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Short Paper

Paleoecology of Beringian "packrat" middens from central Yukon Territory, Canada

Grant D. Zazula[a,*], Duane G. Froese[b], John A. Westgate[c], Catherine La Farge[d], Rolf W. Mathewes[a]

[a]Department of Biological Sciences, Simon Fraser University, 8888 University Drive, Burnaby, BC, Canada V5A 1S6
[b]Department of Earth and Atmospheric Sciences, University of Alberta, Edmonton, AB, Canada T6G 2E1
[c]Department of Geology, University of Toronto, Toronto, ONT, Canada M5S 1A1
[d]Cryptogamic Herbarium, Department of Biological Sciences, University of Alberta, Edmonton, AB, Canada T6G 2E1

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Abstract

Rodent middens from ice-rich loess deposits are important new paleoenvironmental archives for Eastern Beringia. Plant macrofossils recovered from three middens associated with Dawson tephra (ca. 24,000 ^{14}C yr B.P.) at two sites in Yukon Territory include diverse graminoids, forbs, and mosses. These data suggest substantial local scale floristic and habitat diversity in valley settings, including steppe-tundra on well-drained soils, moist streamside meadows, and hydric habitats. Fossil arctic ground squirrel burrows and nesting sites indicate that permafrost active layers were thicker during Pleistocene glacial periods than at present on north-facing slopes.

Keywords: Beringia; Pleistocene; Plant macrofossils; *Spermophilus parryii*; Microtine rodents; Herbivory; Permafrost; Loess; Paleoecology

Introduction

Fossil rodent middens and nests recovered from burrows or rock shelters contain archives of local vegetation. The most extensively studied middens are those made by packrats (*Neotoma* spp.) and other rodents in arid regions of western North and South America where they have been used to reconstruct late Quaternary vegetation responses to climate change (Betancourt et al., 1990; Latorre et al., 2002). Nests and caches within fossil burrows of arctic ground squirrels (*Spermophilus parryii*) and microtine rodents have been reported from Pleistocene deposits of Siberia (Gubin, 2003) and Eastern Beringia (Guthrie, 1990; Harington, 1984, 2003; Pirozynski et al., 1984; Porsild et al., 1967); however, their paleoecological potential remains largely unexplored. Anticipating this potential in Beringia, Harington (1984, p. 521) noted, "Indeed, these ground squirrels could be considered as small, furry botanists, industriously sampling vegetation within a limited range of their nests and storing it away in underground herbaria."

Plant macrofossils from rodent middens can provide new and taxonomically detailed floristic data to test hypotheses regarding how full-glacial ecosystems functioned in Beringia. Previous paleoenvironmental reconstructions of Eastern Beringia are tentative because pollen data alone do not have the taxonomic and spatial precision to reconstruct the floristic details of local vegetation (Birks and Birks, 2000; Guthrie, 1990; Kozhevnikov and Ukraintseva, 1999). Regional herb-dominant vegetation during the last glaciation is well demonstrated by pollen assemblages from numerous lake cores across Alaska and Yukon Territory (Anderson and Brubaker, 1994) and differing interpretations of those pollen data have been central to ongoing debate (Colinvaux, 1996; Cwynar and Ritchie, 1980;

* Corresponding author. Fax: +1 604 291 3496.
E-mail addresses: gdzazula@sfu.ca (G.D. Zazula), duane.froese@ualberta.ca (D.G. Froese), westgate@geology.utoronto.ca (J.A. Westgate), clafarge@ualberta.ca (C. La Farge).

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Guthrie, 1990; Hopkins et al., 1982). Plant macrofossils have proven effective for the reconstruction of local vegetation at specific sites (Elias et al., 1997; Goetcheus and Birks, 2001; Zazula, 2003; Zazula et al., 2003a,b). Here, we report on plant macrofossil analyses for three late Pleistocene rodent middens associated with Dawson tephra (Froese et al., 2002) at two sites in the Klondike gold fields of west-central Yukon Territory (Fig. 1). The detail afforded by these middens permits reconstruction of microsite habitats across an aggrading valley margin 24,000–26,000 ^{14}C yr B.P.

Site locations and methods

Ice-rich sediments exposed by placer mining in the Klondike Placer District preserve a rich paleoenvironmental record, including fossils of diverse Beringian fauna (Fraser and Burn, 1997; Harington, 2003; Kotler and Burn, 2000). Exposures of perennially frozen "muck" consist of unconsolidated, organic rich silt that is found mostly along north and north-easterly facing sites and in the bottom of narrow valleys. These deposits were formed by the aggradation of both primary and colluviated loess (Fraser and Burn, 1997). At these sites Dawson tephra (ca. 24,000 ^{14}C yr B.P.) serves as a marker bed for the onset of silt aggradation during the last glaciation (Froese et al., 2002; Kotler and Burn, 2000; Zazula et al., 2003a). Fossil middens were collected at exposures along Quartz Creek and Last Chance Creek (Fig. 2) in the summers of 2001 and 2002. Unlike packrat and other fossil rodent middens in which the plant material and other debris are cemented in crystalline urine, these Beringian middens consist of frozen amalgamations of plants remains.

