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Early Wisconsinan (MIS 4) Arctic ground squirrel middens and a squirrel-eye-view of the mammoth-steppe

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ABSTRACT

Fossil arctic ground squirrel (*Spermophilus parryii*) middens were recovered from ice-rich loess sediments in association with Sheep Creek-Klondike and Dominion Creek tephras (ca 80 ka) exposed in west-central Yukon. These middens provide plant and insect macrofossil evidence for a steppe-tundra ecosystem during the Early Wisconsinan (MIS 4) glacial interval. Midden plant and insect macrofossil data are compared with those previously published for Late Wisconsinan middens dating to ~25–29^{14}C ka BP (MIS 3/2) from the region. Although multivariate statistical comparisons suggest differences between the relative abundances of plant macrofossils, the co-occurrence of steppe-tundra plants and insects (e.g., *Elymus trachycaulus*, *Kobresia myosuroides*, *Artemisia frigida*, *Phlox hoodii*, *Connatichela artemisiae*) provides evidence for successive reestablishment of the zonal steppe-tundra habitats during cold stages of the Late Pleistocene. Arctic ground squirrels were well adapted to the cold, arid climates, steppe-tundra vegetation and well-drained loessal soils that characterize cold stages of Late Pleistocene Beringia. These glacial conditions enabled arctic ground squirrel populations to expand their range to the interior regions of Alaska and Yukon, including the Klondike, where they are absent today. Arctic ground squirrels have endured numerous Quaternary climate oscillations by retracting populations to disjunct “interglacial refugia” during warm interglacial periods (e.g., south-facing steppe slopes, well-drained arctic and alpine tundra areas) and expanding their distribution across the mammoth-steppe biome during cold, arid glacial intervals.

1. Introduction

The hallmark characteristic of Quaternary environmental change is the cyclical oscillation between warm interglacial and cold glacial climate intervals, largely driven by orbital perturbations and their effects on solar insolation. Evidence for these climate fluctuations is recorded in $\delta^{18}O$ and other proxy data from deep sea marine sediments (Martinson et al., 1987; Shackleton, 1987) and cores taken from the Greenland (Dansgaard et al., 1993) and Antarctic (EPICA, 2004) ice caps. However, long Quaternary terrestrial paleoecological records are rare, especially in the northern hemisphere where continental glacial advances have effectively removed much of the sedimentary archive from previous intervals. Thus, there is limited understanding of the composition or function of high latitude terrestrial ecosystems for much of the Quaternary prior to the Last Glacial Maximum (LGM) or ecological responses to climate change over successive glacial–interglacial cycles. In reconstructing environmental change over glacial–interglacial time scales, it is important to recognize that for approximately 80% of the Quaternary, global climates were colder than the present interglacial (Ehlers and Gibbard, 2004). As such, for many present-day organisms, in the circumpolar region, glacial conditions, or at least conditions characterized by colder than present climates, can be considered to represent the “norm” in terms of their typical ecological adaptations (Rull, 2009).

Unlike most of northern North America, vast areas of Alaska and adjacent Yukon (Eastern Beringia) escaped glaciation, and this region contains a terrestrial sedimentary archive that spans much of the Late Cenozoic (Hopkins et al., 1982; Froese et al., 2009). Since many of these deposits are older than the effective limits of radiocarbon dating (~50 000 ^{14}C yr BP), development of a detailed geochronology for this region has relied on other methods. In

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particular, much of Eastern Beringia is in the fall-out zone of distal tephra from the Aleutian and Wrangell–St. Elias volcanic fields (Preece et al., 1999, 2000; Begét, 2001; Westgate et al., 2008). Tephra can be dated with direct (i.e. fission track, Westgate, 1989) and indirect (i.e. luminscence or from associated radiocarbon ages, Berger et al., 1996; Froese et al., 2002; Demuro et al., 2008) methods and correlated regionally by geochemical analyses. At least 70 tephras have been identified in Eastern Beringia thus far and have facilitated the study of regional Late Cenozoic environmental change (Westgate et al., 1990; Begét, 2001; Westgate et al., 2005).

Frozen "muck" sediments are commonly exposed by placer gold mining in valleys of central Alaska and Yukon, yielding a wealth of Pleistocene fossil biota (Guthrie, 1990; Péwé et al., 1997; Harington, 2003; Zazula et al., 2005, 2007). Muck consists of perennially frozen, unconsolidated, organic-rich loess found commonly along north and north-easterly facing sites and in the bottoms of narrow valleys (Fraser and Burn, 1997; Kotler and Burn, 2000; Froese et al., 2009). Throughout the summer, new exposures of muck are constantly created through natural melting and placer mining.

In the ice-rich loessal deposits of the Klondike goldfields in west-central Yukon, Dawson tephra (Dt), dating to ~25 300^{14}C yr BP (~30 000 cal. yr BP) serves as a stratigraphic marker for the onset glacial conditions at the Marine Isotope Stage (MIS) 3/2 transition (Froese et al., 2002, 2006, 2009; Zazula et al., 2006a), while Sheep Creek tephra-Klondike (SCt-K) and Dominion Creek tephra (DCt), dating to 82 ± 9 ka, mark the onset of the Early Wisconsinan glacial interval of MIS 4 (Westgate et al., 2005, 2008). Reconstructing paleoenvironments associated with these tephras has been the focus of interdisciplinary research (Sanborn et al., 2006; Zazula et al., 2006a). Paleoenvironmental records for early MIS 2 (Late Wisconsinan) from the Klondike include fossil arctic ground squirrel middens (Zazula et al., 2005, 2007), peat and *in situ* vegetation (Zazula et al., 2003, 2006a; Froese et al., 2006) and loessal paleosols (Sanborn et al., 2006). Together, these data provide evidence for zonal cryoxerophilous steppe-tundra vegetation that occupied well-drained loessal soils during the onset of the last major Pleistocene cold stage.

Although many of the paleoecological details are becoming established for Eastern Beringia during the last glaciation (Elias et al., 1997; Goetcheus and Birks, 2001; Guthrie, 2001; Ager, 2003; Bigelow et al., 2003; Zazula et al., 2005, 2007) many questions remain about paleoenvironments during earlier glacial intervals. A prevailing interpretation of this glacial environment has been termed the "mammoth-steppe" (Guthrie 1990, 2001). The mammoth-steppe model as put forth by Guthrie (1990, 2001) is based on two lines of fossil evidence: 1) the dominance of grass (Poaceae), sedge (Cyperaceae), sagebrush (*Artemisia*) and various forbs in regional MIS 2 pollen data, and 2) the dominance of large mammal grazers in regional Late Pleistocene fossil vertebrate faunas, including woolly mammoths (*Mammuthus primigenius*), horses (*Equus* spp.), and steppe-bison (*Bison priscus*). Together, the reconstructed regional ecosystem characterized by high latitude grasslands, or "steppe-tundra" and the associated large mammal grazing community, can be summarized as the mammoth-steppe. Guthrie (1990, 2001) suggests the broadscale uniformity of both pollen and vertebrate data from across the Holarctic, indicates the mammoth-steppe biome stretched from England to Yukon during the last glaciation. Further, Guthrie (1990, 2001) has suggested that the holarctic mammoth-steppe biome responded synchronously with northern hemisphere climate fluctuations, with xerophilous steppe-tundra vegetation and the mammoth-fauna expanding across the unglaciated regions of Eurasia and northern North America during successive Quaternary cold stages. However, detailed, multi-proxy paleoecological records from multiple cold stages in Beringia are not available to test this hypothesis. Knowledge about Beringian biota from multiple intervals can help us understand the nature of northern biotic refugia and address how these ecosystems and organisms respond to climate change over glacial-interglacial time scales.

In this paper, we present plant and insect macrofossil data from 64 fossil arctic ground squirrel (*Spermophilus parryii*) middens (nests and caches) recovered in association with SCt-K/DCt (early MIS 4 marker beds, ca 80 ka) from ice-rich loess exposures in the Klondike goldfields of west-central Yukon (Fig. 1). Pleistocene arctic ground squirrel middens have been recognized and examined from Siberia (Gubin et al., 2001, 2003; Zanina, 2005), Alaska (Guthrie, 1990) and Yukon (Harington, 1984, 2003; Zazula et al., 2005, 2006a, 2007) and consist of frozen amalgamations of plants remains that include both graminoid vegetative materials used by arctic ground squirrels for nests, and seeds and fruits that were cached over the winter (Zazula, et al., 2005, 2006b). Plant and other biotic remains from the middens provide detailed, local paleoecological records because present-day arctic ground squirrels are known to forage in a relatively limited radius from their nests (Batzli and Sobaski, 1980; Zazula et al., 2006b). Although the paleoecological data from midden samples are certainly biased towards preferred cache forage and nest building plant taxa (Zazula et al., 2006b), the wide range of species represented in previously analyzed fossil samples suggest that they adequately represent overall local plant community composition (Zazula et al., 2005, 2007). These midden data are compared with those from 48 fossil middens which date to the Late Wisconsinan glacial interval (MIS 3/2 transition) ~25 and 29 ka^{14}C yr BP (Zazula et al., 2007). Comparison of the Late Wisconsinan (MIS 3/2 transition) and Early Wisconsinan (MIS 4) middens are used to examine vegetation, arctic ground squirrel adaptations and the ecology of mammoth-steppe biome during two successive glacial intervals.

