages and chronology

Two samples of individual graminoid leaves were sampled for AMS radiocarbon dating from the vegetated surface directly underlying Dawson tephra at Site 2 (Froese et al., 2006; Table 1). The two ages are within 1 σ, providing an age for the surface around 25,300 ^{14}C years BP. These ages indicate Dawson tephra buried the vegetation at about 28,700–29,500 cal. years BP, near the onset of the last glaciation (MIS 2). Although we did not obtain any radiocarbon ages on the arctic ground squirrel middens from Site 1, close stratigraphic association with the tephra suggests that their ages are contemporaneous with Dawson tephra (Zazula et al., 2005). The direct stratigraphic association of organic remains with the tephra at Site 3 also suggests that their age also approximates that of Dawson tephra. These AMS ^{14}C dates and stratigraphic association with Dawson tephra suggest that the fossil arctic ground squirrel middens, paleosols, and other data examined from Sites 1, 2, and 3 are contemporaneous, providing paleoenvironmental information for the onset of Marine Isoptope Stage (MIS 2), ca. 25,300 ^{14}C years BP.

Two samples of plant macrofossils were selected for AMS radiocarbon dating at Site 4 (Table 1). A small wood fragment from the apparent paleosol (AVR-04-07-23) which truncates the upper surface of the ice wedge yielded a ^{14}C age of 28,000 + 170/−160 years BP (KIA-26908; 30,400–32,300 cal. years BP). Seeds from the arctic ground squirrel cache (GZ.04.46)

Table 1
AMS radiocarbon ages from Goldbottom Creek

Age ^{14}C years BP	δ^{13}C	Dated material	Lab no.	Context	Reference
25, 410 ± 160	−20.0	grass leaf	KIA25702	in situ surface below Dawson tephra	Froese et al., 2006
25, 210 ± 260	−24.6	grass leaf	KIA25703	in situ surface below Dawson tephra	Froese et al., 2006
28, 000 + 170/−160	−27.9	twig	KIA26908	Organics/paleosol above ice-wedge at Site 4	this paper
29, 450 ± 320	−24.6	seeds	Beta 202418	ground squirrel midden under ice-wedge at Site 4	this paper

KIA = Christian-Albrechts Universität. Beta = Beta Analytic Ltd.

underlying the ice-wedge yielded an age of 29,450 ±320 years BP (Beta-202418; 33,100–34,500 cal. years BP). Radiocarbon ages from Site 4 place this midden and ice wedge within the later stages of the MIS 3 Middle Wisconsinan interstadial between about 28,000 and 29,500 ^{14}C years BP (Anderson and Lozhkin, 2001).

5.2. Vegetation buried under tephra

The remarkable preservation of plant remains buried under Dawson tephra (Sites 2 and 2b) enables us to reconstruct vegetation that was present in the valley bottom at 25,300 ^{14}C years BP (Table 2, Fig. 4). Although graminoid leaves, stems, roots and rhizomes dominate the samples, they are difficult to identify based on macroscopic characteristics. Thus for grass identification, attention was focused on florets and inflorescences. These macrofossils suggest that a diversity of mesophytic grasses and sedges dominated the buried vegetation at Site 2, including *Deschampsia caespitosa*, *Carex* sp., *Alopecurus* sp. (specimens of *Alopecurus* were misidentified as *Phalaris arundinacea* in Froese et al., 2006), and *Hierochloë hirta* ssp. *arctica*. Abundant horsetail (*Equisetum* cf. *palustre*) and mosses were interspersed within graminoid meadow vegetation. Sedges (*Carex* sp.), dwarf willow (*Salix* cf. *arctica*) and bryophytes dominated the surface more proximal to the valley centre (Site 2b). In all subsamples, other seeds and fruits are rare and probably allochthonous in the assemblage because no intact stems with leaves or inflorescences of these taxa were recovered. These include grasses (*Elymus*, *Festuca*), upland sedges (*Kobresia myosuroides*), sage (*Artemisia frigida*) and forbs of at least twelve taxa representing eight families. These forbs include *Bistorta vivipara*, *Cerastium*, *Silene taimyrensis*, *Ranunculus* spp., *Draba*, *Erysimum* cf. *cheiranthoides*, *Potentilla*, *Androsace septentrionalis*, and *Phlox hoodii*. No identifiable macrofossils from arboreal taxa were recovered and coarse woody fragments were rare.

Bryophytes recovered from the buried vegetation support inferences of microtopographic variation in the riparian habitat (Table 3). Bryophytes are sensitive indicators of moisture and pH gradients that are often linked to restricted microhabitat specificity. The eight samples from the in situ vegetation (Sites 2 and 2b) include thirty-seven taxa from eleven families and about 9% of the contemporary Alaskan moss flora (Steere, 1978) (Tables 3 and 4, Fig. 5), which represent a broad range of microhabitats. One sample from Site 2b (GZ.July.04.01) contained an extremely large diversity of taxa (21). *Amblystegium*, *Campylium*

spp., *Catoscopium nigritum*, *Drepanocladus aduncus* var. *kneifii*, *Encalypta procera*, *Climacium dendroides*, *Meesia uliginosa* and *Philonotis fontana* are all indicative of wet meadow, seeps, margins of pools or streambed habitats. Many mosses are indicators of calcareous substrates (Table 3). An especially high diversity of *Bryum* spp. occurs at Site 2, which is typical of contemporary arctic tundra bryophyte communities. *Funaria hygrometrica* and *Ceratodon purpureus* are widespread, mesic species that typically grow on soils in disturbed habitats. *Barbula icmadophila*, *Bryoerythrophyllum*, *Desmatodon* spp., *Distichium* spp., and *Tortula ruralis* grow on soil or rock under variable moisture conditions ranging from mesic to xeric habitats. The macrofossils from Sites 2 and 2b are all gametophytic tissue with the exception of a few sporophytes not determined to species. Excellent preservation of these bryophyte macrofossils rivals that of Holocene in situ seepage fen deposits (La Farge-England et al., 1991).

5.3. Arctic ground squirrel middens

Fossil arctic ground squirrel nests and caches (middens) recovered at Goldbottom Creek are similar to those described from other sites in the Klondike (Harington, 1984; Zazula et al., 2005). These middens are typically about 25 cm in diameter and include bedding material of "hay" and associated caches of seeds and fruits (Table 2). Middens at Site 1 were recovered from ice-rich silt in direct association with Dawson tephra (Fig. 3a,b), thus they are contemporaneous with the buried riparian vegetation at Site 2. Graminoid leaves and stems (hay) dominate plant macrofossil assemblages from the middens, with identifiable florets, inflorescences and/or fruits of *Elymus trachycaulus*, *D. caespitosa*, *H. hirta* ssp. *arctica*, *Poa*, *Festuca*, *K. myosuroides*, *Carex* and *Juncus* (Fig. 4, Table 2). Fossil cache seeds and fruits are dominated by steppe and mesic to dry tundra forbs representing at least eighteen taxa from eleven families. Amongst the most abundant forbs are *B. vivipara*, *Cerastium*, *S. taimyrensis*, *Draba*, *Potentilla*, *Ranunculus* spp. and *P. hoodii*. The midden at Site 4 dating to 29,450 ± 320 ^{14}C years BP (GZ.04.46) is a dense cache composed of fruits and seeds. The assemblage contains many of the same species from Site 1 (*B. vivipara*, *Ranunculus* spp., *Potentilla*, *Draba*, etc.), in addition to *Suaeda* cf. *calceoliformis*, *Anemone patens* var. *multifida* and *K. myosuroides*.

The bryophyte material from the midden samples is of particular interest (Table 3). Although sporophyte

Table 2
Vascular plant macrofossil data from Goldbottom Creek

Samples	GZ.04.47	GZ.04.37	GZ.04.38	GZ.04.46	GZ.05.24	GZ.05.25	GZ.05.26	GZ.04.49	GZ.04.45	GZ. July 04-01	GZ.04.29	GZ.04.30	GZ.04.31	GZ.04.32	GZ.04.33	GZ.04.34	GZ.04.44	AVR-04-07-23	Ecology
Site	1	1	1	4	2	2	1	1	2b	2b	2	2	2	2	2	3	4		
Type	midden	midden	midden	midden	midden	midden	midden	paleosol	buried turf	buried turf	buried turf	buried turf	buried turf	buried turf	buried turf	buried turf	detrital	organics	
Taxon																			
Equisetaceae																			
Equisetum cf. *palustre* (stems, roots)										**	***	***	*	*	*	*			wet woods and meadows, shores and shallow water
Graminoid foliage	5	3	6	3	4	6	5		**	**	***	***	***	***		***			
Poaceae																			
Poaceae undet. floret																			
Deschampsia caespitosa (L.) Beauv, (florets)	1	1	1		1						***	**	*		*				wet meadows, lakeshores, gravel bars
Elymus trachycaulus (Link) Gould ex Shinners (spikes)	2																		
Elymus sp. (florets)		1			2		1		*	*			*	**	*	*			sandy, gravelly riverbanks, hillsides, open, well-drained slopes
Festuca sp. (florets, spikelets)		1	1		2				*	*	*			*	*				grassland, tundra, sandy, gravelly, riverbanks, lakeshores
Hierochloë hirta (Schrank) Borbas sp. *arctica* G. Weim (florets, spikelets)	2	1												*	**	*			sand stream banks, lakeshores and meadows
Alopecurus sp. (florets)											*	*		***	*	*			shallow ponds and moist tundra meadows
Poa sp. (florets, spikelets)	3			2	1	2	2				*	*	**	**	**	**	*		tundra, grassland, meadows, stream banks open well-drained slopes
Cyperaceae																			
Carex sp. (trigonous achenes)				2	2				*	*									mesic to xeric, grassland to tundra, often riparian
Carex sp. (lenticular achenes)	1	1	1		2		3	*	***		*	*	*	*	***	**		*	
Kobresia myosuroides (Vill.) Fiori and Paol. (achenes, spike fragments)					2	3	1	3	*			*	*	*					dry locations, usually calcareous sandy heath and windswept ridges