We collected middens that we observed melting out of ice-rich exposures with a trowel. In the laboratory, we subsampled known volumes of the debris by displacement in water and washed it through a 250-μm sieve. The retained material was sorted and identified under a dissecting microscope. Vascular plant remains were identified by GDZ at the Paleoecology Lab, Simon Fraser University, with the aid of herbarium reference specimens. Vascular plant nomenclature and inferred habitat data follow Cody (2000). Mosses were identified by CL at the University of Alberta Cryptogamic Herbarium. Moss nomenclature follows Crosby et al. (1999) and inferred habitat data are from Nyholm (1954–1969) and Steere (1978).

Middens from Quartz Creek and Last Chance Creek

A fossil nest with a cache was recovered from within a bed of Dawson tephra at Quartz Creek (Fig. 2A), overlain by 12 m of silt and yielded radiocarbon ages of 24,280 ± 130 ^{14}C yr B.P. (Beta 161239) and 23,990 ± 130 ^{14}C yr B.P. (Beta 16238) (Froese et al., 2002). The large size of

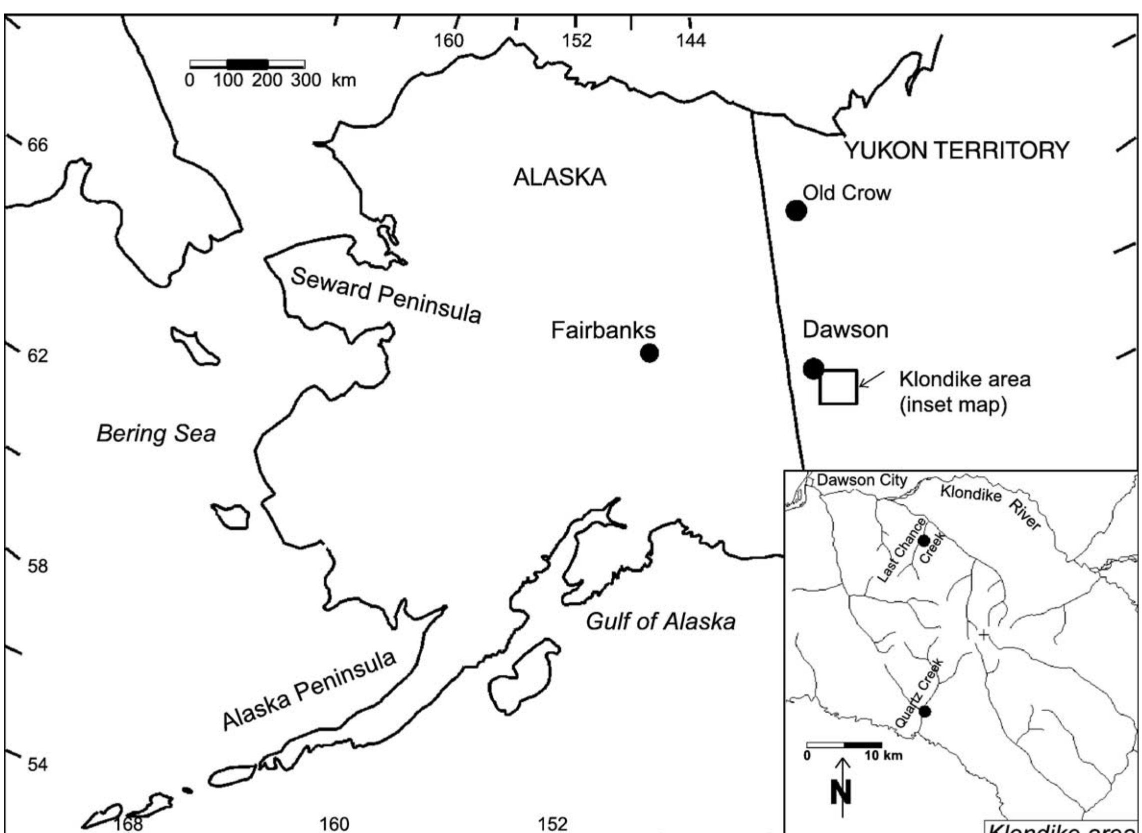

Figure 1. Map of Eastern Beringia with Klondike area and site locations inset.