2. Methods

Fossil arctic ground squirrel middens (Figs. 2 and 3) were collected at exposures of Pleistocene ice-rich silt along Dominion Creek ($n = 38$), Quartz Creek ($n = 17$), and Irish Gulch ($n = 9$) (Fig. 1) during several visits through the summers of 2002–2005. Laboratory methods for midden macrofossil analysis follow Zazula (2006). Middens were immersed in water to disaggregate the plant material before sorting under a dissecting microscope. Plant remains were identified to the most precise taxonomic resolution possible. Identification of plant material was conducted by comparison with herbarium reference specimens from the University of Alberta, University of British Columbia, University of Alaska, Fairbanks, Simon Fraser University and Yukon Palaeontology Program. Vascular plant nomenclature follows the Flora of North America (Flora of North America Editorial Committee, 1993). Inferred habitat data follows Cody (2000) and some ecological and biogeographic information was obtained from Hultèn (1937, 1968). Individual plant taxa from each midden were quantified using a relative abundance index (RAI) where 0 = absent, 1 = <1%, 2 = 1–5%, 3 = 6–25%, 4 = 26–50%, 5 = 51–75% and 6 = >75% of the entire midden contents (Zazula, 2006, 2007). The majority of plant material in each midden was assigned the "miscellaneous vegetation" category which includes graminoid and other unidentified herbaceous foliage and stems presumably used by the squirrels as nesting material. Since the interval distance within each RAI is not uniform, mid-point values for each RAI class interval were used for quantitative analyses (RAI mid-point values: 0 = 0, 1 = 0.5%, 2 = 3%, 3 = 16%, 4 = 38%, 5 = 63% and 6 = 88%). Mid-points are useful approximations for RAI or other ecological class data when the exact abundance value for each taxon is not measured (e.g. Mitchell et al., 1988; Peck et al., 2004). Mean RAI mid-points based on all 64

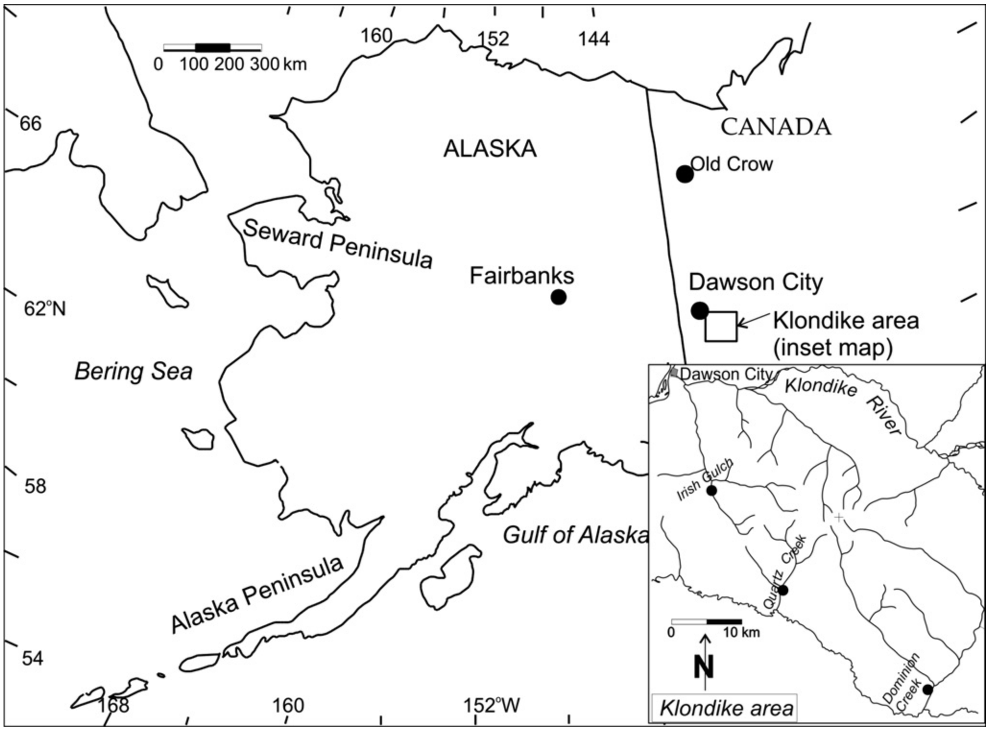

Fig. 1. Map of Alaska and Yukon Territory with Klondike area inset showing locations of study sites in Klondike goldfields.

middens were calculated to estimate each taxon's overall abundance. RAI values of zero (RAI = 0) were included in the mean calculation.

Insects from the middens were picked during midden sorting by G. Zazula and later identified by S. Kuzmina and S. Elias. Ground and rove beetles were used to obtain estimates of seasonal temperature using the Mutual Climatic Range (MCR) method based on estimates of seasonal the species climate envelopes (Elias, 2000). Temperatures presented are uncalibrated MCR estimates based on total climate envelopes of present-day taxa.

Multivariate analyses were conducted to compare the Early Wisconsinan midden data with those previously published of Late Wisconsinan age (Zazula et al., 2007). For numerical analyses, the miscellaneous vegetation class (graminoid and other nesting material) was removed from the data matrix. A Kruskal–Wallis test available in JMP 5.01 (Sall et al., 2001) confirmed there were no significant differences in mean nesting material abundance from the MIS 3/2 and MIS 4 midden samples ($P = 0.5887$). The resultant data matrix was relativized by sample sum of squares (McCune and Grace, 2002) to standardize the amount of cache material (seeds and fruits) in each midden sample and ensure comparison of relatively equal sample sizes. An arcsine square root transformation was applied to these data. This transformation is appropriate for ecological data matrices based on proportional data with abundant zeros and is recommended to improve normality (McCune and Grace, 2002).

All multivariate tests were conducted with PC-Ord 4.14 (McCune and Mefford, 1999). The overall trends and structure in the midden plant macrofossil data were explored using Non-Metric Multidimensional Scaling (NMS) using the autopilot program with the slow and thorough analysis option and the default settings in PC-Ord 4.14 (McCune and Mefford, 1999). NMS is a non-parametric ordination method well suited to non-normally distributed ecological data that avoids many of the assumptions about underlying structures of data made by traditional ordination methods (Kenkel and Orlóci, 1986; Clarke, 1993; McCune and Grace, 2002; Lamb et al., 2003). Samples and species are plotted along n ordination axes as defined by the optimal solution using the Sørensen's (Bray-Curtis) similarity distance (McCune and Grace, 2002). In the NMS solution, each taxon is assigned an r^2 value which reflects the amount of variance in the overall dataset which can be accounted for by that taxon. Difference in plant macrofossil assemblages between MIS 3/2 and MIS 4 was tested using a Multiple Response Permutation Procedure (MRPP) with the Sørensen's distance measure (Zimmerman et al., 1985). MRPP is a non-parametric analogue of Discriminant Function Analysis (DFA), which supports a multivariate test of the null hypothesis of no significant difference between *a priori* groups of samples (Williams, 1983; McCune and Grace, 2002). In the MRPP, and A statistic measured the grouping "effect size", or distinctiveness of groups, on a scale of 0–1. Values of $A > 0.3$ are considered fairly high. Indicator Species Analysis (ISA) was used to identify species that were significantly more frequent and abundant in middens of either the MIS 3/2 or MIS 4 intervals. The indicator values are calculated by multiplying the relative abundance of each taxon in a particular group by the relative frequency of the species' occurrence in that group (Dufrêne and Legendre, 1997; McCune and Grace, 2002).

3. Results

3.1. *MIS 4 loess and paleosol stratigraphy of the Klondike*

Fossil middens and loessal paleosols are commonly observed in the Klondike within ice-rich sediments in association with SCt-K and DCt (Fig. 4). (Westgate et al., 2005, 2008; Sanborn et al., 2006; Froese et al., in preparation). DCt has a glass fission track age of 82 ± 9 ka and occurs stratigraphically above and in close association with SCt-K. Optically Stimulated Luminescence (OSL) ages obtained from sediments associated with SCt-K are consistent with the glass FT age on the DCt (Westgate et al., 2005, 2008). Both

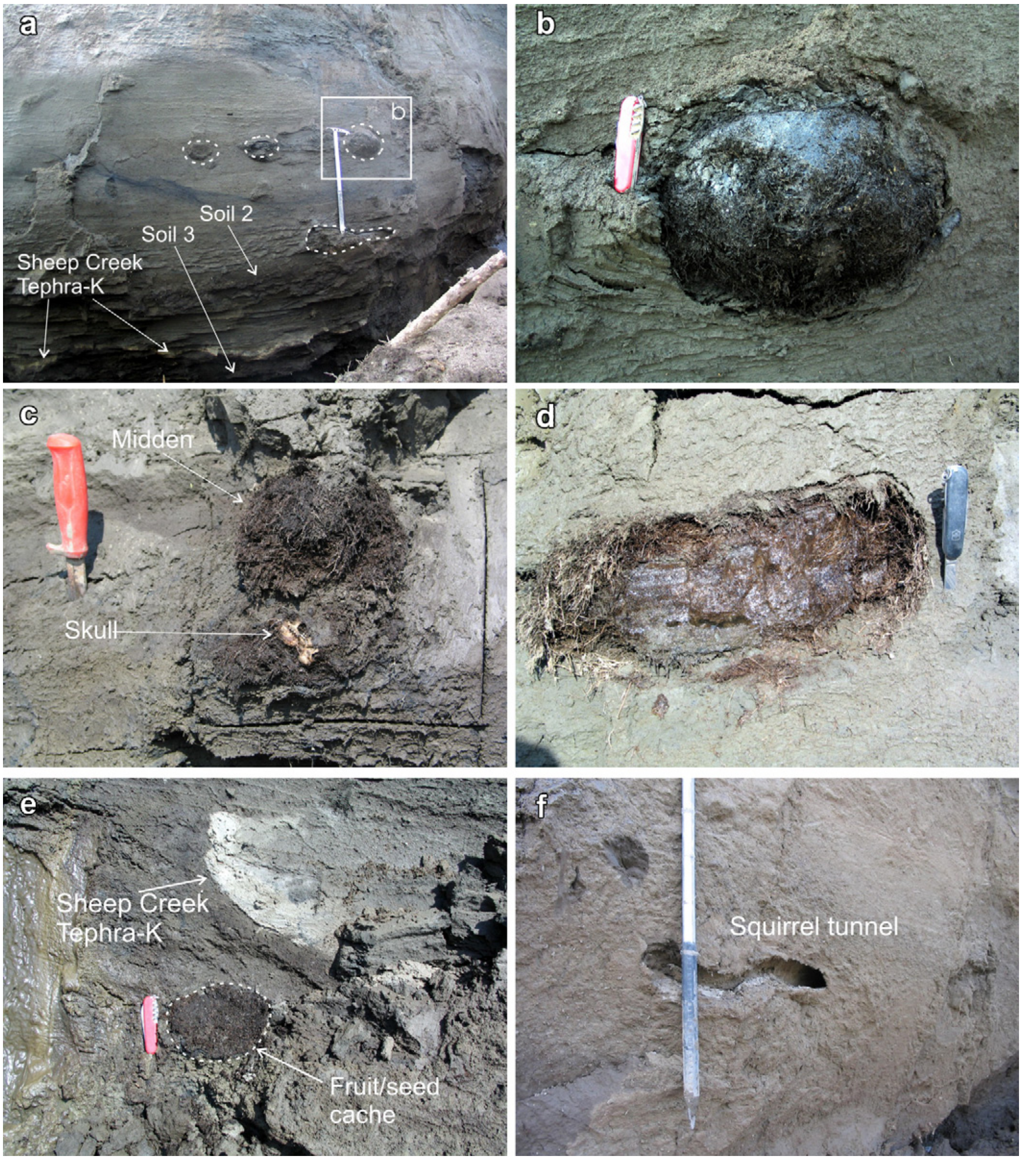

Fig. 2. Various arctic ground squirrel remains from MIS 4 sediments. a) four middens above Sheep Creek tephra – Klondike at Dominion Creek site; b) close up of frozen midden from previous photo with knife handle (9.0 cm long) for scale; c) midden with arctic ground squirrel skull at Dominion Creek site (knife handle is 10.0 cm long); d) arctic ground squirrel midden in MIS 4 loess at Quartz Creek (black knife handle is 9.0 cm long); e) fruit/seed cache associated with Sheep Creek tephra – Klondike at Dominion Creek site (knife handle is 9.0 cm long); f) squirrel tunnel in MIS 4 loess at Quartz Creek.

tephras occur stratigraphically above fossil forest beds and organic-rich deposits correlated with the final substage of the last interglacial, likely MIS 5a (Westgate et al., 2005, 2008; Froese et al., in preparation). Based on this chronology, loessal paleosols and arctic ground squirrel middens associated with these tephra correlate with the onset of glacial conditions during early MIS 4 (Early Wisconsinan). Two middens recovered stratigraphically above SCt-K at Quartz Creek date to $>42\,000\,^{14}$C yr BP (Beta – 202422; Beta – 203420) and are consistent with an MIS 4 age.