Taxon	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	Habitat
Juncaceae																	
Juncus sp. (seeds, capsules)					3		1			*							wet, riverbanks, tundra, gravel bars, lakeshores
Salicaceae																	
Salix cf. *arctica* (twigs, capsules, leaves)	1						1	***	**	*				*			dwarf shrub, herbmats, floodplains in arctic tundra
Polygonaceae																	
Bistorta vivipara (L.) Delarbre (bulbils)	1			3	3		3			*	*	*	*	*	*		turfy places, rocky barrens, moist grassy herbmats, favors manured places
Rumex cf. *arcticus* (achenes)											*						damp turfy places
Chenopodiaceae																	
Chenopodium sp. (seeds)				1						*		*	*	*	*		weedy, disturbed, often halophytic
Suaeda cf. *calceoliformis* (Hook.) Moq. Type (seeds)											*	*		*		*	alkaline flats
Caryophyllaceae																	
Caryophyllaceae undet. (seed)																	
Cerastium sp. (seed, capsules)	2	1	2		2	1	1	*			*	*	*				gravelly slopes, open meadows, disturbed situations
Minuartia sp. (seed)								*									alpine, tundra, open slopes, well-drained, calcareous
Silene taimyrensis (Tolmatchev) Bocquet (seeds)	1	1	2	2		1	1			*		*		*			sandy and rocky open slopes and cliffs
Silene uralensis (Rupr.) Bocquet (seed)																	moist alpine slopes and meadows, calcareous soils, well-drained
Stellaria cf. *calycantha* (seeds, capsules)	2				2	1		*									alpine slopes, meadows, lake and stream shores
Ranunculaceae																	
Anemone narcissiflora L. s.l. (achenes)				1													woodlands to heath to arctic tundra
Anemone patens var. *multifida* Pritzel, L. (achenes)				1													sandy well-drained

Table 2 (*continued*)

Samples	GZ.04.47	GZ.04.37	GZ.04.38	GZ.04.46	GZ.05.24	GZ.05.25	GZ.05.26	GZ.04.49	GZ.04.45	GZ. July 04-01	GZ.04.29	GZ.04.30	GZ.04.31	GZ.04.32	GZ.04.33	GZ.04.34	GZ.04.44	AVR-04-07-23	Ecology
Site	1	1	1	4	2	2	1	1	2b	2b	2	2	2	2	2	2	3	4	
Type	midden	midden	midden	midden	midden	midden	midden	paleosol	buried turf	buried turf	buried turf	buried turf	buried turf	buried turf	buried turf	buried turf	detrital	organics	
Taxon																			
Ranunculus sulphureus-eschscholtzii type (achenes)	2	1	3	4	2		2								*	*		*	alpine tundra herbmats and meadows
Ranunculus pensylvanicus-macounii type (achenes)	2	1	3	3				*											wet meadows, stream banks, moist disturbed
Papaveraceae																			
Papaver sp. (seed)				1															tundra meadows, herbmats, often calcareous soils
Brassicaceae																			
Draba sp. (seeds, silicles)	2	2	4	2		1	2	*	*		**	**	**	**	**		*		arctic-alpine tundra, often calcareous, well-drained, rocky and turfy places
Erysimum cf. *cheiranthoides* (seeds, siliques)	2		1				1				**	**	**	**	**	**			rocky outcrops, dry slopes, river terraces
Eutrema edwardsii R. Br. (seeds)	2	2	4									*	*		*				not too dry turfy tundra and heath, calcareous soils
Lepidium densiflorum Schrad.(seeds, silicles)					1	1													disturbed soils, dry, open
Saxifragaceae																			
Parnassia sp. (seeds, capsules)		2	3				1												moist meadows, lakeshores, by streams
Rosaceae																			
Potentilla sp. (achenes)	3	1		3	2	1	2		*		**	**	**	**	**	**	*	*	riverbanks, dry slopes, alpine, open meadows
Fabaceae																			
Astragalus eucosmus Robins. (seeds, legumes)	1	1					1												open areas, gravel river flats, disturbed

Taxon																	Habitat
Apiaceae																	
Bupleurum americanum Coult. and Rose (carpels)													*				alpine meadows, moist sand, gravel banks, talus
Conioselinum cnidiifolium (Turcz.) A.E. Porsild (carpels)												*	*		*		sandy riverbanks, gravelly slopes, wet meadows
Primulaceae																	
Androsace septentrionalis L. (seeds, capsules)	1					1				*	*	*					dry calcareous sandy or gravelly places
Gentianaceae																	
Gentiana cf. *algida* (seeds, capsules)		1	2		1	1											alpine tundra, heath
Gentiana cf. *prostrata* (seeds, capsules)	1	1	2	1	1	2				*							moist tundra, meadows, lake and stream banks
Gentianella type (seeds, capsules)	1		1		1												alpine tundra, heath, moist stream banks
Polemoniaceae																	
Polemonium sp. (seeds, capsules)								*						*	*		alpine, tundra, turf, sand dunes, dry slopes
Phlox hoodii Richards. (leaves, capsules, seeds)				1	1	1	*	*	*	*	*	**	*	**	***	*	grasslands and foothills
Boraginaceae																	
Lappula sp. (nutlets)	1																roadsides, clearings, fields
Scrophulariaceae																	
Pedicularis cf. *lapponicus* (capsules, seeds)					1	2				*							calcareous tundra, heath
Plantaginaceae																	
Plantago cf. *canescens* (seeds, capsules)				1										*	*		steep open slopes, riverbanks, screes, disturbed
Asteraceae																	
Artemisia sp. (flowers)					1				*	**	**	***	**	**			
Artemisia frigida Willd. (leaves)						2			*	**	**	*		*			steep open slopes and sandy river terraces
Aster/Erigeron type (achenes)								*		*		*					slopes, meadows, river flats, open areas

Table 2 (continued)

Samples	GZ.04.47	GZ.04.37	GZ.04.38	GZ.04.46	GZ.05.24	GZ.05.25	GZ.05.26	GZ.04.49	GZ.04.45	GZ. July 04-01	GZ.04.29	GZ.04.30	GZ.04.31	GZ.04.32	GZ.04.33	GZ.04.34	GZ.04.44	AVR-04-07-23	Ecology
Site	1	1	1	4	2	2	1	1	2b	2b	2	2	2	2	2	2	3	4	
Type	midden	midden	midden	midden	midden	midden	midden	paleosol	buried turf	buried turf	buried turf	buried turf	buried turf	buried turf	buried turf	buried turf	detrital	organics	
Taxon																			
Taraxacum ceratophorum (Ledeb.) DC. s.l. (achenes)	2	1	2	1	2	1	1	*					*	*					woodland and heath to tundra
midden mass (g)	226	143	10.3	65.1	170	114	228												

For the buried vegetation and paleosol samples, vascular plant macrofossils were classed as "absent", "rare (*)", "moderate (**)", or "abundant (***)" based on their relative frequency within the sample. Analysis of fossil arctic ground squirrel middens utilized the entire sample and individual taxa were assigned a relative frequency index: 0=absent, 1=<1%, 2=1–5%, 3=6–25%, 4=26–50%, 5=51–75%, and 6>75%, similar to other fossil rodent midden studies (Betancourt et al., 1990; Latorre et al., 2002).

fragments are extremely rare in fossil bryophyte assemblages, sample GZ.04.47 contained over fifty diplolepideous capsules of cf. Bryaceae that were probably selectively cached (Fig. 5d,e). Bryophyte capsules are forage material for arctic hare and lemmings (C. La Farge, personal observation), though it is unknown whether these are typical components of arctic ground squirrel diet. Each sporophyte was truncated at the seta just below the capsule. The midden bryophytes include three taxa from the Mniaceae family (*Cyrtomnium*, *Rhizomnium*, and *Plagiomnium*) that represent wet depressions or wet meadow species and commonly grow intermixed with other mosses. *Cratoneuron filicinum* is an indicator of calcareous rich fens (high pH) and that grows in wet habitats along streambeds, springs, or lakeshores. *P. fontana*, *Campylium* spp., *Drepanocladus lycopodioides* v. *brevifolius*, *D. aduncus*, *D. aduncus* v. *kneifii*, *Amblystegium serpens*, *Brachythecium turgidum* and *Bryum pseudotriquetrum* are all indicators of wet habitats (edges of ponds, streams, lakes, in wet depressions) or grow intermixed with wet meadow species. Two members of the Brachytheciaceae — *Brachythecium starkei* v. *pacificum* and *Isothecium stoloniferum* potentially suggest tree-related habitats (logs or on trees), although they also are found on soil. *B. icmadophila*, *Bryoerythrophyllum recurvirostre*, *Desmatodon heimii* grow on calcareous substrates with mesic to xeric moisture range. *Bryum arcticum*, *Bryum cryophyllum*, *B. pallens*, and *Bryum* spp. grow in soil habitats with generally open exposure under mesic conditions.

5.4. Other plant macrofossils

Identifiable macrofossils recovered from the paleosols at Sites 1 (GZ.04.49) and 4 (AVR-04-07-23) are rare and poorly preserved, with much of the organic material being highly humified (Table 2). At Site 1, specimens of *Carex*, *K. myosuroides*, *Ranunculus*, *Draba*, *P. hoodii*, and *Taraxacum* cf. *ceratophorum* confirm the presence of these taxa in the upland plant community dating to ca. 25,300 ^{14}C years BP. The paleosol at Site 4 dating to 28,000+170/−160 ^{14}C years BP yielded rare specimens of *Salix*, *Potentilla*, *S.* cf. *calceoliformis*, *Ranunculus*, *Carex,* and *P. hoodii.* No bryophyte remains were recovered from the Site 1 or 4 paleosols.

Plant macrofossils were abundant in the organic detritus underlying Dawson tephra at Site 3, dominated by capsule fragments of *P. hoodii* and unidentified wood fragments, with rare specimens of *Conioselinum cnidiifolium*, *Chenopodium*, *S.* cf. *calceoliformis*, *Draba*, *Poa*, *B. vivipara* and *Potentilla*.

5.5. Fossil pollen

Fossil pollen was recovered from six subsamples of the buried vegetation at Site 2 and 2b (Table 5). Samples from Sites 1 and 4 did not yield sufficient or well-preserved pollen suitable for significant pollen counts. Pollen from Poaceae dominates five out of six samples of the buried vegetation, ranging in frequency from 24.8% to 69.6%. Other dominant taxa include Cyperaceae (1.2–21.8%), *Artemisia* (7.3–50.6%) and *Salix* (0.7–11.1%). Diverse herb taxa are of limited frequency and include Tubuliflorae, Liguliflorae, Chenopodiaceae-*Amaranthus*, Caryophyllaceae, *Potentilla* type, *Polygonum*, *Ranunculus* type, *Plantago*, *Thalictrum*, *Sanguisorba*, Brassicaceae, *Polemonium*, *Eriogonum*, Fabaceae, *Rumex* and *Apiaceae*. Arboreal pollen types, including *Picea*, *Alnus*, and *Betula*, are rare.