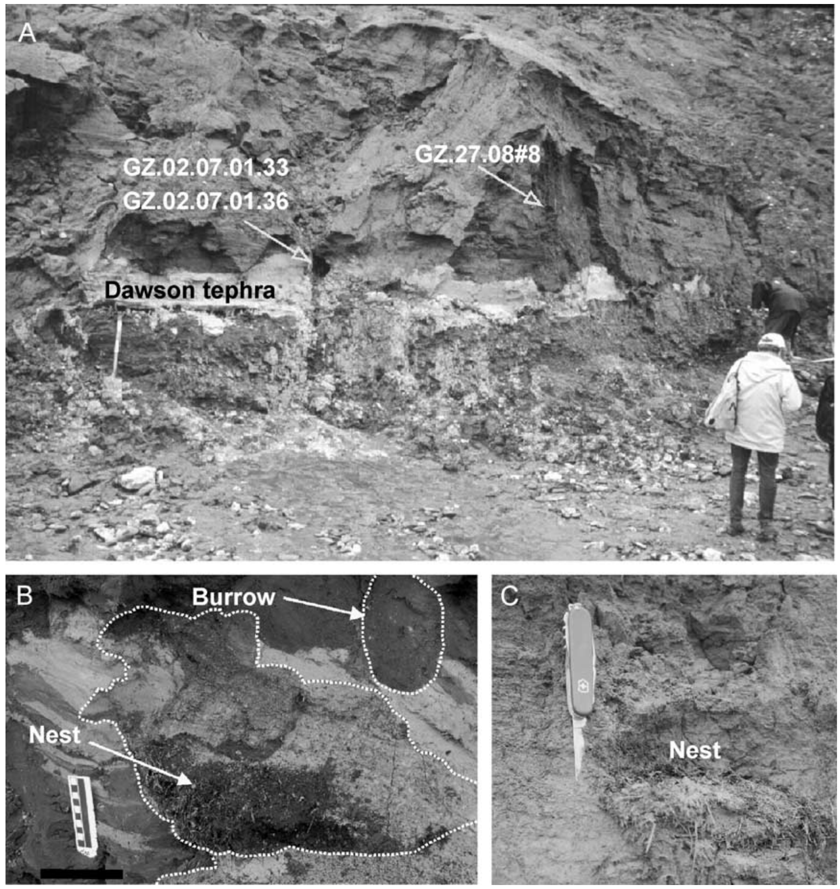

Figure 2. Small mammal middens from exposure at Quartz Creek. (A) Location of middens in relation to Dawson tephra; (B) Arctic ground squirrel midden in Dawson tephra (sample GZ.02.07.01.33 and GZ.02.07.01.36) with in-filled burrow and hibernacula outlined; (C) microtine rodent nest GZ.27.08#8 (knife handle is 9.0 cm long).

the burrow (ca. 10 cm wide), nest (ca. 35 cm wide), and large ovoid/cylindrical shaped fecal pellets (ca. 1.7–2.1 cm long × 0.8 cm wide) suggests that this was an arctic ground squirrel winter hibernaculum (Fig. 2B). A 40-ml subsample of the nest (GZ.02.07.01.33) is composed primarily of fragmented graminoid foliage, with florets from four taxa, while a 5-ml subsample of the cache (GZ.02.07.01.36) yielded seeds and fruits from a variety of forbs. The bryophyte component of the nest consists of gametophytic material (stems, branches, leaves) from two mosses and sporophytes from three taxa.

A small nest (ca. 20 cm wide) at Quartz Creek was recovered 60 cm above Dawson tephra (Fig. 2A). A 10-ml subsample (GZ.02.27#08) was examined and contains primarily fragmented graminoid foliage though a significant proportion (ca. 20%) is the leaves of *Artemisia frigida* (Fig. 2C). It contains abundant small cylindrical shaped fecal pellets (ca. 4.75–6.25 mm long and 2.00 mm wide) deposited by a microtine rodent. Bryophyte material is predominantly gametophytic fragments but included two sporophytes. We believe the age of Dawson tephra approximates the age of the nest because of the close stratigraphic proximity and evidence for rapid silt deposition (Froese et al., 2002).

An arctic ground squirrel food cache (JJD-203-02) was recovered from silt 1.5 m below Dawson tephra and 3 m above creek gravel at Last Chance Creek. Autochthonous peat (GZ.02.07.09.149) within the gravel yielded a diverse plant macrofossil assemblage (Table 1) dating to 25,700 ± 400 ^{14}C yr B.P. (Beta 171748; Zazula et al., 2003a). This cache is ca. 20 cm wide and a 5-ml subsample is dominated by *Carex albo-nigra* fruits, with limited graminoid foliage, gametophytic moss fragments, and ground squirrel fecal pellets.