Within the MIS 4 loess deposits at Dominion Creek and Quartz creek, paleosols and other stratigraphic features provide information on substrates and environmental conditions associated with arctic ground squirrel middens. Three distinct paleosols occur within the loess (Fig. 4; Sanborn et al., 2006). Pedological characteristics suggest more mesic conditions with substantial cryoturbation in the lowermost Soils 2 and 3 (Fig. 4), with generally decreasing moisture stratigraphically upwards and limited cryoturbation in the upper part of the sequence (Soil 1 and above). At Dominion Creek, ice-wedges that are 1–2 m in width disrupt the two lowermost loessal soils, but do not extend as far stratigraphically as Soil 1. Soil 1 probably formed under loess accretion in more xeric conditions than Soil 2 or 3 and is most similar to MIS 2 paleosols associated with Dawson tephra (Sanborn et al., 2006). At Dominion Creek and at an additional site at nearby Whitman Creek (Froese et al., 2003), sand wedges and sandsheets cap the MIS 4 loess-paleosol sequence. Taken together, tephra, loess sediments and paleosols at these sites record increasing aridity during the transition from late MIS 5a through MIS 4. However, soil active layers must have been thicker and better drained than modern throughout the loess/paleosol sequence as evidenced by the abundance of fossil ground squirrel middens (Sanborn et al., 2006; Zazula et al., 2007).

3.2. Midden plant macrofossils

Plant remains from the middens are dominated by miscellaneous vegetative material that includes graminoid foliage nesting

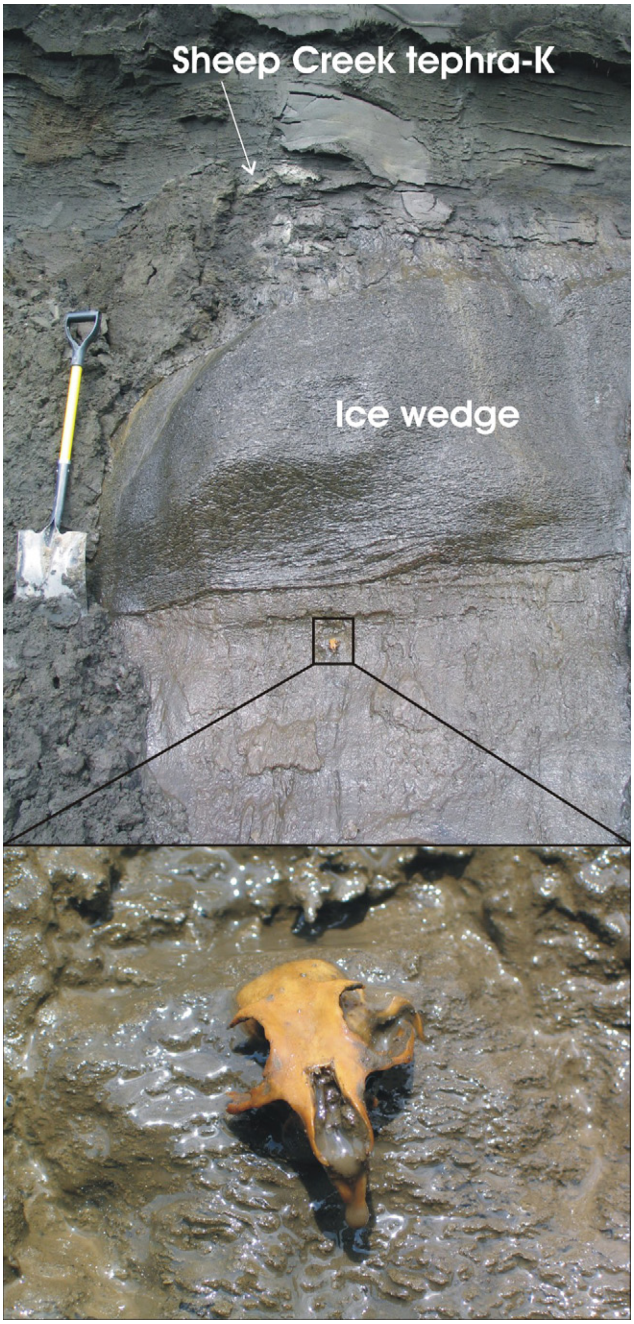

Fig. 3. Fossil arctic ground squirrel cranium recovered within ice-rich silt underneath ice-wedge and Sheep Creek tephra – Klondike.

material (mean RAI mid-point = 50.05, STDV = 33.62). Midden sample sizes vary considerably, with mass ranging from 2.4 to 215 g (mean = 41.84 g, STDV = 44.93). This wide size range reflects the fact that sometimes we were only able to recover partial middens from the exposures. Plant macrofossils from the MIS 4 middens include at least 45 taxa (Table 1) representing 24 families, dominated by forbs (36 taxa), with three kinds of Poaceae (grass), at least two species of dwarf willows (*Salix* cf. *arctica* and *Salix* cf. *polaris*), and one tree (*Picea* spp.; Zazula et al., 2006c; see Figs. 5–7 in Zazula et al., 2007). Several taxa were consistently abundant and frequent in the midden samples (% of samples where taxon present; mean RAI mid-point; maximum RAI), including *Poa* sp. (84.4%; 8.95; 6), *Draba* sp. (75.0%; 11.79; 6), *Potentilla* sp. (73.4%; 5.01; 4), *Salix* spp. (51.6%; 3.58; 5), *Kobresia myosuroides* (50.0%; 3.06; 3), and *Erysimum* cf. *cheiranthoides* type (43.8%; 11.63; 6). Some taxa were recovered frequently, but in low abundance such as *Ranunculus eschscholtzii-sulphureus* type (45.3%; 1.06; 3) and *Elymus* sp. (43.8%, 0.41; 2). Some rare taxa were only recovered from one (*Juncus* sp., *Saxifraga* sp., *Astragalus alpinus*, *Achillea* sp.) or two (*Myosotis alpestris*, *Parnassia* sp.) middens.

3.3. Midden insects

Insect fossils were recovered from 37 out of 64 middens (Table 2). Coleoptera dominated the midden insect fauna, representing at least 7 families. Of these, ground beetles (Carabidae) were the most diverse with at least 9 taxa, including *Amara alpina* and *Pterostichus* (*Cryobius*) species. Weevils (Curculionidae) occur most frequently with *Lepidophorus lineaticollis* recovered from 13 samples (max MNI = 4) and *Connatichela artemisiae* recovered from 9 samples (max MNI = 3). Fly puparia (Diptera) were recovered from 14 samples (max MNI = 4).

There were sufficient numbers of ground and rove beetle species to yield Mutual Climatic Range (MCR) estimates of seasonal temperatures. Our estimate of mean July temperature (TMAX) for the MIS 4 assemblages is 10–10.5 °C. This is about 5 °C colder than modern TMAX at Dawson City (the nearest meteorological station to the study sites). This estimate is similar for Klondike fossil beetle assemblages associated with Dawson tephra and early MIS 2 (Zazula et al., 2006a, 2007). We estimate that mean January temperatures (TMIN) were −16 to −15 °C, which is about 10 °C warmer than modern TMIN at Dawson City. TMIN MCR estimates are poorly constrained (Elias et al., 1996), but our estimate may still be taken to indicate some degree of winter warming, compared to the modern, highly continental climate of interior Yukon.

4. Interpretations

4.1. Reconstructed paleoenvironments for early MIS 4 in west-central Yukon

Plant macrofossils from the middens provide evidence for the onset of cold, dry conditions and establishment of steppe-tundra vegetation during early MIS 4. Macrofossils indicate this vegetation was rich in graminoids (*Elymus* sp., *Poa* sp., *Festuca* sp., *K. myosuroides*, *Carex* spp.), diverse forbs (*Thalictrum alpinum*, *Bupleurum americanum*, *Draba* sp., *E.* cf. *cheiranthoides*, *Phlox hoodii*) and prairie sagebrush (*Artemisia frigida*). Remains of xerophilous steppe plants, such as *A. frigida*, *P. hoodii*, *Androsace septentrionalis* and *Plantago* cf. *canescens* suggest that soils were well-drained and frequently disturbed. The presence of the weevil *C. artemisiae* provides further evidence for the local abundance of prairie sagebush (*A. frigida*) on the early MIS 4 landscape. Plants such as *Alopecurus* sp., *Lloydia serotina*, *Bistorta vivipara* and *T. alpinum* are more typical of present-day mesic to well-drained tundra. This vegetation has compositional and functional affinities to both present low arctic or alpine well-drained tundra (Edwards and Armbruster, 1989; Wesser and Armbruster, 1991; Walker and Everett, 1991; Lloyd et al., 1994; Walker et al., 2001) and azonal steppe vegetation (Laxton et al., 1996; Vetter, 2000). In terms of the present-day biogeographic affinities of these plants, this vegetation is best described as a hybrid between steppe and herbaceous tundra, and thus we use the term “steppe-tundra”.