5.6. Insects

Fossil insects were recovered from samples of the buried vegetation at Site 2, arctic ground squirrel middens and paleosols at Sites 1 and 4, and bedded-organic detritus at Site 3 (Table 4, Fig. 6). Samples from the buried surface are dominated by several members of the ground beetle family (Carabidae) in the genera *Elaphrus*, *Bembidion*, and *Pterostichus (Cryobius).* The other dominant taxa in these assemblages were the weevil *Lepidophorus lineaticollis* (Curculionidae) and fly pupae (Diptera). Insects from detrital organic sediments at Site 3 were very abundant and well preserved. This assemblage is dominated by the ground beetles *Amara alpina* and *Harpalus alaskensis*, and the weevils *L. lineaticollis* and *Connatichela artemisiae*. The middens from Sites 1 and 4 contained a few specimens of *Pterostichus* (*Cryobius*) spp., *A. alpina*, the weevils *L. lineaticollis* and *C. artemisiae*, and abundant fly pupae. The upland paleosol at Site 1 (GZ.04.49) contained specimens of the ground beetle *Pterostichus (Cryobius) tareumiut*, the rove beetle *Tachinus brevipennis*, the pill beetle *Simplocaria metallica*, the leaf beetle *Chrysolina subsulcata*, and the weevil *L. lineaticollis*. The paleosol that truncates the ice wedge at Site 4 (AVR-04-07-23) contained several specimens of *L. lineaticollis* and a variety of less abundant taxa.

MCR paleo-temperature estimates were conducted on the Goldbottom Creek insect fauna. The samples from Sites 1, 2 and 3 are contemporaneous with each other, but not all of the assemblages contained sufficient faunal diversity to yield precise MCR estimates. The most tightly constrained temperature estimate came from the assemblages associated with the buried
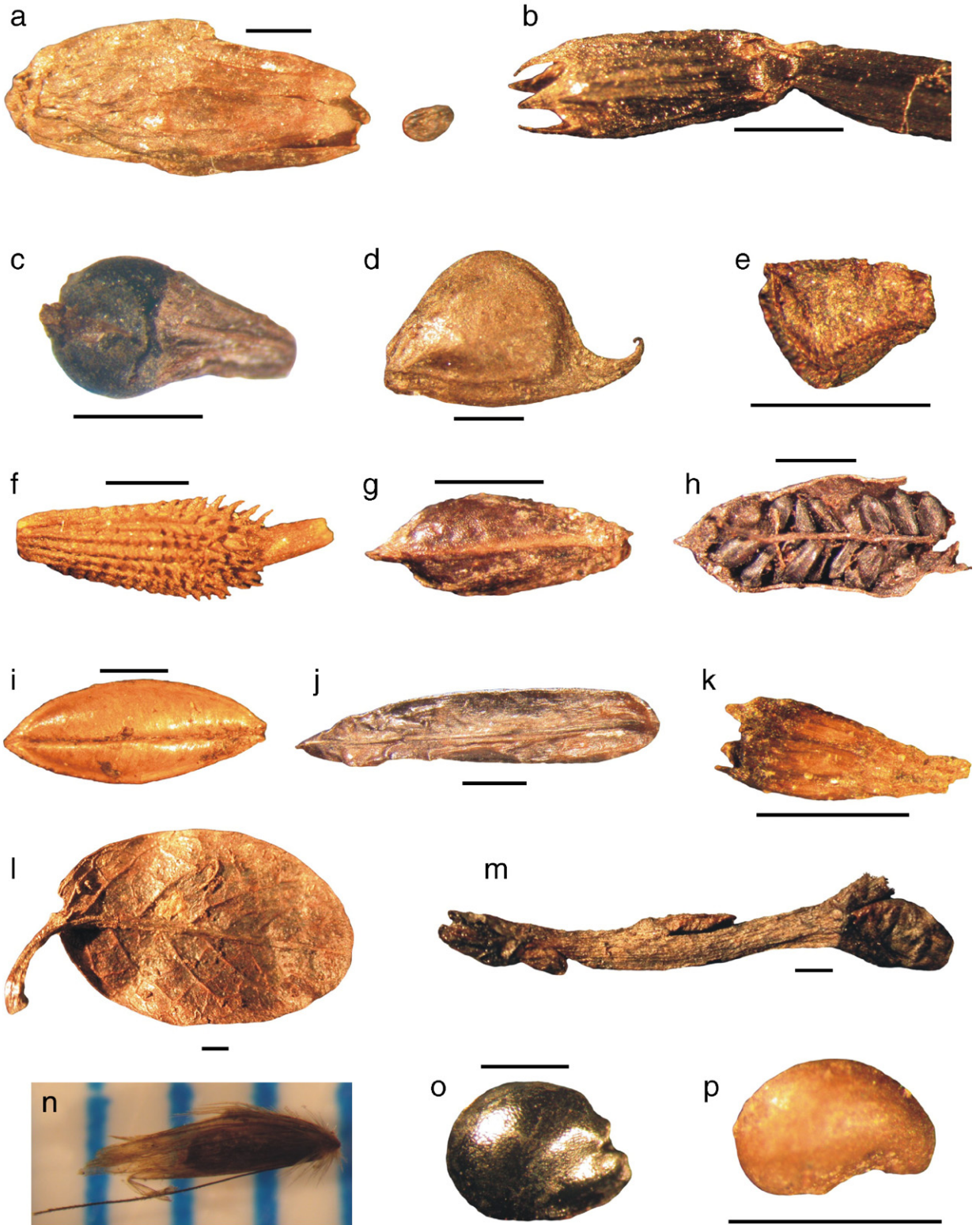
vegetation at Site 2. This fauna yielded a mean temperature estimate for the warmest month of the year (TMAX) of 9–10 °C. It yielded a mean temperature estimate for the coldest month of the year (TMIN) of −32 to −27 °C. Modern TMAX and TMIN at Dawson City, Yukon, are 15.6 °C and −27.6 °C, respectively (Environment Canada, 2001). These estimates suggest that average summer temperatures were depressed by 5.6–6.6 °C, and average winter temperatures were depressed by as much as 4.4 °C in the Klondike region at ca. 25,300 ^{14}C years BP. The TMAX estimates are in close agreement with previous TMAX estimates for last-glacial faunal assemblages in Yukon Territory, but the TMIN estimates are noticeably cooler than the other site estimates (Elias, 2000).

5.7. Paleosols

A 2-cm-thick calcareous A horizon directly beneath Dawson tephra at Site 1 has slightly higher concentrations of organic C than the associated loess-derived C horizons (2.5% vs. 2.0%). Comparable organic C concentrations are observed in morphologically similar Static Cryosol paleosols in loess sequences of equivalent age elsewhere in the Klondike region (Sanborn et al., 2006). This lack of horizon differentiation is consistent with the location of this site in an accretionary, lower slope position.

The strongest differentiation of soil horizons occurs at Site 2 (Fig. 7, Tables 6 and 7). In situ fossil vegetation is rooted in a 20-cm-thick silty, dark-coloured Ah horizon containing approximately 2% organic C. Thin sections reveal abundant root detritus and a spongy fabric that displays the intimate mixing of mineral and organic components characteristic of A horizons of loess-derived soils in modern steppe-like plant communities (cf. Marsh et al., in review) (Figs. 3c and 7a,b). The olive brown colour and absence of mottling in the underlying IIBmkb horizon suggest somewhat better soil drainage conditions and a more stable surface at this location on the margin of the former floodplain than in the valley centre at Site 2b. Only modest concentrations of extractable Fe and Al were present, consistent with the limited degree of chemical weathering that is expected in such calcar-

eous materials. The lack of disrupted horizon boundaries suggests that cryoturbation was largely absent, and prior to burial this soil would have resembled a modern Static Cryosol.

At Site 2b, a thin (~1 cm thick) and discontinuous organic matter-enriched horizon separated Dawson tephra and underlying gravel. There is no evidence of disruption of soil horizons by cryoturbation. Equivalent modern soils with similarly limited morphological development in an active floodplain setting would be classified as Orthic Regosols, or Static Cryosols if permafrost occurs within 1 m of the surface (Soil Classification Working Group, 1998).

All silt-rich paleosol horizons and overlying sediments at Sites 1, 2 and 2b are calcareous (1.5–4.0% $CaCO_3$-equivalent) providing an alkaline mineral substrate for the vegetation. The underlying coarser fluvial sediments (>90% sand) at Sites 2 and 2b contain <1% $CaCO_3$-equivalent.

6. Interpretations and discussion

6.1. Goldbottom Creek habitat mosaic at the onset of Marine Isotope Stage (MIS) 2

The exceptional record of in situ vegetation buried by Dawson tephra ca. 25,300 ^{14}C years BP affords a detailed "snapshot" of the valley bottom riparian meadow community in west-central Yukon Territory during the onset of the last glaciation. The preservation of an intact biotic community by tephra is rare in the Pleistocene stratigraphic record and provides a unique opportunity to compare paleoecological data obtained from various contexts at the site. Together, our data provide detailed evidence for a habitat mosaic within the Goldbottom Creek valley, likely related to landscape position (i.e. upland vs. lowland), moisture and substrates. AMS radiocarbon ages and stratigraphic evidence indicate the paleoecological data from the arctic ground squirrel middens at Site 1, buried in situ vegetation at Site 2, and detrital macrofossils at Site 3 are contemporaneous and document local ecosystem heterogeneity at the onset of glacial conditions of MIS 2. MCR temperature estimates based on the Goldbottom Creek insect fossils suggest temperatures were

Fig. 4. Selected plant macrofossils from Goldbottom Creek. Scale bars are 1 mm. (a) *Stellaria* cf. *calycantha* capsule and seed, sample GZ.04.47; (b) *Equisetum* cf. *palustre* sheath, sample GZ.04.30; (c) *Bisorta vivipara* bulbil, sample GZ.04.45; (d) *Ranunculus pensylvanicus-macounii* type achene, sample GZ.04.47; (e) *Silene taimyrensis* seed, sample GZ.04.47; (f) *Taraxacum ceratophorum* achene, sample GZ.05.24; (g) *Kobresia myosuroides* achene, GZ.05.24; (h) *Juncus* sp., capsule with seeds, sample GZ.05.24; (i) *Phlox hoodii* capsule fragment, GZ.05.24; (j) *Elymus* sp. caryopsis, sample GZ.04.32; (k) *Artemisia* flower, sample GZ.04.32; (l) *Salix* cf. *arctica* leaf, GZ.04.45; (m) *Salix* twig with buds, sample GZ.July.04.09; (n) *Deschampsia caespitosa* floret, sample GZ.04.29; (o) *Suaeda* cf. *calceoliformis* seed, sample GZ.04.32; (p) *Potentilla* sp., sample GZ.04.47 achene.