Results and discussion

The exceptional preservation of frozen Pleistocene middens enabled us to make several plant macrofossil identifications to genus or species level and thus generate detailed ecological data (Table 1; Fig. 3). We recovered taxa from 18 mosses, 16 herbaceous dicots, 7 graminoids, and 1 shrub. This assemblage provides a glimpse of local vegetation at two sites in the continental interior of Eastern Beringia around 26,000–24,000 ^{14}C yr B.P.

Biases resulting from herbivore selectivity and foraging range are important to consider when interpreting paleo-

Table 1
Plant macrofossil taxa identified from fossil small mammal middens and autochthonous peat

Plants	GZ.27.08.#8 Quartz Ck.	GZ.02.07.01.33 Quartz Ck.	GZ.02.07.01.36 Quartz Ck.	JJD-203-03 Last Chance	GZ.02.07.09.149 Last Chance peat[a]	Habitat
Shrubs and trees						
Salicaceae						
Salix sp. (buds)					x	mesic to moist, arctic, alpine, riparian, tundra
Salix cf. *polaris* (leaves, capsules)	x					not to dry mossy tundra, late snow beds, alpine slopes
Forbs						
Polygonaceae						
Oxyria digynia (achene)					1	moist tundra, snowbeds
Polygonum vivparum. (bulbil)				693		turfy, rocky barrens, moist grassy herbmats; favors manured places, animal dens
Chenopodiaceae						
Chenopodium sp. (seed)					1	disturbance, ruderal, dry
Caryophyllaceae						
Caryophyllaceae undet. (seed)					2	
Cerastium sp. (seed)	7	7	5		4	open, disturbance, dry mineral soils
Minuartia sp. (seed)					2	well-drained, tundra, slopes
Silene involucrata (seed)					1	rocky, gravelly, river terraces
Silene uralensis (seed)					2	sandy, rocky, open slopes
Stellaria sp. (seed)			3	1		alpine slopes, meadows, edges of lakes, streams
Ranunculaceae						
Ranunculus sp. (achene)	3	3	21	5	15	moist, streamsides, shorelines, meadows
Papaveraceae						
Papaver sp. (seed)			113		4	tundra, rocky outcrops, gravelly
Brassicaceae						
Brassicaceae undiff. (seed)	173		735			
Draba type (seed)		243		1	13	tundra, slopes, herbmats, calciphilous
Draba sp. (silicle fragment)	13	134	182	1		tundra, slopes, herbmats, calciphilous
Erysimum cf. *cheiranthoides* (silique fragment)	2		5			moist turfy places, near settlements, lake or creek shores, grassy slopes, disturbance
Erysimum cf. *cheiranthoides* type (seed)			66			moist turfy places, near settlements, lake or creek shores, grassy slopes, disturbance
Lepidium densiflorum (silicle fragment)	34					dry, open, disturbance, ruderal
Lepidium sp. (seed)	45					dry, open, disturbance, ruderal
Saxifragaceae						
Parnassia sp. (seed)			1			wet meadows, lakeshores, along streams
Rosaceae						
Potentilla sp. (achene; not. *P. palustris* or *P. fruticosa*)	3	1			19	grassy meadows, tundra, open slopes
Primulaceae						
Androsace septentrionalis (seed)	45				15	dry, calcareous, sandy, gravelly
Gentianaceae						
Gentiana cf. *algida* (seed)			9			alpine meadows, tundra, heath lands