Steppe-tundra vegetation probably occupied well-drained, xeric to mesic substrates on upland habitats developed under cold and arid glacial conditions with active loess aggradation (Sanborn et al., 2006). Since arctic ground squirrels preferably burrow, construct their nests and hibernate about 1 m below the surface (Buck and Barnes, 1999), plant remains within the fossil middens reflects vegetation that occupied former surfaces stratigraphically above

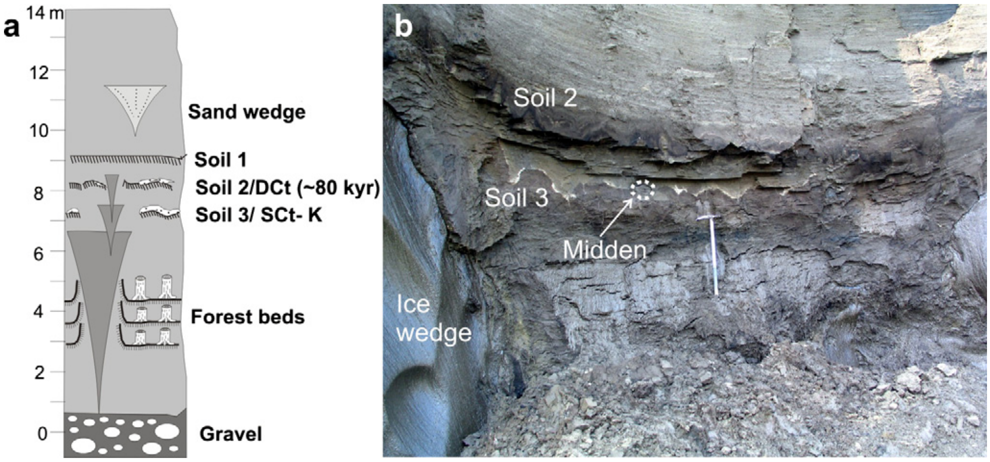

Fig. 4. a) Lithostratigraphy of MIS 4 deposits at Dominion Creek site showing association of Sheep Creek tephra – Klondike (SCT-K) and Dominion Creek tephra (DC-t) with three distinct generations of ice-wedges and paleosols; b) overview of loess-paleosol stratigraphy at Dominion Creek.

the middens. As such, the midden vegetation data probably reflects the environment associated with the upper well-drained paleosol (Soil 1), rather than the more mesic conditions suggested by the lower paleosols (Soils 2, 3) (Fig. 4; Sanborn et al., 2006). The steppe-tundra formed a mosaic that also included dwarf willow shrubs in more mesic microhabitats and rare spruce trees that were probably confined to sheltered valley bottoms (see Zazula et al., 2006c).

The fossil insect assemblages from these samples are similar in composition, and we treat them here as a single assemblage for the paleoenvironmental reconstruction. Interpretation of a cryoxeric steppe-tundra for early MIS 4 based on plant macrofossils is supported by fossil weevils such as *L. lineaticollis* and *C. artemisiae* which are well-established members of the MIS 2 fauna from Eastern Beringia (Matthews and Telka, 1997; Zazula et al., 2006a, 2007). In addition, there are clear indicators of mesic to moist tundra in this fauna, including *Pterostichus ventricosus* and members of the *Cryobius* group of the genus *Pterostichus*. But, the greatest beetle diversity is among taxa associated with dry herbaceous vegetation (*A. alpina*, *Dicheirotrichus cognatus*, *Harpalus alaskensis*, *Harpalus amputatus*, and *Harpalus opacipennis*). The pill beetles of the genus *Morychus* (including *Morychus* sp. in North America and *Morychus viridis* in Asia) are additional indicators of steppe-tundra environments in both Eastern and Western Beringia during the Pleistocene (Elias et al., 2000; Kuzmina and Sher, 2006). *M. viridis* is an important inhabitant of extant cryoxerophilous sedge steppe communities in Siberia (Berman, 1990; Berman et al., in this volume). The taxonomic status and ecology of its closest relative in Eastern Beringia is less clear, however, because the species is probably extinct. We can presume that *Morychus* species in both areas played a similar ecological role during Pleistocene cold stages because they are recorded as fossils synchronously across Beringia, while becoming virtually extirpated during interglacials (Berman, 1990; Berman et al., in this volume). As evidenced by the midden insect fossils, the environments in the vicinity of the ground squirrel nests appear to have been a mixture of more mesic tundra, perhaps in poorly drained valley bottoms, and arid steppe-tundra on better-drained hill slopes. This reconstruction is supported by paleobotanical evidence from the squirrel middens.

4.2. Comparison between Late and Early Wisconsinan midden records

Fossil arctic ground squirrel middens from MIS 3/2 and MIS 4 are compositionally different in several ways, although both assemblages provide evidence for steppe-tundra communities. Even though there were fewer MIS 3/2 midden samples (48), they contained a greater diversity of plant taxa than the larger MIS 4 midden record (64 samples); there were at least 60 taxa recovered in the MIS 3/2 middens, while only 45 are present in the MIS 4 samples (Table 1). Some plant taxa recovered within the MIS 3/2 record are conspicuously absent from MIS 4 middens. Interestingly, some taxa that are absent from the MIS 4 samples but present in MIS 3/2 middens are important ecological indicators of alkaline (*Suaeda* cf. *calceoliformis*), disturbed (*Lappula* sp.) or steppe habitats (*Anemone patens* var. *multifida*, *Penstemon gormanii*). Further, some grasses (*Deschampsia ceaspitosa*, *Alopecurus* sp., and *Hierochloë hirta* ssp. *arctica*) and other taxa (*Conioselinum cnidiifolium*, cf. *Spiraea beauverdiana* and *Sanguisorba* sp.) typically associated with mesic and/or riparian habitats are also absent in the MIS 4 record.

4.2.1. Multiple Response Permutation Procedure

The MRPP demonstrates that there are highly significant differences between the MIS 4 and MIS 3/2 midden assemblages (Table 3). The MRPP test statistic is very low (−15.6844) with high significance ($P < 0.00001$). These results are supported by the apparent pattern of separation of MIS 3/2 and MIS 4 on the scatterplot of sites in the NMS ordination (Figs. 5–7). However, the low MRPP *A* value (0.03156) indicates that there is high within group heterogeneity in the data.

4.2.2. Indicator Species Analysis

The ISA demonstrates that some taxa are significantly more abundant and frequent in either the MIS 3/2 or MIS 4 middens (Table 4). However, the ecological importance of these results may be difficult to assess. There are several significant indicator taxa for MIS 3/2, including *Carex* sp. (lenticular type), *B. vivipara*, *Cerastium* sp., *Stellaria* cf. *calycantha*, and *Ranunculus pensylvanicus-macounii* type. The analysis only revealed *Salix* spp., *B. americanum* and *T. alpinum* as significant indicators for MIS 4 middens. These species are present during both time intervals and are expected within steppe-tundra vegetation developed under cold, dry Pleistocene conditions. Some possible vegetation differences revealed in our ISA are the significance of *Carex* spp. (including *Carex albo-nigra*) remains in MIS 3/2 middens and *Salix* spp. (dwarf species including *S.* cf. *polaris* and *S.* cf. *arctica*) remains during MIS 4. This result may be taken to suggest a greater proportion of *Carex* spp. during MIS 3/2 and dwarf willow ground cover at our sites during early MIS 4.

Table 1
Plant macrofossil data from MIS 4 and MIS 3/2 middens (after Zazula, 2006, 2007).

Vascular Plants	MIS 4 middens				MIS 3/2 middens		Ecology
	Number of middens where taxon present (n, %)	Mean RAI mid-point	Standard deviation	Maximum RAI	Number of middens where taxon present (n, %)	Mean RAI mid-point	
Pteropsida							
Gymnosperma							
Equiseticaeae							
Equisetum cf. *palustre* L. (sheath)	$n = 0$, 0%	na	na	na	$n = 1$, 2.1%	0.01	Wet meadows, lakeshores, woods, shallow waters
Pinaceae							
Picea sp. (needle)	$n = 3$, 4.7%	0.02	0.11	1	$n = 2$, 4.2%	0.02	Forests, treeline
Angiosperm*a*							
Poaceae							
Deschampsia caespitosa (L.) Beauv, (florets)	$n = 0$, 0%	na	na	na	$n = 17$, 35.4%	1.41	Wet meadows, lakeshores, gravel bars
Elymus sp. (floret, spikelet, glumes) incl. *Elymus trachycaulus* (Link) Gould ex Shinners	$n = 28$, 43.8%	0.41	0.80	2	$n = 29$, 60.4%	0.83	Open slopes, well-drained, riverbanks
Festuca sp. (floret, spikelets)	$n = 15$, 23.4%	0.56	2.12	3	$n = 17$, 35.4%	0.93	Sandy, gravelly, tundra, open slopes, dunes, lakeshores, woodlands
Hierchloë hirta (Schrank) Borba ssp. *arctica* G. Weim (florets, spikelets)	$n = 0$, 0%	na	na	na	$n = 6$, 12.5%	0.11	Sandy stream banks, lakeshores, meadows
Alopecurus sp. (floret)	$n = 0$, 0%	na	na	na	$n = 7$, 14.6%	0.45	Shallow ponds, wet meadows
Poa sp. (floret, spikelets)	$n = 54$, 84.4%	8.95	19.04	6	$n = 42$, 87.5%	7.28	Open slopes, tundra, stream banks
Cyperaceae							
Carex sp. (lenticular achene)	$n = 14$, 21.9%	0.43	2.05	3	$n = 42$, 87.5%	4.43	Moist, stream sides, shorelines, meadows
Carex sp. (trigonous achenes)	$n = 4$, 6.3%	0.07	0.39	2	$n = 8$, 16.7%	0.19	Moist, stream sides, shorelines, meadows
Kobresia myosuroides (Vill.) Fiori & Paol. (achenes, spike fragments)	$n = 32$, 50.0%	3.06	5.71	3	$n = 23$, 47.9%	3.13	Dry locations, calcareous, heath, ridges
Juncaeae							
Juncus sp. (seeds, capsules)	$n = 1$, 1.6%	0.01	0.06	1	$n = 5$, 10.4%	0.43	Wet meadows, arctic-alpine, river flats, borders of ponds, lakes, streams
Liliaceae							
Llyodia serotina (L.) Rchb.	$n = 3$, 4.7%	0.02	0.11	1	$n = 2$, 4.2%	0.02	alpine tundra, rocky, polygonal ground, heaths
Salicaceae							
Salix sp. (capsules, buds, twigs, leaf fragments) incl. *S. polaris*, *S. arctica*	$n = 33$, 51.6%	3.58	9.76	5	$n = 17$, 35.4%	0.92	
Salix cf. *arctica* Pall.	[a]	[a]	[a]	[a]	[a]	[a]	Dry tundra, heath, sedge meadows
Salix cf. *polaris* Wahlenb.	[a]	[a]	[a]	[a]	[a]	[a]	Not too dry tundra, late snowbeds, scree slopes
Polygonaceae							
Bistorta vivipara (L.) Delarbre (bulbils)	$n = 10$, 15.6%	1.79	6.04	4	$n = 30$, 62.5%	7.06	Turfy, rocky, moist grassy herbmats, manured places
Rumex acetosa L. (achenes, calyx)	$n = 0$, 0%	na	na	na	$n = 3$, 6.3%	0.03	Moist alpine or subalpine meadows
Chenopodiaceae							
Chenopodium sp. (seeds)	$n = 3$, 4.7%	0.06	0.38	2	$n = 1$, 2.1%	0.01	Disturbed situations, often halophytic
Suaeda cf. *calceoliformis* (Hook.) Moq. (seeds, bracts)	$n = 0$, 0%	na	na	na	$n = 8$, 16.7%	0.14	Alkaline flats
Caryophyllaceae							
Cerastium sp. (seeds, capsules)	$n = 16$, 25.0%	1.15	5.14	3	$n = 29$, 60.4%	1.15	Rocky, gravelly or sandy, alpine tundra to heath to meadows
Minuartia sp. (seeds)	$n = 5$, 7.8%	0.04	0.14	1	$n = 3$, 6.3%	0.14	Alpine tundra, snowbeds, gravelly, dry open slopes
Silene involucrata (Cham.&Schlecht.) Bocquet (seeds, capsules)	$n = 5$, 7.8%	0.32	2.03	3	$n = 2$, 4.2%	0.02	Stony, gravelly, river terraces
Silene taimyrensis (Tolmatchev) Bocquet (seeds, capsules)	$n = 26$, 40.6%	2.25	4.96	3	$n = 28$, 58.3%	1.83	Sandy and rocky open slopes and cliffs
Silene uralensis (Rupr.) Boquet (seeds)	$n = 0$, 0%	na	na	na	$n = 2$, 4.2%	0.02	Moist alpine slopes and meadows, dunes, seepages