Table 3
Bryophyte macrofossil data recovered from Goldbottom Creek

Samples	GZ.04.47	GZ.04.37	GZ.04.38	GZ.04.46	GZ.05.24	GZ.05.25	GZ.05.26	GZ.04.49	GZ.04.45	GZ. July 04-01	GZ.04.29	GZ.04.30	GZ.04.31	GZ.04.32	GZ.04.33	GZ.04.34	GZ.04.44	AVR-04-07-23	Ecology
Site	1	1	1	4	2	2	1	1	2b	2b	2	2	2	2	2	2	3	4	
Type	midden	midden	midden	midden	midden	midden	midden	paleosol	buried turf	buried turf	buried turf	buried turf	buried turf	buried turf	buried turf	buried turf	detrital	organics	
BRYOPHYTA	*	*		*	*	*	*		***	***	***	***	***	***	*	*			
Funariaceae/ Splachnaceae																			wet meadow mosses or dung habitats
capsule							*												
leaves and stem										*									
Funariaceae cf. *Funaria hygrometrica* Hedw.														*					usually on calcareous or element enriched soil, disturbed sites, post-burn
Catascopiaceae *Catoscopium nigritum* (Hedw.) Brid.											*	*							wet calcareous, rich fens, wet meadow, often along streams or near lakes
Ditrichaceae *Ceratodon purpureus* (Hedw.) Brid.										*									on soil or burned wood, disturbed sites
Distichium hagenii Ryan ex Philibert										*									calcareous soil, often in frost boils
Distichium capillaceum (Hedw.) Bruch and Schimp. in B.S.G	*								*	*	*								moist calcareous soil open exposure or in soil crevices
Rhabdoweisiaceae *Oncophorus virens* (Hedw.) Brid.							*												on wet soil in fens or marshy tundra, often with standing water
Pottiaceae									*	*cfr									
Barbula icmadophila Schimp. ex C. Müll. Hal.		*		*					*					*					calcareous soil in frost boils or rock crevices
Barbula sp.																*			
Bryoerythrophyllum recurvirostre (Hedw.) Chen Pan-chieh	*	*		*															calcareous soil or rock

Species								Habitat
Desmatodon heimii (Hedw.) Mitt.	*							on calcareous silt and rock, especially common near the sea coast
Desmatodon heimii var. *arctica* (Lindb.) Crum				*	*			arctic species on bare calcareous soil, on cliffs or bluffs
Desmatodon latifolius (Hedw.) Brid.			*	*	*	*		on calcareous silt and soil
Desmatodon latifolius var. *muticus* (Brid.) Brid.				*	*			growing in moist habitats compared to the type variety
Desmatodon laureri (Schultz) Bruch and Schimp.				*			*	moist calcareous soil
Desmatodon sp.		*						
Didymodon asperifolius (Mitt.) Crum, Steere and Anderson			*	*		*	*	calcareous silt and soil
Encalypta procera Bruch				*				very moist to wet soil and on limestone, in wet fens and in rock crevices
Tortula ruralis (Hedw.) Gaertn., Mey. and Scherb.						*		on calcareous soil or rock
Mniaceae								
Cyrtomnium hymenophyllum (B.S.G.) Holmen		*						on moist soil and sand in open tundra usually in crevices or other sheltered niches
Plagiomnium ellipticum (Brid.) Koponen	*	*						various wet habitats — springs, lakeshores, streambeds, wet tundra meadows, marshes, fens, humus or mixed with other bryophytes
Rhizomnium andrewsianum (Steere) Koponen		*	*					in wet depressions in open tundra, frost produced depressions around boulders or wet depressions on steep Mnt. sides

Table 3 (*continued*)

Samples	GZ.04.47	GZ.04.37	GZ.04.38	GZ.04.46	GZ.05.24	GZ.05.25	GZ.05.26	GZ.04.49	GZ.04.45	GZ. July 04-01	GZ.04.29	GZ.04.30	GZ.04.31	GZ.04.32	GZ.04.33	GZ.04.34	GZ.04.44	AVR-04-07-23	Ecology
Site	1	1	1	4	2	2	1	1	2b	2b	2	2	2	2	2	2	3	4	
Type	midden	midden	midden	midden	midden	midden	midden	paleosol	buried turf	buried turf	buried turf	buried turf	buried turf	buried turf	buried turf	buried turf	detrital	organics	
BRYOPHYTA	*	*		*	*	*	*		***	***	***	***	***	***	*	*			
Bryaceae											*			*					
Bryum arcticum (R. Brown) Bruch and Schimp. in B.S.G.	*													*					moist calcareous soil in exposed tundra
Bryum cf. *calophyllum* R. Brown													*	*					moist sandy soil, usually along rivers
Bryum cryophilum Martensson												*							moist soil and rocks in and near stream, often in late snow-melt areas
Bryum pallens Swartz	*																		moist sand or clay
Bryum cf. *pallescens* Schleicher ex Schwaegr.											*								moist soil often in rock crevices
Bryum pseudotriquetrum (Hedw.) Gartner, B. Meyer and Scherbius		*																	soil or soil over rock, wet habitats
Bryum cf. *nitidulum* Lindb.														*					moist soil usually calcareous
Bryum (1)		*		*		*			*	*	*	*	*		*				
Bryum (2)		*		*		*			*	*	*	*	*		*				
Bryum (3)		*		*					*	*			*						
Bryum (4)									*		*	*				*			
Bryum (5)									*			*							
Bryum (6)									*										
~50 Bryaceae/ Diplolepideous moss capsules	*																		
Bryum/Pohlia									*										various habitats
Pohlia											*								various habitats
Meesiaceae																			
Meesia uliginosa Hedw.									*										wet soil, fens, wet rock in streams, moist rock crevices, calcareous habitats
Bartramiaceae																			
Philonotis fontana (Hedw.) Brid.		*		*					*	*				*					calcareous fens, wet meadows, along streambeds slow moving water

										Habitat
Amblystegiaceae										
Amblystegium serpens (Hedw.) B.S.G.	*								*	*	moist to wet habitats usually on soil
cf. *Amblystegium*									*		
Campylium arcticum (Williams) Broth.								*			wet tundra habitats
Campylium stellatum (Hedw.) Jensen	*					*	*		*		wet calcareous fens, meadow, springs, lakeshores
Cratoneuron filicinum (Hedw.) Spruce	*					*					moist to very wet calcareous substrates, usually soil and limestone near or in streams and springs especially waterfalls, where water is aerated
Drepanocladus aduncus (Hedw.) Warnstorf		*		*							fens, seepage areas, besides lakes and pools in calcareous areas
Drepanocladus aduncus var. kneiffii (Schimp.) Mönk.						*					rich fens, sedge meadows, often submerged
Drepanocladus lycopodioides var. brevifolius (Lindb.) Mönk.	*				*	*					wet calcareous fens, ponds and tundra depressions, rarely floating
cf. *Drepanocladus*				*					*		
Brachytheciaceae											
Brachythecium turgidum (Hartman) Kindb.	*					*					moist soil in wet meadows frequently near pools or streams
Brachythecium starkii var. *pacificum* (Ren. and Card.) Lawton		*									soil, logs and litter,
Isothecium cf. *stoloniferum* Brid.			*								soil, rocks, or trees
pleurocarp				*							various habitats
Climaceaceae											
Climacium dendroides (Hedw.) Weber and Mohr									*		wet habitats usually with percolating water, along streams and lakes
Undetermined material											
Stem and leaves w/ growth increments									*		
Capsules		*				*					
Setae		*									

The proportion of bryophytic material per sample was indicated by rare (*), intermediate (*), abundant (***) based on comparison with other samples.

Table 4
Insect fossils data from Goldbottom Creek

Samples	GZ.04.47	GZ.04.37	GZ.04.38	GZ.04.46	GZ.05.24	GZ.05.25	GZ.05.26	GZ.04.49	GZ.04.45	GZ. July 04-01	GZ.04.29	GZ.04.30	GZ.04.31	GZ.04.32	GZ.04.33	GZ.04.34	GZ.04.44	AVR-04-07-23	Ecology
Site	1	1	1	4	2	2	1	1	2b	2b	2	2	2	2	2	2	3	4	
Type	midden	midden	midden	midden	midden	midden	midden	paleosol	buried turf	buried turf	buried turf	buried turf	buried turf	buried turf	buried turf	buried turf	detrital	organics	
Insects																			
Ord. Coleoptera **Fam. Carabidae**																			
Elaphrus sp.					1								1						mostly riparian, common in forest, rare in southern tundra.
Elaphrus parviceps VD.									6										southern arctic region both tundra and forest, near small lakes and ponds
E. tuberculatus Mäkl.									2										strictly riparian, south of the tree line, on silt beaches with *Equisetum*
Bembidion (Peryphanes) dauricum Motsch.											1	2	2					1	mostly tundra, on dry fine sand or peaty soil
B. (Peryphanes) grapii Gyll.														2					in forest and rare coastal tundra, on dry thin sandy soil, sparse vegetation cover.
Bembidion (Peryphanes) sp.			1																probably one of the riparian species
B. (Trechonepha) kuprianovi Mann.									8										strictly riparian, mostly in forest, sometime in southern tundra
B. (Asioperyphus) umiatense Lindrt.																1			in Asia both in forest and tundra, in America mostly in tundra on gravel near water
B. (Asioperyphus) sordidum Kby																1			Both in forest and tundra, on moist clayey soil with sparse vegetation often along large rivers in some depth of water