Gentiana cf. *prostrata* (seed)	2		6			moist arctic and alpine tundra, meadows, banks of streams and lakes
Gentianella type seed	2					
Asteraceae						
Asteraceae undiff. (achene)					2	
Achillea millefolium (achene)					1	open slopes, disturbance, riverbanks
Artemisia (tubular flower)	4	5			1	open, disturbance, riverbanks
Artemisia frigida (leaves)	xxx	11				dry open grassland slopes, disturbance
Taraxacum ceratophorum (achene)			1			woodland and heath to tundra, disturbance
Graminoids						
Poaceae						
Poaceae undet. (floret)			2		14	
Deschampsia caespitosa (floret)		255				wet meadows, lakeshores, gravel bars
Deschampsia brevifolia (floret)	16					moist alpine meadows, tundra, rocky slopes
Deschampsia sp. (floret)	7				1	
Elymus sp. (floret)	3	14			2	open slopes, well-drained, riverbanks
Festuca sp. (floret)		11			2	tundra, open woodlands, rocky, gravelly,
Hierochloë hirta ssp. *arctica* (spikelet)		42				sandy stream banks, lakeshores, dunes
Poa sp. (floret)	51			563	29	open slopes, tundra, stream banks
Cyperacae						
Cyperaceae undet. (achene)					2	
Carex albo-nigra (achene, spike)				1151		turfy places in dry alpine tundra
Carex sp. (achene)	1				297	moist, streamsides, shorelines, meadows
Juncaceae						
Juncaceae undet. (seed)					3	moist, meadows, riparian
Moss						
Sphagnaceae						
Sphagnum sp.	x					forms hummocks in wet or moist habitats in bogs or fens, margins of lakes or rivers
Bryaceae						
Bryum sp. 1 (long lanceolate leaves, subpercurrent costa)	x				x	cosmopolitan genus occurring mostly on soil and rock
Bryum sp. 2 (percurrent costa)	x					
Bryum sp. 3 (excurrent costa, broadly recurved below)		?			x	
Bryum sp. 4 (excurrent costa, recurved margins to apex)	x	x				
Bryum sp. 5 (broad leafed)	x					
Bryum sp. cfr. (capsules only)	x	x, cfr. (2 spp)				
Bryaceae undet. (gametophyte)					x	
Bartramiaceae						
Philonotis tomentella	x	x, cfr.				on moist to wet soil in percolated flushes on slopes
Pottiaceae						
Bryoerythrophyllum recurvirostre	x					calcareous soil and rock
Desmatodon cf. *cernuus*	x, cfr.					calcareous soil and rock
Desmatodon heimii var. *arctica*	x, cfr.					calcareous soil and on cliffs and bluffs

(continued on next page)

Table 1 (*continued*)

Plants	GZ.27.08.#8 Quartz Ck.	GZ.02.07.01.33 Quartz Ck.	GZ.02.07.01.36 Quartz Ck.	JJD-203-03 Last Chance	GZ.02.07.09.149 Last Chance peat[a]	Habitat
Moss						
Desmatodon heimii	x	x, cfr.				calcareous soil and rock
Didymodon rigidulous var. *icmadophila*					x	on calcareous soil typically in frost boils or rock crevices
Pottiaceae undet. (gametophyte)		x				
Mniaceae						
Palgiomnium ellipticum					x	wet habitats (springs, lakes shores, stream banks, wet tundra meadows, marshes fens, on humus
Cyrtomnium hymenophylloides				x		on moist calcareous soil
Amblystegiaceae						
Campylium polygamum					x	in wet or moist habitats on calcareous soil or humus
Calliergon giganteum					x	wet habitats standing or percolating water
Drepanocladus cf. *aduncus*					x	wet habitats, pools, not necessarily submerged
Cratoneuron filicinum					x	moist to wet calcareous substrates, in streams or springs, especially near waterfalls where water is well aerated

Vascular plant nomenclature and habitat information follows Cody (2000) and personal observations. Moss nomenclature follows Crosby et al. (1999) and inferred habitat data are from Nyholm (1954–1969) and Steere (1978).

[a] Vascular macrofossil counts for GZ.02.07.09.149 based on analysis of 500 ml of bulk sample; x = present; xxx = abundant; cf. = similar to; cfr. = with fruit.