Table 1 (*continued*)

Vascular Plants	MIS 4 middens				MIS 3/2 middens		Ecology
	Number of middens where taxon present (*n*, %)	Mean RAI mid-point	Standard deviation	Maximum RAI	Number of middens where taxon present (*n*, %)	Mean RAI mid-point	
Stellaria cf. *calycantha* (Ledeb.) Bong. (seeds, capsules)	*n* = 9, 14.1%	0.07	0.18	1	*n* = 18, 37.5%	0.34	Alpine tundra, meadows, riverbanks, dry slopes
Ranunculaceae							
Anemone narcissflora L. s.l. (winged achenes)	*n* = 0, 0%	na	na	na	*n* = 6, 12.5%	0.06	Woods and heaths to tundra
Anemone patens var. *multifida* Pritzel, L. (achenes)	*n* = 0, 0%	na	na	na	*n* = 2, 4.2%	0.43	Sandy well-drained
Ranunculus eschscholtzii-sulphureus type (achenes)	*n* = 29, 45.3%	1.06	2.26	3	*n* = 38, 79.2%	4.35	Moist alpine meadows, herbmats
Ranunculus pensylvanicus-macounii type (achenes)	*n* = 3, 4.7%	0.27	2.00	3	*n* = 29, 60.4%	6.74	
Thalictrum alpinum L. (achenes)	*n* = 12, 18.8%	0.73	2.86	3	*n* = 2, 4.2%	0.07	Alpine herbmats
Papaveraceae							
Papaver sp. (seeds, capsules) incl. *Papaver mcconnellii* Hultén (and *Papaver keelei* A.E. Porsild only in MIS 4)	*n* = 7, 10.9%	0.78	3.40	3	*n* = 15, 31.3%	1.88	Gravelly sandy soil, tundra
Brassicaceae							
Draba sp. (seeds, silicles) incl. *Draba cinerea* Adams, *Draba fladnizensis* Wulfen	*n* = 48, 75.0%	11.79	20.80	6	*n* = 34, 70.8%	8.82	Calcareous rocky barrens and sunny cliffs, rocky, gravelly alpine slopes
Erysimum cf. *cheiranthoides* L. (seeds, siliques)	*n* = 28, 43.8%	11.63	25.19	6	*n* = 24, 50.0%	8.54	Moist turfy places, disturbed situations, lakeshores, creek banks
Eutrema edwardsii R. Br. (seeds)	*n* = 4, 6.3%	0.11	0.53	2	*n* = 8, 16.7%	0.97	Not too dry tundra, heath, calciphile
Lepidium densiflorum Schrad.(seeds, silicles)	na	na	na	na	*n* = 10, 20.8%	1.18	Dry open, disturbed soils
Saxifragaceae							
Parnassia sp. (seeds)	*n* = 2, 3.1%	0.02	0.09	1	*n* = 12, 25.0%	0.50	Moist meadows, along streams, lakeshores
Saxifraga cf. *razshivinii* Zhmylev (seeds)	*n* = 1, 1.6%	0.05	0.38	2	*n* = 7, 14.6%	0.13	Gravelly, rocky, alpine, turfy tundra, herbmats, often calcareous
Rosaceae							
Potentilla sp. not *Potentilla palustris*, *Potentilla norvegica*, *Potentilla fruiticosa* (achenes, aggregate)	*n* = 47, 73.4%	5.01	10.02	4	*n* = 38, 79.2%	3.93	Gravelly, sandy, open slopes, alpine tundra
Sanguisorba sp. (winged achenes)	*n* = 0, 0%	na	na	na	*n* = 9, 18.8%	0.15	Riverbanks to alpine slopes
cf. *Spiraea beauverdiana* Scneid. (seeds, follicles)	*n* = 0, 0%	na	na	na	*n* = 1, 2.1%	0.01	Borders of muskeg, alpine and subalpine meadows and dry slopes
Fabaceae							
Astragalus alpinus L. (seed, legume)	*n* = 1, 1.6%	0.01	0.06	1	na	na	Grassy slopes, heath, moraine, riverbeds
Astragalus eucosmus Robins. (seeds, legumes)	*n* = 14, 21.9%	1.58	5.76	4	*n* = 13, 27.1%	0.14	Gravelly, stony slopes, meadows
Apiaceae							
Bupleurum americanum Coult. & Rose (carpels)	*n* = 14, 21.9%	1.36	4.31	3	*n* = 4, 8.3%	0.42	Alpine meadows, moist sand, gravel, scree
Conioselinum cnidiifolium (Turcz.) A.E. Porsild (carpels)	*n* = 0, 0%	na	na	na	*n* = 6, 12.5%	0.39	Sandy riverbanks, gravelly slopes, wet meadows.
Primulaceae							
Androsace septentrionalis L. (seeds, capsules)	*n* = 22, 34.4%	0.61	2.11	3	*n* = 17, 35.4%	1.03	Dry calcareous, gravelly, disturbed
Gentianaceae							
Gentiana cf. *algida* Pall. (seeds, capsules)	*n* = 7, 10.9%	0.34	2.03	3	*n* = 13, 27.1%	0.67	Alpine meadow, tundra, heath, calcareou.
Gentiana cf. *prostrata* Haenke (seeds, capsules)	*n* = 14, 21.9%	1.48	8.09	5	*n* = 20, 41.7%	0.90	Moist arctic or alpine tundra, meadows, banks of streams or lakes
Gentianella type (seeds, capsules)	*n* = 8, 12.5%	0.42	2.08	3	*n* = 6, 12.5%	0.06	Tundra slopes, heath, stream banks

(*continued on next page*)

Table 1 (*continued*)

Vascular Plants	MIS 4 middens				MIS 3/2 middens		Ecology
	Number of middens where taxon present (*n*, %)	Mean RAI mid-point	Standard deviation	Maximum RAI	Number of middens where taxon present (*n*, %)	Mean RAI mid-point	
Polemoniaceae							
Phlox hoodii Richards. (seeds, capsules, leaves)	$n=28$, 43.8%	0.70	2.12	3	$n=19$, 39.6%	0.30	Dry prairies and foothills
Polemonium sp. (seeds, capsules)	$n=8$, 12.5%	0.59	2.82	3	$n=13$, 27.1%	1.61	Moist humus, alpine meadows, tundra turf, sand dunes, grassy slopes
Boraginaceae							
Lappula cf. *anisacantha* (Turcz. ex Bunge) Guerke. (nutlets)	$n=0$, 0%	na	na	na	$n=5$, 10.4%	0.16	Dry, disturbed habitats
Mertensia sp. (nutlets)	$n=0$, 0%	na	na	na	$n=6$, 12.5%	0.06	Woodlands to tundra, riverbanks
Myosotis alpestris Schm. (nutlets)	$n=2$, 3.1%	0.02	0.09	1	$n=12$, 25.0%	0.33	Moist tundra, late snow patches, sandy banks
Scrophulariaceae							
Castilleja sp. (seeds, capsules)	$n=0$, 0%	na	na	na	$n=2$, 4.2%	0.07	Upland tundra, stony slopes, meadows, heath, riverbanks
Pedicularis cf. *lapponica* (seeds, capsule)	$n=3$, 4.7%	0.02	0.11	1	$n=8$, 16.7%	0.62	Dry to moist tundra, heath, calcareous
Penstemon gormanii Greene (capsule whole, seeds)	$n=0$, 0%	na	na	na	$n=8$, 16.7%	0.08	Dry, gravelly, disturbed soils
Plantaginaceae							
Plantago cf. *canescens* Adams (seeds, capsules)	$n=14$, 21.9%	0.75	2.86	3	$n=15$, 31.3%	1.45	Alkaline meadows
Asteraceae							
Aster/Erigeron type (achenes)	$n=6$, 9.4%	0.05	0.15	1	$n=6$, 12.5%	0.17	Slopes, meadows, river flats, open areas
Achillea sp. (achenes)	$n=1$, 1.6%	0.01	0.06	1	$n=2$, 4.2%	0.02	
Artemisia frigida Willd. (flowers, leaves)	$n=23$, 35.9%	1.87	11.13	6	$n=18$, 37.5%	0.51	Steep open slopes, dry, disturbed
Hieracium type (achenes)	$n=0$, 0%	na	na	na	$n=11$, 22.9%	0.49	Alpine meadows, open areas
Taraxacum ceratophorum (Ledeb.) DC. s.l. (achenes, clusters)	$n=23$, 35.9%	2.66	9.57	3	$n=28$, 58.3%	1.56	Woodland and heath to tundra
Miscellaneous vegetation (nesting material)	$n=64$, 100%	50.05	33.62	6	$n=48$, 100%	47.25	Mostly graminoid leaves, stems

na = no data available (taxon not present).

[a] Present but not quantified.