Taxon	1	2	3	4	5	6	7	8	9	10	11	12	13	Ecology
Poecilus (Derus) nearcticus Lth.												5		in tundra on very dry patches with *Artemisia* cover, almost extinct now but common in the Pleistocene
Stereocerus haematopus (Dej.)												1		Common in tundra on dry, sandy soil with crowberry (*Empetrum*).
Pterostichus (Cryobius) pinguedineus Esch.	1					1			1			1		both in forest and tundra, in forest on river banks, wet meadows; on tundra among rich vegetation, in High Arctic on dry soil
P. (Cryobius) ventricosus Esch.											1			both in forest and tundra up to High Arctic, in forest on river banks under leaves, on tundra on moist soil
P. (Cryobius) brevicornis (Kirby)												2		in tundra on heath and meadow, among grass and leaves, near treeline under alders
P. (Cryobius) similis Mann.										1		1		in tundra on sandy soil among dead leaves
P. (Cryobius) arcticola Chaud.						1						1	3	in tundra and mountain tundra
P. (Cryobius) tareumiut Ball					1									only tundra, on wet peaty soil.
Pterostichus (Cryobius) spp.			2				2		1			2		mostly tundra on moist patches, in forest on open boggy places and river banks.
Amara alpina Payk.		1	3	1			1	1	1		1	33	1	Mostly tundra on rather dry soil among grass vegetation, in taiga near treeline meadows
Amara sp.?									1					widespread genus
Dicheirotrichus (Oreoxenus) mannerheimi? Sahlb.													1	in tundra on open dry ground and steep slopes, in forest near timbler limit on dry sandy slopes with low vegetation.

(continued on next page)

Table 4 (*continued*)

Samples	GZ.04.47	GZ.04.37	GZ.04.38	GZ.04.46	GZ.05.24	GZ.05.25	GZ.05.26	GZ.04.49	GZ.04.45	GZ. July 04-01	GZ.04.29	GZ.04.30	GZ.04.31	GZ.04.32	GZ.04.33	GZ.04.34	GZ.04.44	AVR-04-07-23	Ecology
Site	1	1	1	4	2	2	1	1	2b	2b	2	2	2	2	2	2	3	4	
Type	midden	midden	midden	midden	midden	midden	midden	paleosol	buried turf	buried turf	buried turf	buried turf	buried turf	buried turf	buried turf	buried turf	detrital	organics	
Insects																			
Harpalus alaskensis Lth																	27		in tundra on dry sandy slopes with sparse grass and *Artemisia* vegetation
Fam. Silphidae																			
Thanatophilus coloradensis Wickh.									1										tundra-alpine species, Alaska, north of British Columbia and Colorado above tree line, carrion feeder
Fam. Leiodidae																			
Agathidium sp.											1	1		1					in litter, beetles develop in fungi and myxomycetes.
Fam. Staphylinidae																			
Tachinus instabilis Mäkl.																		1	In forest and tundra, usually with mammal dung, also in ground squirrel burrows
T. brevipennis Sahlb.	1							1	2		1	1		1				2	in tundra, among flood debris on river banks and sea cost, on clay soil under plant litter.
Tachinus sp.?									1										widespread genus, under plant debris
Philonthus sp.									1										widespread genus, under plant debris
Quedius sp.											1	1		1				1	widespread genus, under plant debris
Aleocharinae gen. indet.																2		1	widespread subfamily
Fam. Hydrophilidae																			
Cercyon limbatus Mann?				1															forest and tundra, on moist patches in dung or on mushrooms, under bones.

Taxon												Ecology
Fam. Lathridiidae												
Corticaria sp.?					1		1				1	mostly in forest or in southern tundra, in plant litter, feed on fungi (mustiness)
Lathridiidae gen. indet.?											1	in plant litter, feed on fungi (mustiness)
Fam. Scarabaeidae												
Aphodius sp.	1			2		2	1			4	1	widespread genus, in the Pleistocene common in steppe-tundra assemblages, common in the fossil ground squirrel nests.
Fam. Byrrhidae												
Simplocaria metallica (Sturm)			1	1								Mostly in tundra, on dry soil with thin moss
S. semistriata F.						1					1	Mostly in forest, on dry soil with thin moss
Morychus sp.	3	2		1		2	1		1	7	2	it is probably undescribed species associated with tundra-steppe fossil assemblages, most of *Morychus* beetles live now on the dry soil with tine moss cover
Fam. Elateridae												
Ctenicera sp.						1	1					this beetle belongs to one of small subarctic species, on meadows or dry grassy patches in tundra
Fam. Chrysomelidae												
Chrysolina septentrionalis Men		1						1			1	Abundant in arctic tundra, occurs in southern tundra and polar desert; polyphagous, commonly on Ranunculaceae.
Ch. subsulcata Mnnh.			2									Abundant in arctic tundra, less common in typical tundra and polar desert; polyphagous, often on sedges.

Table 4 (continued)

Samples	GZ.04.47	GZ.04.37	GZ.04.38	GZ.04.46	GZ.05.24	GZ.05.25	GZ.05.26	GZ.04.49	GZ.04.45	GZ. July 04-01	GZ.04.29	GZ.04.30	GZ.04.31	GZ.04.32	GZ.04.33	GZ.04.34	GZ.04.44	AVR-04-07-23	Ecology
Site	1	1	1	4	2	2	1	1	2b	2b	2	2	2	2	2	2	3	4	
Type	midden	midden	midden	midden	midden	midden	midden	paleosol	buried turf	buried turf	buried turf	buried turf	buried turf	buried turf	buried turf	buried turf	detrital	organics	
Insects																			
Chrysolina sp.												1					2	1	widespread genus
Phaedon cyanescens Stål								1										1	On herbs of moist meadows and river banks.
Galeruca rudis (LeC.)																	2		meadows
Fam. Anobiidae																			
Anobiidae? *Dermescidae*?																	1		
Fam. Nitidulidae																			
Meligethes? sp.																	1		meadows
Fam. Curculionidae																			
Lepidophorus lineaticollis Kby	3			7	3	2	3	5	2		10	23		6	3	4	66	15	In tundra on dry sandy soil with poor vegetation, common on azonal steppe-like patches. One of most common beetle in the Pleistocene in American Arctic.
Connatichela artemisiae And.				1							1		1		1		163		In forest zone (Yukon Territory and southern Alaska) on azonal steppe-like slopes, on sandy soil with *Artemisia*, common in the Late Pleistocene, rare now.
Vitavitus thulius Kiss.				1													2		in tundra only, on dry open ground, common in the Pleistocene, rare now.

Taxon	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	Notes
Ceutorhynchus sp.									1										widespread genus, on Brassicaceae
Coniocleonus sp.							1										3		In tundra on dry open ground with Fabaceae, rare, mostly on steppe-like pathes to south from timber limit.
Notaris aethiops ? Fab.																	2		Sedge meadows in stream valleys
Hypera sp.											1						1		mostly xerophilous
Ord. Diptera																			
fly puparia	6	34				25			2		15	9	22	10	89	7	5	3	indicate of rather wet condition
Ord. Hymenoptera																			
Parasitic wasps												2							
Ord. Heteroptera																			
Fam. Corixidae																			
Sigara sp.														1					in lakes and ponds
Fam. Saldidae																			
Saldula sp.				2					1			1							near waters
Fam. Pentatomidae																			
Pentatomidae gen. indet.						1													
Heteroptera fam. indet.																1			
Ord. Homoptera																			
Cicadellidae gen. indet.							2												meadows
Total Insect MNI for sample	11	34	1	22	4	28	12	10	34	–	35	42	36	28	97	16	332	39	

Values indicate Minimum Number of Individuals (MNI) for each sample.
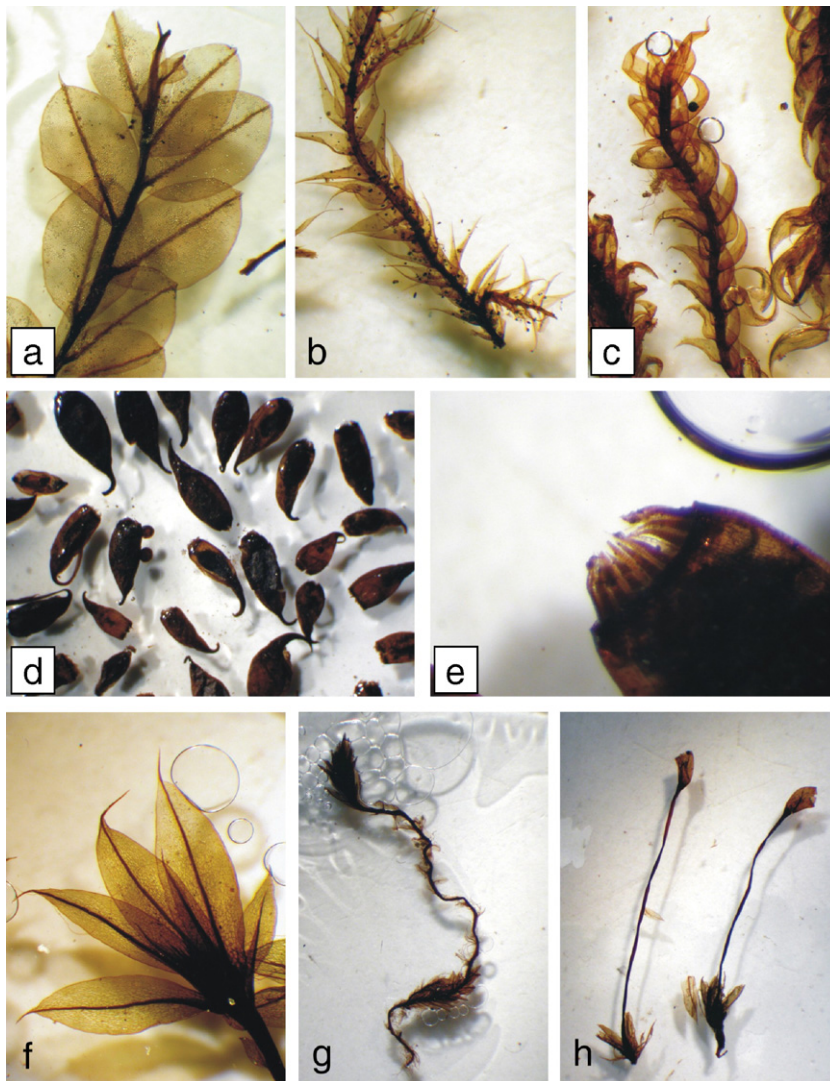
Fig. 5. Selected fossil bryophytes from Goldbottom Creek. (a) *Plagiomnium ellipticum* stem with leaves, sample GZ.05.24; (b) *Campylium stellatum* stem with leaves and branching visible, sample GZ.04.47; (c) *Drepanocladus lycopodioides* var. *brevifolius* stem with leaves, sample GZ.05.26; (d) Bryaceae and/or diplolepideous capsules many with peristomes intact with severed setae just below neck of capsules, sample contained ∼50 capsules, sample GZ.04.47; (e) Bryaceae detail of capsule mouth—diplolepideous alternate peristome with inner peristome perforate, sample GZ.04.47; (f) *Bryum* sp. Showing cell detail and excurrent costae; (g) cf. Bryaceae growth increments visible, sample GZ.July.04.09; (h) Pottiaceae preserved gametophyte with attached sporophyte, peristome lacking (papillae visible on upper leaf cell surface, basal cells smooth), sample GZ.04.29.