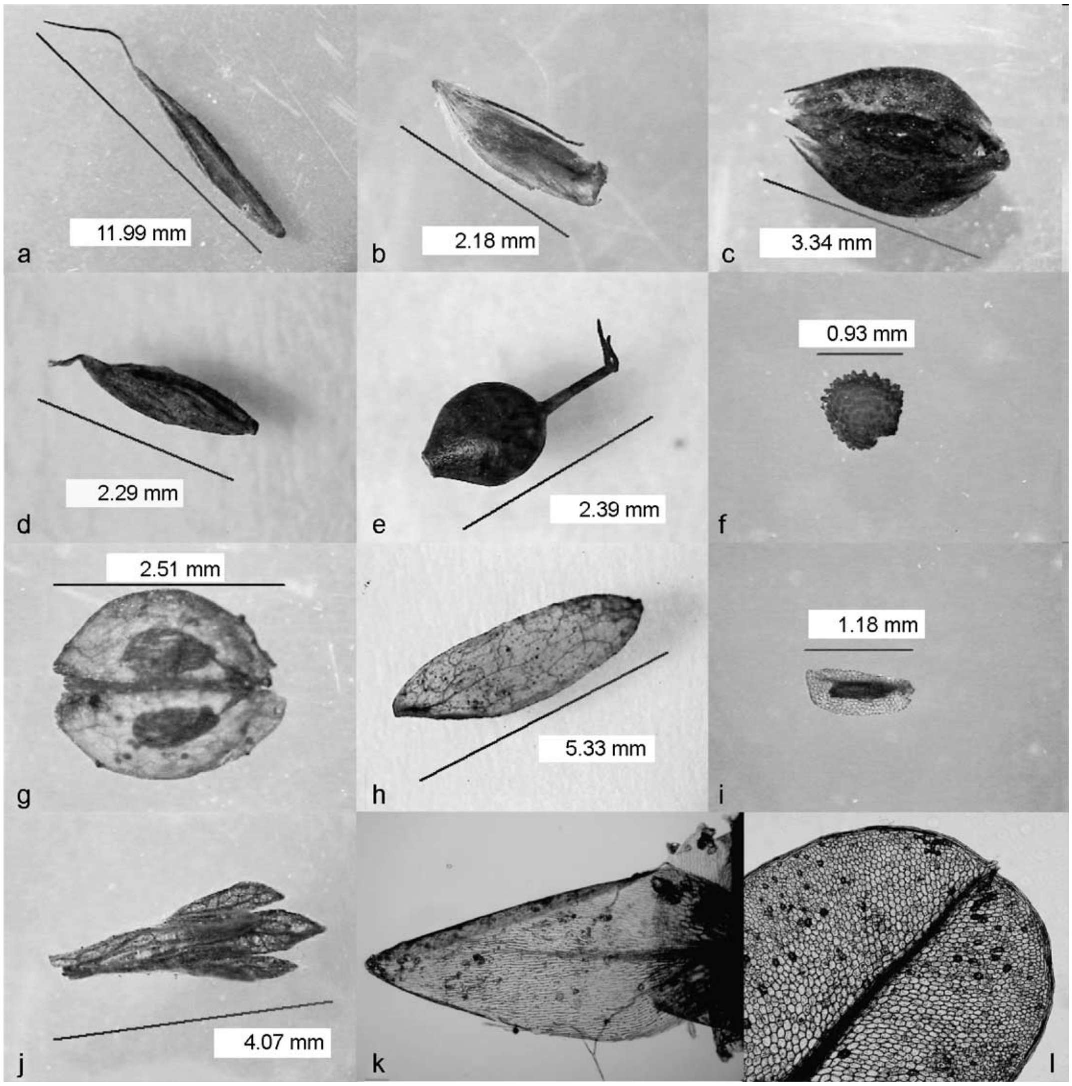

Figure 3. Selected plant macrofossils from small mammal middens: (a) *Elymus* sp. floret; (b) *D. caespitosa* floret; (c) *Hierochloë hirta* ssp. *arctica*; (d) *Poa* sp. floret; (e) *Carex* sp. achene; (f) *Cerastium* sp. seed; (g) *L. densiflorum* silicle; (h) *Draba* sp. silicle; (i) *Parnassia* sp. seed; (j) *A. frigida* leaves; (k) *C. giganteum*; (l) *Crytomnium hymenophylloides*.

botanical data from fossil middens. McLean (1985) indicates that arctic ground squirrels in the southwestern Yukon Territory consume a wide variety of plants but selectively forage on a small number of taxa that are not necessarily abundant on the landscape. Males cache seeds and fruits during the late growing season (Krog, 1953; Mayer, 1953; McLean and Towns, 1981), which are consumed in spring to regain body mass lost during hibernation and undergo sexual maturation (Buck and Barnes, 1999a). Their nests are known to be composed of dry "hay" or graminoid foliage, lichens, mosses, mammal fur, and other leaves (Krog, 1953; Mayer, 1953). Batzli and Sobaski (1980) indicate that arctic ground squirrels on the North Slope of Alaska typically forage within 30 m of their burrows, but not in the immediate vicinity of burrow entrances. Microtine rodents (*Microtus* sp., *Dicrostonyx* sp., *Lemmus* sp.) each prefer different habitats and selectively consume a wide variety of different plants that are variable seasonally (Batzli and Jung, 1980). Despite herbivore behavioral biases, macrofossils from the middens provide local records of Pleistocene plants that inhabited a limited radius surrounding the sampling sites. Furthermore, the middens provide new data on diet and forage selection for Pleistocene rodents, especially for arctic ground squirrel caching.