4.2.3. Non-metric Multidimensional Scaling

The NMS identified a three dimensional optimal solution (Figs. 5–7). The solution is strong as the correlations (r^2) between the distances in the final solution and the distances in the *n*-dimensional species space are 0.272, 0.183, and 0.246 for the first, second and third axes, respectively. This gives a cumulative r^2 of 0.702, indicating that most of the variance structuring the dataset has been accounted for. In general, there is a large amount of overlap between samples of the two time intervals, which is especially evident between Axis 1 and 2 (Fig. 5) but some samples from each time interval show clear differences. However, according to the analysis, samples from MIS 3/2 separate well from the MIS 4 samples in species space along all three axes. Axis 1 appears to separate samples with large amounts of *Cerastium* sp. ($r = -0.574$; $r^2 = 0.329$), *S. taimyrensis* ($r = -0.524$; $r^2 = 0.274$), and *Ranunculus eschscholtzii-sulphureus* type ($r = -0.416$; $r^2 = 0.173$) from those with large amounts of *E.* cf. *cheiranthoides* ($r = -0.560$; $r^2 = 0.313$). Because *Cerastium* sp. and *Ranunculus eschscholtzii-sulphureus* type are significant indicators for MIS 3/2 taxa, Axis 1 seems to separate samples from the two time intervals (Fig. 5). Axis 2 appears to separate middens with large amounts of *Draba* sp. ($r = 0.695$; $r^2 = 0.483$) from the rest of the dataset. Since *Draba* sp. is abundant and frequent in middens from both time intervals, and is not a significant indicator taxon, it is difficult to assess the ecological meaning of Axis 2 (Fig. 6). Axis 3 appears to separate middens with large amounts of *Draba* sp. ($r = -0.493$; $r^2 = 0.243$) and *Ranunculus pensylvanicus-macounii* type ($r = 0.425$; $r^2 = 0.181$) from those with high amounts of *E.* cf. *cheiranthoides* ($r = 0.686$; $r^2 = 0.471$) (Fig. 7). The separation of significant indicator taxa is also most apparent on Axis 3, where the MIS 4 indicators (*Salix* spp., *T. alpinum*, and *B. americanum*) cluster distinctly from MIS 3/2 indicators (e.g., *B. vivipara*, *Ranunculus pensylvanicus-macounii* type, and *Deschampsia caespitosa*). The separation of indicator species from each time interval in ordination space supports the MRPP result of significant differences between the MIS 3/2 and MIS 4 midden assemblages.

5. Discussion

5.1. The Early Wisconsinan (MIS 4) glacial environments of Beringia

MIS 4 or the Early Wisconsinan cold stage (~ 90–56 ka) is recorded in $\delta^{18}O$ marine records as a time of pronounced Northern Hemisphere glaciation and global sea-level fall, although of lesser magnitude than MIS 2 (Martinson et al., 1987). However, local ice advances were more extensive during MIS 4 than MIS 2 in many areas of Beringia, including; Chukotka Peninsula (Brigham-Grette, 2001), Seward Peninsula (Kaufman et al., 1996), southwest Alaska (Kaufman et al., 2001), western Alaska Range (Briner et al., 2005); Yukon Tanana Upland, (Weber, 1986; Briner et al., 2005) the Brooks

Table 2
Insects recovered from MIS 4 middens.

Taxon	Number of middens where taxon is present	Maximum MNI per midden	Ecology
Ord. Coleoptera			
Fam. Carabidae			
Bembidion sp.?	1	1	Mostly riparian species
P. (*Cryobius*) *ventricosus* Esch.	1	1	On both forest and tundra up to the High Arctic; in forest on riverbanks under leaves, on tundra on moist soil
Pterostichus (*Cryobius*) sp.	1	1	Mostly on moist tundra; in forest on open boggy places and riverbanks
Pterostichus (Cryobius) sp.?	1	1	
Amara alpina Payk.	5	2	Mostly on dry tundra among herbaceous vegetation; in taiga near tree limit on meadow. One of the most common tundra species today
Dicheirotrichus (*Trichocellus*) *cognatus* Gyll.	1	1	Circumpolar, mostly in forest, but may occur in coastal tundra, on open, dry places, sandy soil with sparse vegetation
Harpalus alaskensis Lth	1	1	On dry tundra with sandy slopes and sparse herbaceous vegetation with *Artemisia*
H. (*Harpalomerus*) *amputatus* Say	1	2	Found south of the tundra, on dry sandy grassland
Harpalus opacipennis Hald	1	2	Found south of the tundra, on rather dry ground with sparse vegetation
Carabidae indet	2	2	
Fam. Staphylinidae			
Olophrum consimile Gyll.?	1	1	Widely distributed Holarctic riparian species, mostly boreal, but single sites also in tundra, in leaf litter (*Alnus* and *Salix*)
Philonthus duplicatus Bern&Sch.	1	1	Boreal species, live in leaf litter or carrion woods, prey on mycophagous flies
Fam. Scarabaeidae			
Aphodius albertanus Brown?	1	1	North of North America, boreal
Fam. Byrrhidae			
Morychus sp.	3	1	Probably an undescribed species associated with tundra-steppe fossil assemblages; most *Morychus* beetles live today on dry soils with thin moss cover
Fam. Chrysomelidae			
Chrysolina basilaris (Say)	1	1	Rocky Mountains from Colorado to British Columbia, northern Yukon, common in the Pleistocene steppe-tundra community
Galeruca rudis (LeC.)	1	1	From Yukon Territory to California, on lupines
Fam. Curculionidae			
Lepidophorus lineaticollis Kby	13	4	In tundra on dry sandy soil with poor vegetation, in forest zone on open dry places, common on steppe-like patches. One of the most common Pleistocene beetles in the American Arctic
Connatichela artemisiae And.	9	3	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
Connatichela artemisiae And.?	2	1	
Vitavitus thulius Kiss.?	1	1	Only on tundra, on dry open ground, common in the Pleistocene, rare now
Fam. Cicadellidae			
Leafhopper	1	1	In meadows
Ord. Hymenoptera			
parasitic wasps	4	2	
Ord. Lepidoptera			
Caterpillar	1	1	
Ord. Diptera			
Fly	6	6	
Fly puparia	13	4	Indicates rather wet conditions
Insect varia			
Larvae	1	3	

Table 3
Results of the MRPP testing the null hypothesis of no significant difference in composition between MIS 3/2 and MIS 4 middens. Average distance is the mean Sørensen's distance between each pairwise combination of middens from each particular time interval: *N* is the number of middens samples in each time interval. The observed delta is calculated from the data while the expected delta is derived from a null distribution; *T* is the MRPP test statistic, and *A* is the chance corrected within-group agreement. The MRPP was significant ($P < 0.00001$).

Time interval	Average distance	*N*	MRPP statistics
MIS 3/2	0.67926	48	Observed delta = 0.69794
MIS 4	0.71195	64	Expected delta = 0.72068 $T = -15.6844$, $A = 0.03155$, $P < 0.00001$

Ranges (Hamilton, 1994; Briner et al., 2005) and the St. Elias mountains of southern Yukon (Ward et al., 2008). The collective MIS 4 geologic record suggests that glaciations in Beringia are asynchronous with global ice volume, likely the result of greater moisture availability during MIS 4 since lower MIS 2 sea levels may have drove Beringian moisture sources much further away from the interior (Brigham-Grette, 2001). Regardless of the glacial geologic record, the aeolian stratigraphic record of loess and sandsheets in the Klondike supports the notion of an arid-continental, full-glacial climate during MIS 4 in the interior of Eastern Beringia.

Little is known about ecosystems of Eastern Beringian during Pleistocene cold stages prior to MIS 2. Several sites in central Alaska contain loess deposits correlated with the MIS 4 cold stage, though paleoecological data are limited (Begét, 2001). Only two Alaskan lakes contain sediments with pollen records that extend back to MIS 4; Imuruk Lake on the Seward Peninsula (Colinvaux, 1964, 1996) and Squirrel Lake in northwest Alaska (Anderson, 1985, Berger and Anderson, 2000). Both of these lacustrine records reveal a return to "herb tundra" vegetation following the last interglacial (MIS 5e). Unfortunately, the limited taxonomic detail and age uncertainties with these two lacustrine records hinder detailed interpretations about the structure and composition of MIS 4 vegetation or how it relates compositionally to MIS 2 communities.

In central Yukon, new dates on SCt-K (Westgate et al., 2005, 2008) indicate that organic-rich silt (loess) overlying Reid glacial deposits at the Ash Bend locality (Hughes et al., 1987; Westgate et al., 2001) records the MIS 5/4 transition. Schweger's (2003) pollen record from Ash Bend documents the transition between spruce dominated dense boreal forest during the last interglacial (MIS 5) to forest-tundra (Zone I), birch shrub tundra (Zone II) and then herb tundra (Zone III) associated with glacial conditions of early MIS 4. Importantly, pollen-spectra immediately below and above the SCt-K contain only 5 and 2% *Picea* with 18 and 5% *Betula*, respectively, and the assemblages are dominated by Cyperaceae, Poaceae, and *Artemisia*. Thus, in central Yukon during the MIS 5/4 transition, pollen data suggests that SCt-K fell on forest-tundra