significantly lower than modern at 25,300 ^{14}C years BP and climates were typical of the Last Glacial Maximum in Eastern Beringia (Elias, 2000). Our data substantially add to the growing macrofossil evidence for upland dry tundra or steppe environments that inhabited well-drained loessal soils (Goetcheus and Birks, 2001) and regional-scale habitat variability in Eastern Beringia during the last glaciation (Elias et al., 1997). However, the strength of the Goldbottom Creek record lies in the multi-proxy evidence for several habitat types within a local setting.

6.2. Mesic riparian meadow

Buried vegetation at Goldbottom Creek represents a mesic riparian meadow that was buried by winter deposition of Dawson tephra at about 25,300 years ^{14}C BP (Froese et al., 2006). To our knowledge, this is the first record of a buried in situ Beringian riparian community. This grassy meadow grew upon a Static Cryosol soil that was moderately well-drained, but occasionally flooded, and composed of fine-grained, calcareous, colluviated loess and alluvium on the

Table 5
Fossil pollen data from Goldbottom Creek

| Taxa | GZ.04.31 | | GZ.04.32 | | GZ.04.33 | | GZ.04.34 | | GZ.04.45 | | GZ.July.04.01 | |
| | Site 2 | | Site 2 | | Site 2 | | Site 2 | | Site 2b | | Site 2b | |
	#	%	#	%	#	%	#	%	#	%	#	%
Picea	0	0	2	0.35	1	0.19	0	0	1	0.46	0	0
Alnus	1	0.19	0	0	0	0	0	0	0	0	0	0
Betula	3	0.57	1	0.18	0	0	0	0	0	0	1	0.24
Myrica gale	0	0	1	0.18	0	0	0	0	0	0	0	0
Salix	6	1.14	5	0.97	9	1.7	5	1.21	24	11.1	3	0.72
Cyperaceae	94	17.9	124	21.8	70	13.5	5	1.21	42	19.4	31	7.5
Poaceae	355	67.8	300	52.6	360	69.6	214	51.7	97	44.7	103	24.8
Artemisia	38	7.25	91	16	40	7.73	160	38.7	31	14.3	210	50.6
Tubuliflorae	5	0.95	13	2.28	7	1.35	5	1.21	10	4.6	17	4.1
Liguliflorae	1	0.19	1	0.18	11	2.12	1	0.24	1	0.46	1	0.24
Bistorta vivipara type	1	0.19	0	0	0	0	0	0	0	0	0	0
Polygonum persicaria type	3	0.57	5	0.87	1	0.19	7	1.7	2	0.9	8	1.9
Eriogonum type	0	0	0	0	0	0	0	0	0	0	5	1.2
Rumex	1	0.19	0	0	0	0	0	0	0	0	0	0
Chenopodiaceae-*Amaranthus*	5	0.95	11	1.92	8	1.55	5	1.21	4	1.8	14	3.4
Caryophyllaceae	2	0.38	9	1.58	0	0	9	2.17	3	1.4	4	0.96
Ranunculus type	0	0	0	0	4	0.78	0	0	0	0	3	0.72
Thalictrum	4	0.76	0	0	0	0	0	0	0	0	1	0.24
Brassicaceae	2	0.38	4	0.7	2	0.38	2	0.48	1	0.46	5	1.2
Rosaceae	3	0.57	1	0.18	2	0.38	0	0	0	0	5	1.2
Potentilla type	0	0	0	0	0	0	0	0	0	0	1	0.24
Sanguisorba	0	0	1	0.18	0	0	0	0	0	0	0	0
Fabaceae	0	0	1	0.18	0	0	0	0	0	0	0	0
Apiaceae	0	0	0	0	0	0	0	1	1	0.46	0	0
Ericaceae	0	0	0	0	0	0	0	0	0	0	1	0.24
Polemonium	0	0	0	0	1	0.19	0	0	0	0	0	0
Plantago maritima type	0	0	0	0	1	0.19	1	0.24	0	0	2	0.48
Pollen sum	524		570		517		414		217		415	
Indeterminate pollen	63		67		56		274		48		137	

floodplain margin that probably was not underlain by permafrost. In some samples, in situ grass inflorescences had already expelled their florets, and together with evidence for a surface icing (Aufeis), suggest that the buried surface represents winter riparian-margin vegetation (Froese et al., 2006).

Plant macrofossils recovered from turf samples at Site 2 and 2b indicate local-scale heterogeneity within the riparian meadow and across the floodplain. On the riparian margin (Site 2), vegetation was nearly continuous with bryophyte mats in between vascular plants. Identifiable florets with caryopses found in abundance, including *Deschampsia caespitosa*, *Alopecurus*, and *Poa*, suggest a diversity of dominant grass taxa at different locales upon the buried surface. *Equisetum* was also abundant, but not uniformly distributed in the meadow. The bryophyte component includes *P. fontana*, which is commonly associated with *B. cryophyllum*. *A. serpens*, *C. nigritum*, *Bryum* spp., *Distichium* spp. and *E. procera* in small streamside meadows and other hygric habitats with impeded drainage in arctic-alpine ecosys-

tems. *B. icmadophila*, *Desmatodon* spp., *Didymodon asperifolius*, and *T. ruralis* occupy more mesic or sometimes xeric soils. Macrofossils recovered more proximal to the valley centre (Site 2b) indicate vegetation with limited grass, and are dominated by sedge, dwarf willow shrubs, horsetail and a diverse moss cover. At present, *S. arctica* commonly forms mats of prostate shrubs in arctic or alpine tundra floodplains. Fluvial activity in the central floodplain limited soil development and vascular plant diversity. However, the diverse bryophytes from Site 2b represent disturbed microsites as well as mesic and hydric microsites with *Campylium arcticum*, *C. stellatum*, *P. fontana*, and *Drepanocladus* v. *kneifii* typical of wet meadow sites. The bryophyte assemblages from Sites 2 and 2b indicate selected species with a preference for calcareous substrates from xeric, mesic and hydric habitats related to microtopographic variation on the floodplain (e.g., *Desmatodon latifolius*, *P. fontana*, *M. uliginosa*). In general, the dominance of Poaceae pollen over Cyperaceae recovered across the buried surface supports macrofossil evidence for a grass-
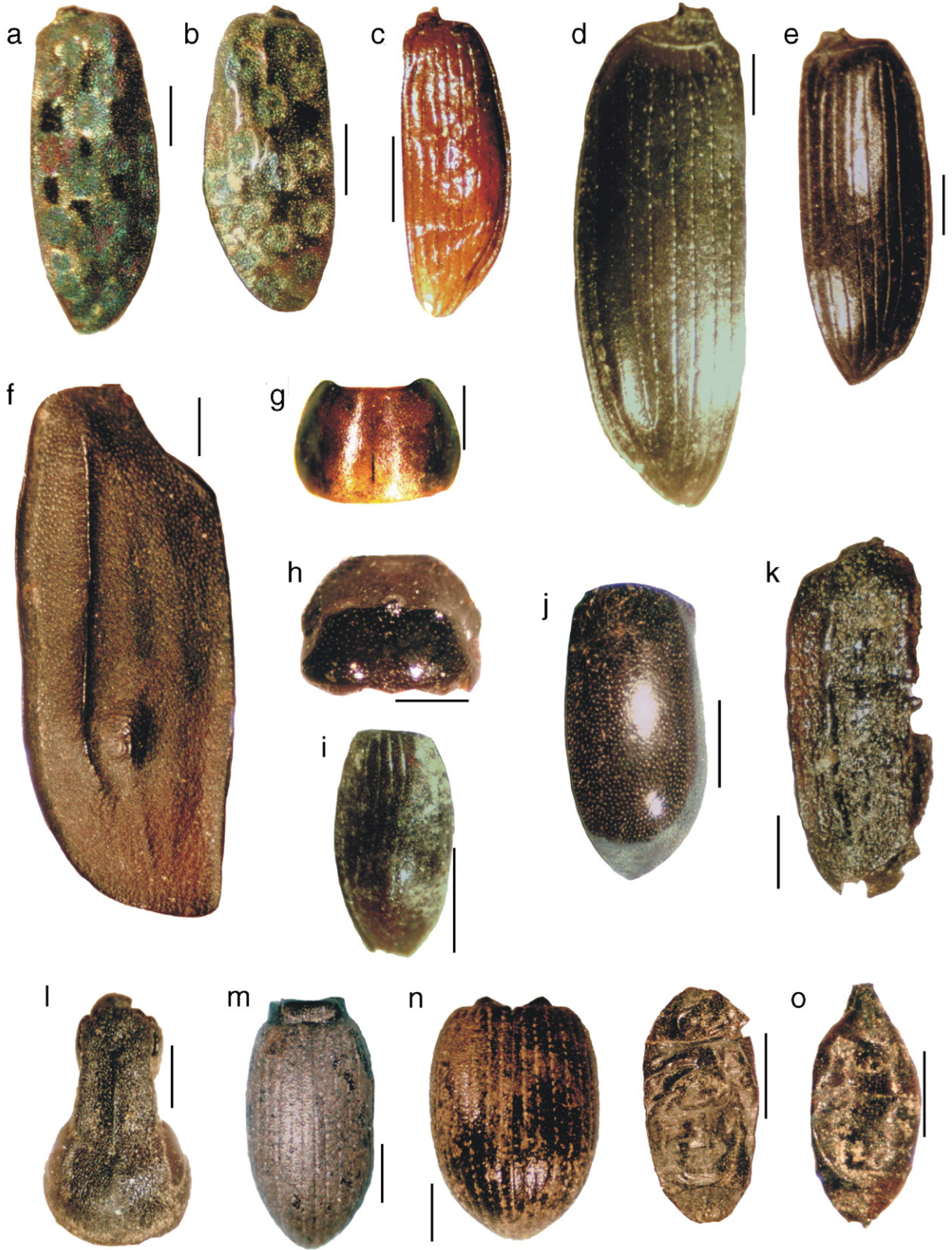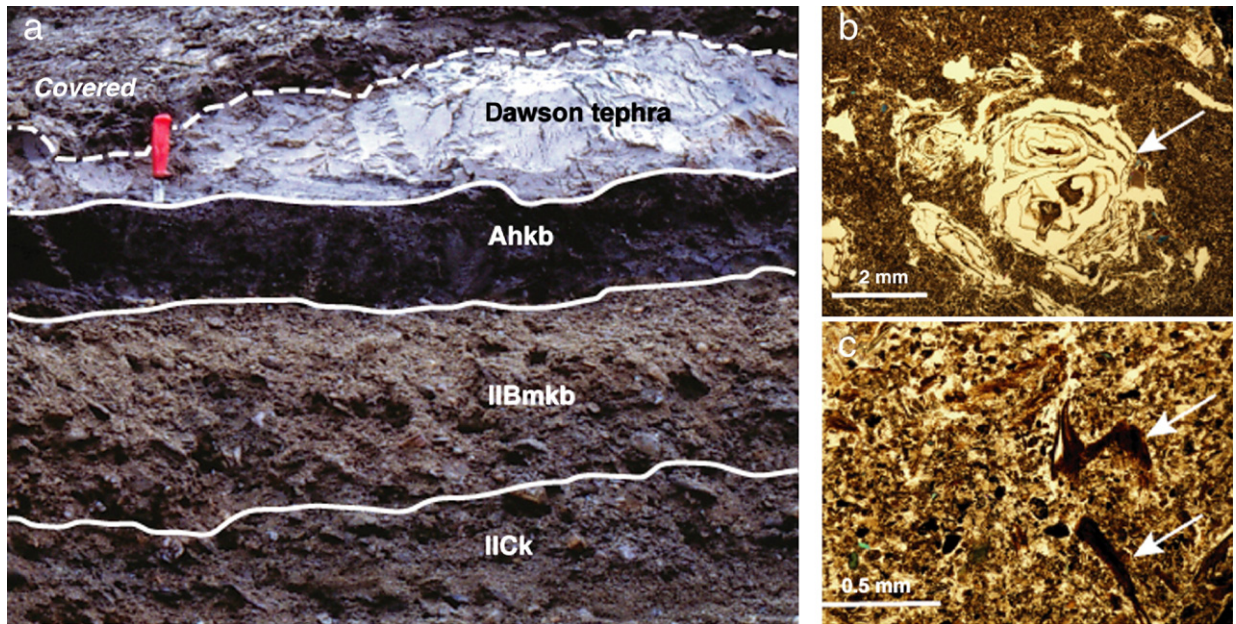
Fig. 7. (a) Paleosol profile at Site 2. Knife handle is 11 cm long. Horizon nomenclature after Soil Classification Working Group (1998) with suffixes indicating burial (b), enrichment with organic matter (h), presence of carbonates (k), and slight alteration by chemical weathering (m), and prefix (II) indicating a soil parent material differing in texture and/or geological origin. (b) Thin section view (plane light) of root residues (arrow) in Ahkb horizon, 1 cm below contact with Dawson tephra. (c) Thin section view (plane light) of Ahkb horizon matrix with organic residues (arrows), 1.5 cm below contact with Dawson tephra.