Vascular plant macrofossils from the middens are diverse (Table 1) and suggest complex patterns of local vegetation in geomorphically active valley bottom and valley margin settings near the onset of the last glaciation. Habitat preferences and probable ecological affinities suggest that these areas include well-drained substrates (*Androsace septentrionalis*, *Artemisia frigida*), moist substrates and riparian meadows (*Ranunculus* sp., *Parnassia* sp., *Deschampsia caespitosa*), and mesic to well-drained herb tundra (*Polygonum viviparum*, *Gentiana* spp., *Deschampsia brevifolia*, *Draba* sp., *Papaver* sp.). Many of the taxa are pioneer plants that colonize recently disturbed or exposed mineral soils (*Cerastium* sp., *Lepidium densiflorum*, *Taraxacum ceratophorum*). Members of at least five genera of Poaceae suggest significant local grass diversity. Dwarf shrubs are represented by *Salix polaris*. The presence of *A. frigida* is important because it is often associated with *Poa glauca*, *Elymus* spp., *Potentilla* sp., and *A. septentrionalis* in azonal subarctic steppe communities (Edwards and Armbruster, 1989; Laxton et al., 1996; Vetter, 2000). The middens are dominated by plants that presently inhabit open areas with well-drained, calcareous substrates that are often disturbed within alpine or arctic tundra, subarctic steppe slopes, and riparian communities. Our data provide evidence for substantial local-scale floristic diversity in the Klondike valleys within the zonal "mammoth-steppe" biome of Eastern Beringia (Guthrie, 1990; Schweger et al., 1982). Slope, drainage, and aspect associated with local topography, geomorphic agents such as slope wash, cryoturbation, and fluvial activity, and other features such as persistence of late season snow banks in the valleys were probably important controls on the local habitat diversity exemplified by our plant macrofossil data.

Macrofossils from autochthonous peat (GZ.02.07.09.149) at Last Chance Creek (Zazula et al., 2003a) assist in the interpretation of the midden data (Table 1). Steppe vegetation is supported by fossils of the weevil *Connatichela artemisiae*, presently known to inhabit southern steppe and dry south-facing slopes where it feeds on *Artemisia* (Anderson, 1984; Zazula et al., 2003a). Herb-tundra plants include *Oxyria digyna*, *Papaver* sp., and members of Caryophyllaceae. Fossils from the peat also include *Salix* sp. and the fly *Xylophagus*, whose larvae live in decaying wood, suggesting the local presence of some shrubs (Zazula et al., 2003a). No tree macrofossils or insects were identified in the peat or middens, even though *Picea* persisted in sheltered valleys in the 60-mile district of West-Central Yukon until at least 26,080 ± 300 ^{14}C yr B.P. (Beta 13870; Matthews et al., 1989). This suggests that the rapid loess aggradation and factors associated with full-glacial climates around 25,000 ^{14}C yr ago created unfavorable conditions for spruce stands.

Moss in both the peat and middens also suggests a broad range of habitats that represent hydric sites including seeps and pools (*Calliergon giganteum*, *Drepanocladus aduncus*), percolating seepage (*Philonotis tomentella*), in streams or springs (*Cratoneuron filicinum*), wet meadows or tundra (*Bryum* spp., *Plagiomnium ellipticum*, *Sphagnum* sp.), wet to moist habitats on calcareous soil or humus (*Campylium polygamum*), and moist calcareous soil and rock habitats (*Bryoerythrophyllum recurvirostre*, *Desmatodon* cf. *cernuus*, *D. heimii* var. *heimii*, *D. heimii* var. *arcticum*, *Didymodon rigidulus* var. *icmadophila*). All of the mosses represent taxa found within modern arctic, arctic-alpine, and boreal ecosystems.

The activities of arctic ground squirrels and other herbivores are important agents that help maintain local floristic diversity and patchiness. Disturbance by burrowing has been shown to bury vegetation (Murray and Murray, 1969), while deposition of waste redistributes soil nutrients (McKendrick et al., 1980) and selective foraging can affect vegetation composition and patterns (Batzli and Jung, 1980; Batzli and Sobaski, 1980; Vetter, 2000). Mallory and Heffernan (1987) note that arctic ground squirrel foraging and disturbance caused a 70% floristic change in a low arctic tundra plant community at Eskimo Point, Northwest Territories. One must consider the possible importance of Pleistocene ground squirrel foraging and disturbance on the maintenance of grazing habitats for Beringian megaherbivores, similar to observations of preferential bison grazing on areas with prairie dog colonies (*Cynomys ludivicianus*) in the mixed-grass prairies of North America (Dyer et al., 1982).

Well-drained loessal substrates

Regional climatic and local geomorphic processes played important roles on local full-glacial substrates. Conditions for regional loess activation and deposition in northern and central Yukon commenced around 25,000 ^{14}C yr B.P. (Cinq-Mars and Morlan, 1999; Froese et al., 2002; Zazula et al., 2003a). Spring melt and runoff would wash much of the upland loess downslope to form thick beds of valley bottom and valley margin silt in the Klondike (Guthrie, 1990; Fraser and Burn, 1997). These fine-grained, calcareous, and nutrient-rich mineral soils provided habitats suitable for colonization for pioneer plants with both steppe and herb tundra affinities. In present circumpolar steppe and tundra, loess deposition is a significant factor that increases plant productivity, diversity, and alters community composition (Laxton et al., 1996; Walker and Everett, 1991).