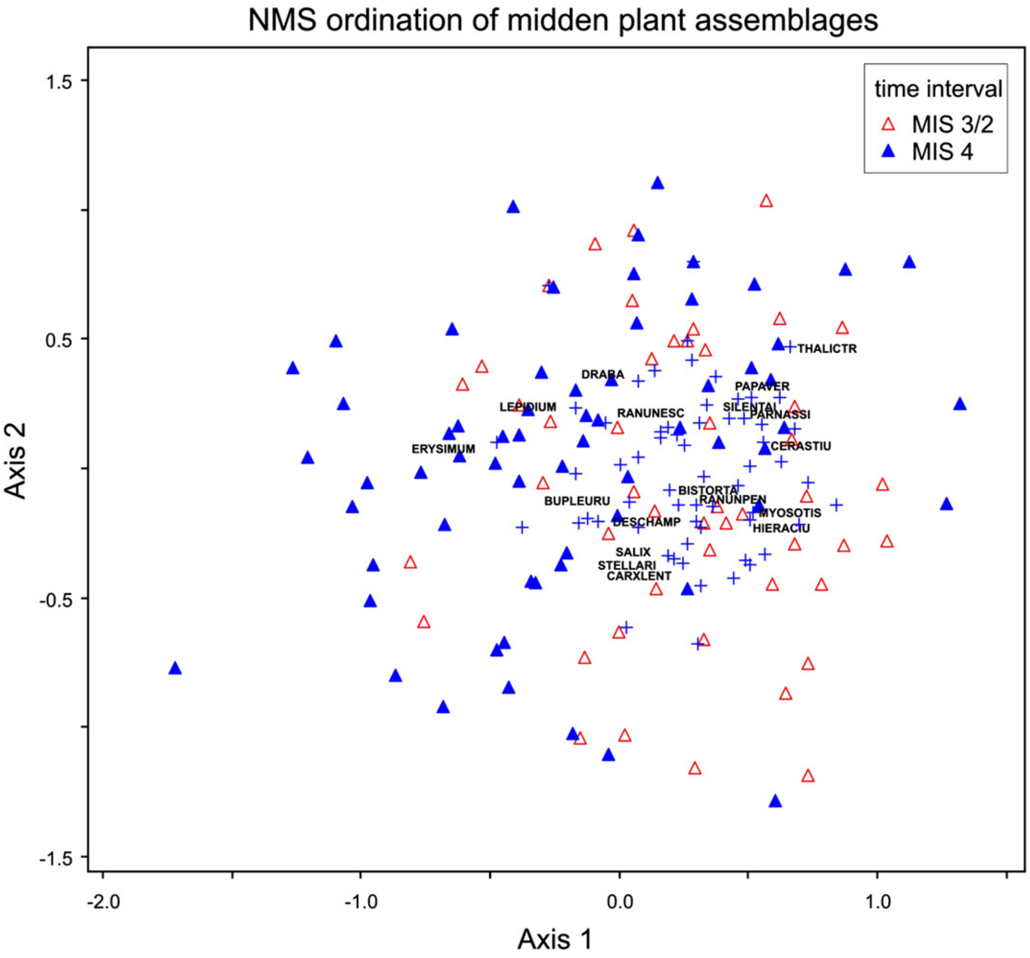

Fig. 5. NMS ordination of all midden samples and plant taxa on Axis 1 and 2. Blue triangles represent MIS 4 samples. Red triangles represent MIS 3/2 samples. Blue crosses represent plant taxa. Axis 1 appears to separate samples with abundant *Cerastium* ($r = -0.574$; $r^2 = 0.329$), *Silene taimyrensis* ($r = -0.524$; $r^2 = 0.274$), and *Ranunculus eschscholtzii-sulphureus* type ($r = -0.416$; $r^2 = 1.73$) from those with abundant *Erysimum* cf. *cheiranthoides* ($r = 0.560$; $r^2 = 0.313$). Axis 2 appears to separate middens with abundant *Draba* ($r = 0.695$; $r^2 = 0.483$) with the rest of the dataset.

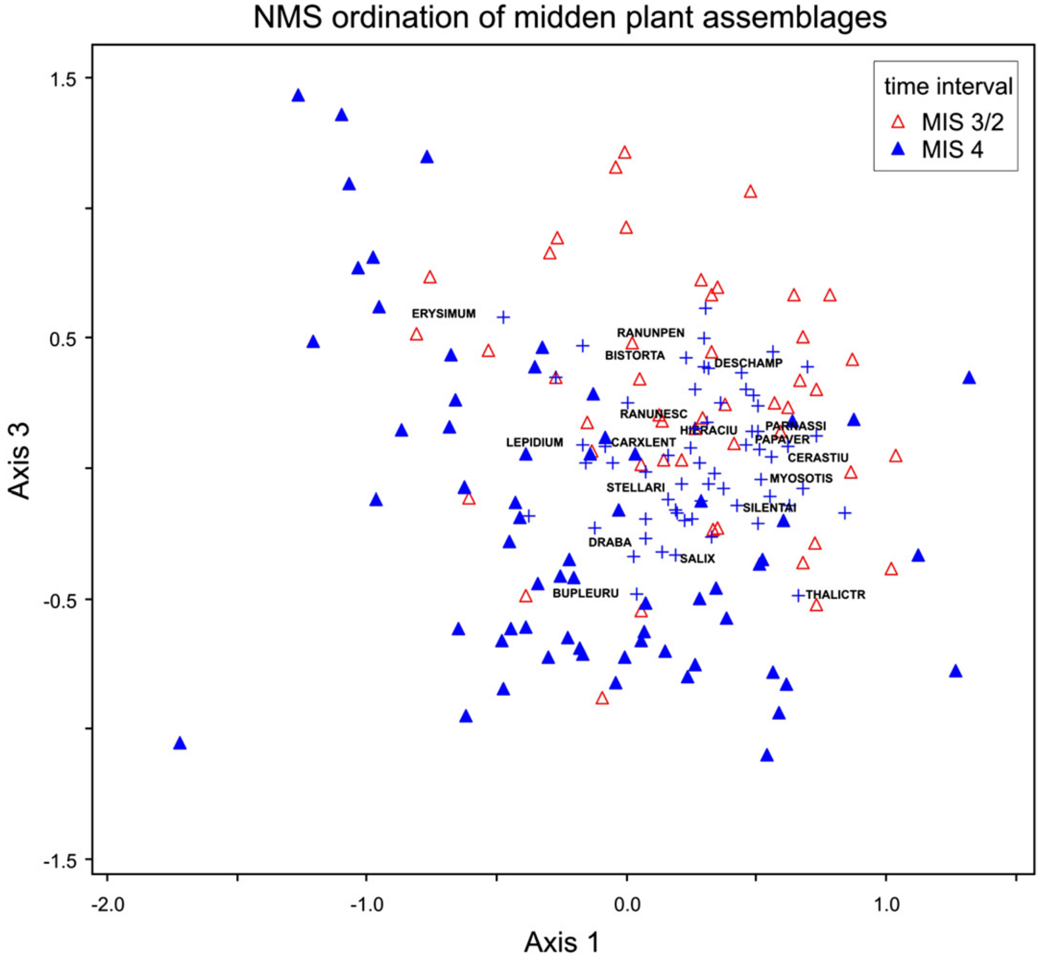

Fig. 6. NMS ordination of all midden samples and plant taxa on Axis 1 and 3. Blue triangles represent MIS 4 samples. Red triangles represent MIS 3/2 samples. Blue crosses represent plant taxa. Axis 1 appears to separate samples with abundant *Cerastium* ($r = -0.574$; $r^2 = .329$), *Silene taimyrensis* ($r = -0.524$; $r^2 = 0.274$), and *Ranunculus eschscholtzii-sulphureus* type ($r = -0.416$; $r^2 = 1.73$) from those with abundant *Erysimum* cf. *cheiranthoides* ($r = 0.560$; $r^2 = 0.313$). Axis 3 appears to separate middens with abundant Draba ($r = 0.493$; $r^2 = 0.243$) and *Ranunculus pensylvanicus-macounii* type ($r = 0.425$; $r^2 = 0.181$) from those with abundant *Erysimum* cf. *cheiranthoides* ($r = 0.686$; $r^2 = 0.471$). The seperation of taxa identifies as significant in the Indicator Species analysis is most apparent on Axis 3, where the MIS 4 indicators (*Salix*, *Thalictrum alpinum*, and *Bupleurum americanum*) cluster towards the bottom distinctly from MIS 3/2 indicators (e.g. *Bistorta vivipara*, *Ranunculus pensylvanicus-macounii* type, and *Deschampsia caespitosa*) which cluster towards the top.

ecotonal vegetation that may have resembled extant birch shrub tundra communities near latitudinal treeline (Schweger, 2003). This vegetation was replaced by herb or steppe-tundra more typical of full-glacial conditions during early MIS 4. This pollen inferred moisture gradient at Ash Bend through the MIS 5/4 transition is similar to evidence for increasing aridity during this interval based on loess paleosols in the Klondike (Sanborn et al., 2006). Further, the reconstructed steppe-tundra from the Klondike arctic ground squirrel middens is probably correlative to Schweger's (2003) herb-zone pollen-spectra (Pollen Zone III) from Ash Bend.

5.2. Steppe-tundra during two successive Late Pleistocene glacial intervals

Although our multivariate analyses indicate that floristic composition of MIS 3/2 middens differ statistically from those of MIS 4, these distinctions may not be very important for the overall paleoenvironmental reconstruction. Differences revealed by our multivariate analyses of plant remains are more likely the result of minor differences in cache foraging activity in relation to site specific differences in vegetation (see Gillis et al., 2005a; Zazula et al., 2006b), rather than substantial differences in zonal vegetation composition or structure (i.e. steppe-tundra). As such, the multivariate results suggest that the midden contents may be highly influenced by foraging upon dense concentrations of particular plants that produce relatively large numbers of seeds and fruits in close proximity to individual arctic ground squirrel burrows (e.g. *E.* cf. *cheiranthoides*, *Draba* sp., *Cerastium* sp., *Ranunculus* spp.). Most of the plant taxa indicative of steppe-tundra vegetation are common between the MIS 3/2 and MIS 4 middens (Table 1) as suggested by the high overlap in samples revealed in the NMS (especially Axis 1 and 2 as demonstrated in Fig. 5), though they may differ in frequency and abundance (Zazula et al., 2007). Plant taxa shared between the two time intervals include graminoids (*Elymus* sp., *Poa* sp., *Festuca* sp., *K. myosuroides*), prairie sagebrush (*A. frigida*), diverse forbs (*Draba* sp., *E.* cf. *cheiranthoides*, *Potentilla* sp., *S. taimyrensis*, *P.* cf. *canescens*, *P. hoodii*), dwarf shrubs (*S.* cf. *polaris*, *S.* cf. *arctica*) and rare conifers (*Picea* spp.). The co-occurrence of many of the important steppe-tundra indicator plants suggests that that vegetation was probably compositionally and structurally similar during the onset of both major glacial intervals of the Late Pleistocene. This overall similarity is consistent with evidence from loessal paleosols (Sanborn et al., 2006) and insect faunas which are dominated by *L. lineaticollis* and *C.*