dominated, rather than sedge-dominated mesic riparian meadow. The presence of abundant grass macrofossils and up to 69.6% Poaceae pollen suggests much of the pollen from this taxon is derived from the riparian meadow. Herbs were rare in the riparian vegetation since no in situ remains were recovered. The presence of sea-blite fruits (*S.* cf. *calceoliformis*) is particularly informative because it is currently restricted to alkaline flats within the interior of Alaska and Yukon. These suggest that widespread aridity formed alkaline evaporative habitats in some areas of the valley bottom. However, moisture from the creek was a primary factor that enabled the mesic grassy meadow to persist within the generally arid full-glacial environment.

6.3. Upland steppe–tundra

The mesic riparian community (Sites 2 and 2b) contrasts significantly with the upland steppe and mesic-

dry tundra communities evident by the dominant taxa in the arctic ground squirrel middens and other vascular plant macrofossils (Sites 1 and 3) that are contemporaneous with Dawson tephra. Here, the term "upland" is used to describe habitats on the valley slopes beyond the floodplain, and not necessarily high elevation sites. Since moisture availability was probably a crucial factor in determining the floristic composition at any given site during Pleistocene glacials, "uplands" with xeric substrates may only be a few meters above the riparian zone. Macrofossils provide evidence for steppe–tundra vegetation rich in upland grasses (*Elymus*, *Festuca*), sedges (*K. myosuroides*), xerophilous steppe forbs (*P. hoodii*, *Plantago* cf. *canescens*, *A. patens* var. *multifida*, *Chenopodium*), sage (*A. frigida*), and tundra forbs typically found above present tree-line (*B. vivipara*, *Eutrema edwardsii*, *Silene uralensis*). These macrofossils support paleosol data that point to generally dry, calcareous, well-drained, accretionary loessal soils that

Fig. 6. Selected insect fossils from Goldbottom Creek. Scale bars are 1 mm. (a) *Elaphrus parviceps* right elytron, sample GZ.04.45; (b) *Elaphrus tuberculatus* left elytron, sample GZ.04.45; (c) *Bembidion* (*Trechonepha*) *kuprianovi* right elytron, sample GZ.04.45; (d) *Poecilus nearcticus* left elytron, sample GZ.04.44; (e) *Harpalus alaskensis* right elytron, sample GZ.04.44; (f) *Thanatophilus coloradensis* left elytron, sample GZ.04.44; (g) *Tachinus brevipennis* pronotum sample GZ.04.45; (h) *Aphodius* sp. head sample GZ.04.44; (i) *Simplocaria metallica* right elytron, sample GZ.04.45; (j) *Morychus* sp. right elytron, sample GZ.04.44; (k) *Galeruca rudis* right elytron, sample GZ.04.45; (l) *Coniocleonus* sp. head, sample GZ.04.44; (m) *Connatichela artemisiae* left and right elytrons connected with abdomen, sample GZ.04.44; (n) *Lepidophorus lineaticollis* left and right elytrons connected with abdomen, sample GZ.04.44; (o) two fly pupae, sample GZ.04.44.

Table 6
Description of Static Cryosol paleosol (Site 2), Horizon nomenclature and descriptive terminology after Soil Classification Working Group (1998)

Horizon	Depth (cm)	Description
Dawson tephra	>20–0	Grayish brown (10YR 5/2 m); silt loam; massive; friable; abrupt, wavy boundary; ~1 m thick.
IIAhkb1	0–10	Black (10YR 3/1 m); silt loam; moderate, medium granular; friable; abundant fine and very fine roots; weak effervescence.
IIAhkb2	10–20	Very dark grayish brown (10YR 3/2 m); silt loam; massive; friable; plentiful fine and very fine roots; weak effervescence; abrupt, wavy boundary; Ahb1 and Ahb2 total thickness range 18–22 cm.
IIIBmkb	20–50	Olive brown (10YR 4/4 m); coarse sand; single grain; loose; very few, very fine roots (in upper 5 cm); 30–50% gravel; very weak effervescence; gradual, wavy boundary; 25–35 cm thick.
IIICk	50–70+	Dark grayish brown (2/5YR 4/2 m); coarse sand; single grain; loose; 30–50% gravel; very weak effervescence.

are frequently disturbed (e.g. *Lappula*, *Lepidium densiflorum*), similar to those reconstructed elsewhere in Yukon Territory for the last glaciation (Zazula et al., 2005, 2006; Sanborn et al., 2006). Differences in moisture availability and their effects on substrate between the upland slopes and riparian zone produced the dramatic floristic differences present between these landscape positions. Upland steppe and tundra forbs dominate midden assemblages, though are rare allochthonous components of the riparian vegetation. Specimens of these taxa from the in situ meadow were probably transported downslope into the valley bottom by periodic sheet wash processes that are also responsible for the thick valley bottom, colluviated loess (Fraser and Burn, 1997) and over-thickened tephra bed (Froese et al., 2006). The presence of *K. myosuroides* macrofossils is important because this taxon dominates the upland full-glacial plant community that was buried by tephra on the Seward Peninsula in western Alaska (Goetcheus and Birks, 2001). Thus,

the presence of this *Kobresia* in central Yukon Territory suggests it formed an important component of regional zonal vegetation in Eastern Beringia and probably favored cold, windswept upland loessal substrates during the last glaciation. The diverse forb pollen recovered from samples of in situ vegetation (e.g. Caryophyllaceae, *Thalictrum*, *Plantago*, Apiaceae, *Potentilla*) supports the macrofossil assemblage of upland steppe–tundra vegetation. The pollen of *Eriogonum* is significant since only one species or subspecies is presently found in the region (*Eriogonum flavum* var. *aquilinum*). This taxon is rare and restricted to dry, azonal steppe slopes which are disjunct from widespread prairie populations far to the south (Cody, 2000).