The presence of fossil rodent burrows and hibernacula provides information about full-glacial valley soils. At present, active layer depths and permafrost distribution are important factors limiting arctic ground squirrel distribution and they burrow in sites that are open and well drained, with permafrost deep below the surface and not prone to spring flooding (Batzli and Sobaski, 1980; Carl, 1971; Mayer, 1953). Favorable sites include upland sites on tundra, open meadows, eskers, river bluffs, and dunes (Batzli and Sobaski, 1980; Carl, 1971; McLean, 1985). Buck and Barnes (1999b) note that arctic ground squirrels selectively hibernate underground at tundra sites with an average thaw depth of 97 cm on the North Slope of Alaska. At present, our north-facing study sites with black spruce (*Picea mariana*) forests, thick moss and organic humus overlying poorly drained substrates with shallow permafrost are not suitable for ground squirrel burrowing. These sites with ice-rich silt sediments where the fossil middens were recovered must have had deeper active layers during the Pleistocene full glacial to enable burrow excavation and hibernation. Fossil middens support previous hypotheses that suggested that full-glacial climates favored discontinuous vegetation on exposed, warm, well-drained soils with deeper active layers than found today in Beringia (Guthrie, 1990; Schweger, 1997). Soils with deeper active layers would have enabled greater nutrient turnover essential for productive, herbaceous steppe-tundra vegetation (Laxton et al., 1996).

Full-glacial macrofossils in Eastern Beringia

Fossil middens in West-Central Yukon Territory add to the limited full-glacial plant macrofossil data from Eastern Beringia (Elias et al., 1997; Goetcheus and Birks, 2001; Zazula, 2003). Examining similarities and dissimilarities in the plant assemblages from our sites in the Klondike with sites elsewhere suggests several possibilities. Our plant data are different from that of Elias et al. (1997) who obtained macrofossils from peat on the now-submerged Bering shelf dominated by local lowland mesic birch-graminoid tundra and emergent taxa, with little evidence for steppe or well-drained habitats. The buried tundra surface under an 18,000-yr-old tephra on the Seward Peninsula (Goetcheus and Birks, 2001) provides a good floristic comparison with our data since it is a small sample of local plants that grew on a calcareous loessal soil. The Seward Peninsula paleovegetation is dominated by the upland xerophilous sedge *Kobresia myosuroides* and includes many plants similar at the genus or species level to those found in our Klondike samples, including *Salix* spp., *Draba* sp., *Potentilla* sp., *O. digyna*, *Papaver* sp., several Caryophyllaceae, *Bryum* sp., *Campylium* sp., *B. recurvirostre*, *Desmatodon* sp., *D. rigidulus* var. *icmadophila*, and *P. ellipticum*. Of particular significance are the vascular plant macrofossils that we have recovered from the Klondike that are absent so far from both aforementioned sites, including the grasses, some forbs such as *A. septentrionalis*, *Gentiana* spp., *L. densiflorum*, and *A. frigida*. However, our results from the Klondike are similar floristically to the full-glacial steppe and tundra reconstructed from macrofossils along the Bluefish River in northern Yukon (Zazula, 2003). These comparisons suggest that well-drained steppe-tundra vegetation with tufted grasses, *Artemisia*, and diverse forbs was more extensive in interior Yukon Territory and Alaska than on the central Bering land bridge (Elias et al., 1997; Guthrie, 2001; Zazula et al., 2003b).

Conclusions

Our data indicate that C.R. Harington was correct; the middens of arctic ground squirrels and other small mammals contain a wealth of paleoecological information. Plants from Quartz Creek and Last Chance Creek middens reflect locally diverse vegetation and habitats between 26,000 and 24,000 ^{14}C yr B.P., including steppe on dry substrates, moist riparian areas with stream side meadows, tundra herbmats, hydric pools, and seepage slopes. Disturbance from primary loess deposition, retransportation of loess, valley bottom fluvial activity, and rodent herbivore activity undoubtedly contributed to this diversity. Fossil burrows and hibernacula suggest well-drained Pleistocene substrates with thicker active layers than presently found at the sampling sites. Macrofossil data from the middens also provide a unique record of arctic ground squirrel diet and forage selection during the late Pleistocene. This paper represents a promising start to ongoing research on rodent middens from Yukon Territory. Like other rodent middens in the Americas, Beringian middens will eventually furnish a rich archive of well-dated plant and animal material suitable for a suite of biological, geochemical, and paleoecological studies.

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