6.4. Late MIS 3 (Middle Wisconsinan) steppe–tundra

Steppe–tundra macrofossil assemblages from our samples that are contemporaneous with Dawson tephra (ca. 25,300 ^{14}C years BP) are similar compositionally to those from Site 4 dated between 28,000 and 29,500 ^{14}C years BP. Radiocarbon ages from Site 4 place the paleosol, ice-wedge and midden chronologically within the Middle Wisconsinan (MIS 3) interstadial (Anderson and Lozhkin, 2001). Fossil weevils, such as *C. artemisiae* and *L. lineaticollis*, and plants, such as *K. myosuroides*, *P. hoodii*, *A. patens* var. *multifida*, *Papaver*, and *S. taimyrensis*, suggest that steppe–tundra vegetation and habitats generally associated with the MIS 2 full-glacial were established by at least 29,500 ^{14}C years BP in west-central Yukon Territory. The ice-wedge also provides evidence for periglacial conditions between 28,000 and 29,500 ^{14}C years BP. Similar conclusions were reached based on multi-proxy paleoecological data dated to 29,600 ± 300 ^{14}C years BP (TO-292) at the Mayo Indian Village site in central Yukon Territory (Matthews et al., 1990). The development of steppe–tundra vegetation during late MIS 3 in west-central Yukon correlates with the onset of glacial conditions and increased loess aggradation in western Alaska by ca. 28,000 ^{14}C years BP (Muhs et al., 2003).

Table 7
Selected analytical data for Static Cryosol paleosol (Site 2)

Horizon	Depth (cm)	Clay (%)	Silt (%)	Sand (%)	Organic C (%)	Total N (%)	CaCO$_3$ (%)	Fe$_o$ (%)	Al$_o$ (%)
Ahkb1	0–10	7.7	63.3	29.0	2.07	0.197	2.29	0.83	0.03
Ahkb2	10–20	9.3	61.7	29.0	1.65	0.160	2.39	1.10	0.13
IIBmkb	20–50	1.4	5.0	93.6	0.16	0.021	0.42	0.16	0.02
IICk	50–70+	1.4	5.9	92.7	0.06	0.017	0.73	0.42	0.04

All data reported on oven-dry basis. Fe$_o$, Al$_o$ = oxalate-extractable Fe, Al.

6.5. Bryophyte habitat variability

The diverse ecological preferences for bryophytes recovered within the arctic ground squirrel middens at Site 1 point to microhabitat variation. Members of the Pottiaceae (e.g., *Barbula, Desmatodon*) found in the midden macrofossil assemblages indicate sampling of the drier steppe–tundra habitats. Members of the Ditrichaceae (*Ditrichum* spp.) and Rhabdoweisiaceae (e.g., *Oncophorus*) include taxa with a broad tolerance from drier growing conditions to moist habitats. The bryophyte data include two species that grow on rock or trees and suggest a drier steppe–tundra or the proximity of deciduous trees. Abundant Bryaceae capsules, many of which having intact opercula, suggest selective foraging for these by ground squirrels. Bryaceae taxa can occupy a broad spectrum of niches from hydric wet meadows to exposed xeric soil microsites. The members of the Amblystegiaceae (*Campylium* spp., *Cratoneuron, Drepanocladus*) and Bartramiaceae (*Philonotis*) represented in the middens indicate that the ground squirrels sampled wet meadow habitats as well as drier sites. Thirty taxa from eight families were identified from the midden record, which represent a broad range of microsite diversity. Therefore, bryophytes from the middens may reflect more ecologically diverse habitats than the midden vascular plant data. These mosses may have been collected by arctic ground squirrels during foraging excursions more randomly than selection for vascular plant cache items.

6.6. Insect ecological variability and biogeographic anomalies

Insect remains from our sites at Goldbottom Creek also point to a local diversity of riparian, mesic tundra, dry tundra, and steppe habitats within the valley at ca. 25,300 ^{14}C years BP. In particular, the riparian ground beetles *Elaphrus parviceps, Elaphrus tuberculatus*, and *Bembidion* spp. were only found in samples of the buried vegetation and support our interpretation of a mesic riparian meadow, based on in situ plant macrofossils. The presence of open ground, dominated by steppe and mesic to dry tundra habitats on the surrounding valley slopes, is well documented by the abundance of the weevils *L. lineaticollis* and *C. artemisiae*. Recovery of these specimens along with upland plant macrofossils at Sites 2, 2b and 3 suggests they were transported downslope and incorporated into the now-buried riparian surface. Most importantly, *C. artemisiae* is a weevil that is

presently endemic to dry steppe slopes in the Yukon and southern Alaska, where it feeds on *A. frigida* (Anderson, 1989, 1997). The abundance of *C. artemisiae* and *A. frigida* macrofossils suggests that a cold, dry steppe–tundra environment, rich in sage, was more prominent in the interior of the Yukon Territory than further west in Alaska during the last glaciation (Zazula et al., 2003b). The common feature of all these insect assemblages at Goldbottom Creek is the presence of species found today in open, treeless landscapes. *E. tuberculatus* is known today only from the forest zone but lives in open ground habitats and is not ecologically linked with trees. Such species as the ground beetle *Poecilus nearcticus*, the pill beetle *Morychus* sp., and the weevils *C. artemisiae* and *Coniocleonus* sp. were typical members of the Western Beringian steppe–tundra fauna during the Pleistocene. They are rare or almost extinct in the modern regional fauna. The abundance of fly pupae probably reflects moist conditions in the nests. We have found only a few pupae in the sample that reflect the upland valley slope environments at Site 3 (GZ.04.44).

Some interesting anomalies were found in the development of the MCR estimates for the Goldbottom Creek insect faunas. The species climate envelope for *H. alaskensis* based on its modern North American distribution falls outside the MCR of the fauna as a whole. Its North American distribution includes only sites that have warmer climatic parameters than the rest of the faunal assemblage, which is essentially arctic/ subarctic in character. However, the modern Siberian distribution of *H. alaskensis* includes localities in the arctic tundra region, such as near the mouth of the Indigirka River (Kataev, 1990). Thus it appears that in postglacial times, this amphi-Beringian species has split into two populations: a North American group that represents the more warm-adapted populations of the species, and a northeast Siberian group that is adapted to a broader range of temperatures. Based on our MCR analysis, it appears that the Eastern Beringian populations of *H. alaskensis* included the more cold-adapted variety of the species.

The *Artemisia*-feeding weevil *C. artemisiae* was not used in the MCR reconstruction, but its modern range in the Yukon also falls outside of the MCR of the fauna as a whole. Its northernmost known collecting locality is 50 km east of Old Crow, Yukon (Anderson, 1997) where modern TMAX is 14.6 °C and modern TMIN is −31.1 °C (Wahl et al., 1997). Thus, this species' known modern range falls well south of the climate zone in which TMAX is 9–10 °C. It has also been

found as a fossil from a number of other Pleistocene faunal assemblages indicative of cold climate. For instance, its presence within the Eva Creek fossil assemblage near Fairbanks, Alaska (Matthews and Telka, 1997) coincides with an MCR-estimated climatic regime of TMAX 8.5–9.5 °C. It is not understood how this beetle was able to live under climatic conditions that are apparently outside its thermal tolerance limits, based on its modern distribution. We cannot rule out the possibility that additional modern collecting in the arctic regions of the Yukon and Alaska may yield the discovery of more northerly populations of this weevil. The distribution of its host plant, *A. frigida*, is largely determined by soil aridity and disturbance, not air temperature, and extends to the arctic coast of the Yukon and the northern foothills of the Brooks Range (Hultén, 1968). Modern TMAX in the former region averages around 10 °C (Wahl et al., 1997), and in the latter region it averages about 9.5 °C (NOAA, 2002).

6.7. Forage diversity for arctic ground squirrels

The mesic grassy meadow and upland steppe–tundra vegetation mosaic would have provided diverse forage resources for Pleistocene mammals, including arctic ground squirrels (Harington, 1984, 2003). Midden cache contents are dominated by upland steppe–tundra forbs that were probably rare or absent in the riparian community. Thus, late growing-season foraging by arctic grounds squirrels for winter cache material was probably focused on the xeric valley slopes. However, growing season foraging studies of modern arctic ground squirrels on the Alaskan North Slope indicate that selection of foods for immediate consumption is correlated strongly with water content, with *Equisetum* being the most commonly taken plant (Batzli and Sobaski, 1980). *Equisetum* was abundant in the riparian meadow community and absent from our fossil midden contents. These results suggest that there was limited foraging for food caches in the valley bottom. However the riparian grassy meadow may have been an important source for nesting material, including grass foliage and mosses, and forage source for plants such as *Equisetum* for growing season consumption. As such, this habitat mosaic of vegetation related to topography, moisture availability and substrates played a key role in the seasonal and spatial foraging patterns of arctic ground squirrels. This habitat differentiation of forage resources may have been important for other members of the diverse Pleistocene mammal community in Eastern Beringia.

7. Conclusions

To our knowledge, fossil vegetation at Goldbottom Creek represents the first documented buried in situ riparian community in Beringia. This in situ vegetation represents a mesic riparian meadow that was buried by deposition of Dawson tephra at about 25,300 ^{14}C years BP, near the onset of full-glacial conditions in Eastern Beringia (Froese et al., 2006). Contemporaneous paleoecological data from the buried surface, arctic ground squirrel middens and other samples provides information on local scale habitat heterogeneity related to differing landscape positions when regional climates were characterized by aridity and colder-than-modern temperatures. Most importantly, our data clearly demonstrates the striking differences in steppe–tundra dominated upland vs. mesic and hydric lowland riparian meadow habitats at a single locality. Fossil bryophytes from the buried vegetation and fossil middens indicate that significant microhabitat differences existed within both the riparian and upland communities. This ecological mosaic undoubtedly provided a variety of forage types that were exploited by arctic ground squirrels and other mammals. From a regional perspective this study documents how local scale heterogeneity may have contributed to ecosystem function and habitat structure within the mammoth steppe biome (Guthrie, 1990). Our reconstruction of local habitat heterogeneity suggests that physiognomically similar steppe–tundra covered slopes and rolling plains with mesic riparian meadows in the valley bottoms were established across the continental interior of the mammoth–steppe. Steppe–tundra plant and insect macrofossils that are contemporaneous with Dawson tephra (ca. 25,300 ^{14}C years BP) are similar compositionally with those dating between 28,000 and 29,500 ^{14}C years BP, suggesting the transition to full-glacial environments was well underway in west-central Yukon during the later stages of the MIS 3 interstadial.

From a methodological perspective, any single proxy that we employed (e.g. pollen, plant macrofossils, bryophytes, fossil insects) taken independently would have provided a somewhat biased and limited view of the paleoecological conditions at this site. However, taken together, each data type provides corroborating information that enabled us to develop a holistic reconstruction of several interacting components of this ecosystem. Ecological and biogeographical details about this ecosystem variability would be difficult to determine with paleoecological approaches based on single proxies, such as lacustrine derived fossil pollen data.

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