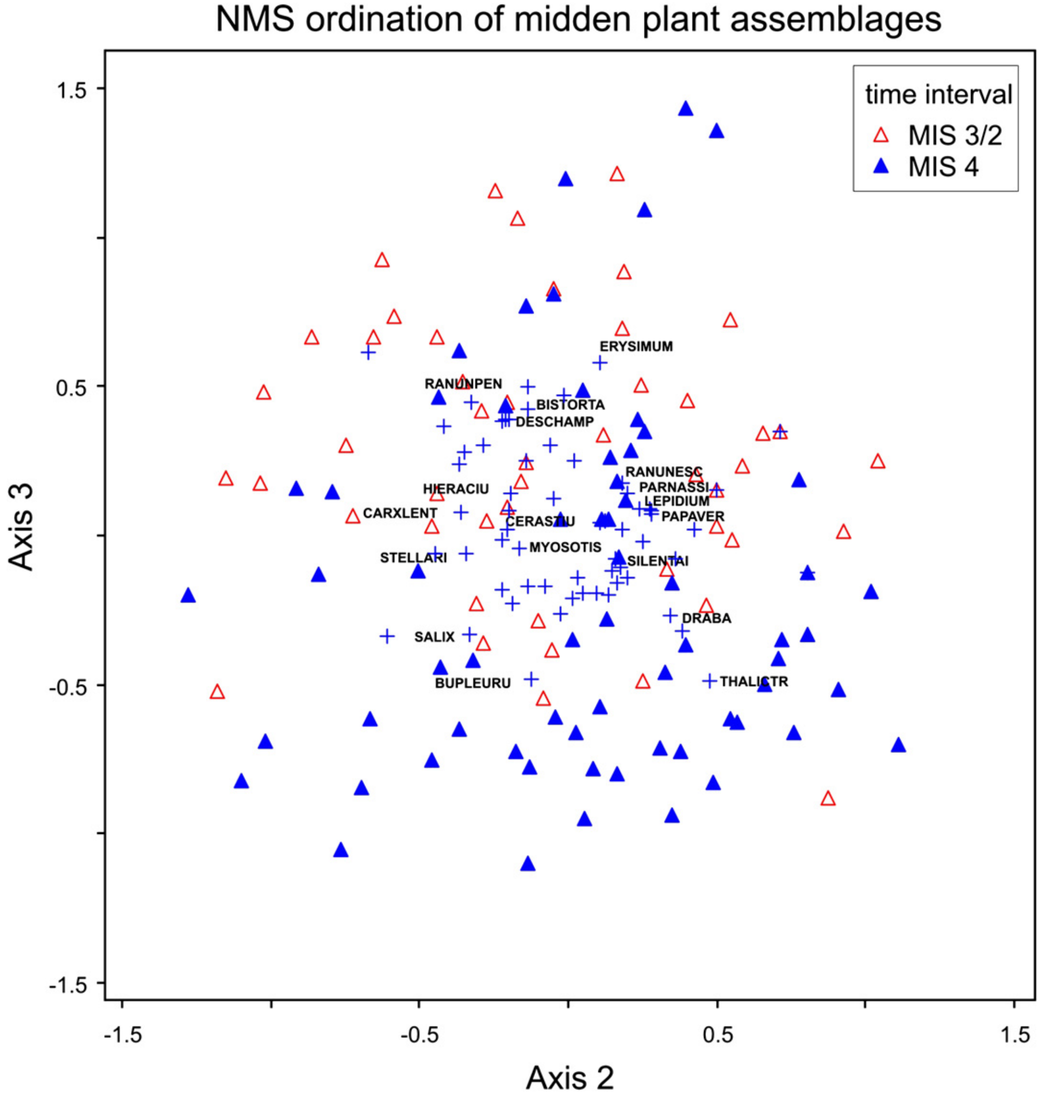

Fig. 7. NMS ordination of all midden samples and plant taxa on Axis 2 and 3. Blue triangles represent MIS 4 samples. Red triangles represent MIS 3/2 samples. Blue crosses represent plant taxa. Axis 2 appears to separate middens with abundant *Draba* ($r = 0.695$; $r^2 = 0.483$) with the rest of the dataset. Axis 3 appears to separate middens with abundant *Draba* ($r = 0.493$; $r^2 = 0.243$) and *Ranunculus pensylvanicus-macounii* type ($r = 0.425$; $r^2 = 0.181$) from those with abundant *Erysimum* cf. *cheiranthoides* ($r = 0.686$; $r^2 = 0.471$). The separation of taxa identifies as significant in the Indicator Species Analysis is most apparent on Axis 3, where the MIS 4 indicators (*Salix*, *Thalictrum alpinum*, and *Bupleurum americanum*) cluster towards the bottom distinctly from MIS 3/2 indicators (e.g. *Bistorta vivipara*, *Ranunculus pensylvanicus-macounii* type, and *Deschampsia caespitosa*) which cluster towards the top.

artemisiae. MCR paleotemperature reconstructions for MIS 3/2 (Zazula et al. 2006a) and MIS 4 suggest that growing season temperatures were similar, characterized by reductions of about 5 °C. The growth of extensive glaciers in the northern Cordillera during MIS 4 and MIS 2 would have resulted in a reduction of moisture sources and increased continentality in the interior of Alaska and Yukon.

5.3. Glacial and interglacial refugia

Much research in Beringia has focused on the concept of “glacial refugia” with aim to reconstruct the composition of past communities and distribution of arctic species during the most recent Pleistocene cold stage (Hopkins et al., 1982). A recent synthesis of refugia theory by Rull (2009) provides a critical distinction between the concepts of glacial refugia and “interglacial refugia”. This distinction is rooted in the notion that the Earth has been effected by glaciation, or at least interstadial conditions that are colder than present, for most (~80%) of the Pleistocene (Ehlers and Gibbard, 2004). As such, glacial or interstadial conditions associated with Pleistocene cold intervals are considered to represent the climatic “norm” for many organisms, while interglacial conditions, such as the Holocene epoch, may be viewed as temporary “disturbances” that glacial-adapted organisms endured by migrating to suitable habitats (Rull, 2009). During the most recent glacial cycle, species that could not endure the transition to the present interglacial by establishing themselves within interglacial refugia became extinct or locally extirpated.

Beringia was a glacial refugium for arctic species during Pleistocene cold periods when much of northern North America was covered by continental ice (Hultèn, 1937; Hopkins et al., 1982). Conversely, small, disjunct habitats within the zonal environment of present-day Beringia serve as interglacial refugia for glacial-adapted species. These interglacial refugia in Beringia are generally characterized as “microrefugia”, which are often small diffuse areas and result in highly fragmented populations for many glacial-

Table 4
Indicator and randomized indicator values for species that are significant ($P < 0.05$) indicators of one of the two time intervals in the midden dataset.

Time interval	Species	Indicator value	Randomized indicator value	*P*-value
MIS 3/2 (~24–29^{14}C ka BP)	*Carex* sp. (lenticular achenes)	76.7	29.6	0.0010
	Bistorta vivipara	48.9	22.2	0.0010
	Cerastium sp.	40.5	24.5	0.0030
	Ranunculus eschscholtzii-sulphureus type	54.0	34.3	0.0010
	Ranunculus pensylvanicus-macounii type	58.5	18.3	0.0010
	Deschampsia caespitosa	35.4	10.8	0.0010
	Stellaria cf. *calycantha*	26.9	15.9	0.0100
	Parnassia sp.	23.8	9.4	0.0010
	Myosotis alpestris	22.8	9.3	0.0010
	Hieracium type	22.9	7.9	0.0010
	Lepidium densiflorum	20.8	7.2	0.0010
	Papaver sp.	21.8	13.4	0.0070
MIS 4 (~82 kyr)	*Salix* spp. (dwarf)	36.1	27.1	0.0300
	Thalictrum alpinum	16.5	9.4	0.0190
	Bupleurum americanum	17.0	11.5	0.0410

adapted arctic and alpine species. Interglacial refugia represent at least partial structural and functional analogues to conditions that were formerly widespread and continuous across the former habitat range for these species during glacial intervals. A good example is the arctic/alpine dwarf shrub *Dryas octopetala* which has populations that are highly fragmented as a result of enduring numerous glacial and interglacial cycles, a complex post-glacial history and reliance on specific microhabitats (Max et al., 1999; Skrede et al., 2006). Rull's concept of interglacial refugia for arctic organisms that are adapted to glacial conditions provides a valuable framework for reconstructing past glacial environments in Beringia and for understanding present-day biogeographic patterns of steppe-tundra vegetation, and associated fauna such as arctic ground squirrels.

5.4. Arctic ground squirrel adaptations

> *This squirrel is best adapted to carry on the life processes of feeding, hibernating and evading enemies in areas where permafrost is several feet below the surface of the ground* (Bee and Hall, 1956: 47).

Present-day arctic ground squirrel populations range in distribution from northeast Siberia across mainland northern North America to Hudson Bay (Figs. 8 and 9; Nadler and Hoffmann, 1977). However, within this geographic range, their populations are highly fragmented, and largely confined to well-drained alpine and arctic tundra or open areas within the boreal forest (Fig. 8). This patchy distribution and restriction to suitable azonal habitats indicates that the species is confined at present within interglacial refugia. There is a conspicuous absence of arctic ground squirrels in the dense boreal forest of interior Alaska and Yukon at present (Nadler and Hoffmann, 1977; Kurtén and Anderson, 1980; Fig. 9). This zone of absence separates the northern populations (*S. parryii* ssp. *parryii*) from the southern clade (*Spermophilus parryii plesius*) and is likely the result of Quaternary biogeographical range disruptions (Eddingsaas et al., 2004), rather than the complete lack of suitable habitat, because this zone does contain alpine ecosystems and open areas within the boreal forest. In contrast, the fossil midden record indicates that arctic ground squirrel populations were much more widespread and abundant throughout the interior of Alaska and Yukon during Late Pleistocene glacial intervals, extending well beyond their modern interglacial range, (Harington, 2003; Zazula et al., 2005, 2007).

The present-day ecology and distribution of arctic ground squirrels is informative to address how this species and some other aspects of the mammoth-steppe may have responded to Quaternary climatic-environmental oscillations in Beringia. In particular, there are three critical aspects of arctic ground squirrel ecology that must be considered in this discussion. Firstly, the present distribution of arctic ground squirrels is largely determined by the presence of permafrost because they cannot burrow into frozen soils and require well-drained substrates suitable for burrowing, nesting and successful hibernation. As such, they tend to establish their colonies in well-drained areas of alpine or arctic tundra, or dry, open meadows (Fig. 8; Bee and Hall, 1956; Carl, 1971; Nadler and Hoffmann, 1977; McLean, 1985; Buck and Barnes, 1999; Gillis et al., 2005a,b). Secondly, arctic ground squirrels are at less risk of predation in open habitats (e.g. tundra or steppe-tundra) with minimal visual obstruction because they require a clear line of site to detect predators and escape to their burrow for protection (Karels and Boonstra, 1999; Hik et al., 2001; Gillis et al., 2005b). This risk of predation resulting from vegetation cover has important implications for overall population fitness for arctic ground squirrels (Hik et al., 2001). Thirdly, arctic ground squirrels can subsist on

Fig. 8. Southwest facing slope with steppe vegetation, well-drained loessal soil and arctic ground squirrel colony in the boreal forest of southwest Yukon near Kluane Lake. These habitats are disjunctly dispersed within the boreal forest of southern Yukon and may be considered interglacial refugia for some organisms that were more widespread in Beringia during Pleistocene cold intervals (Laxton et al., 1996; Zazula et al., 2006b, 2007).

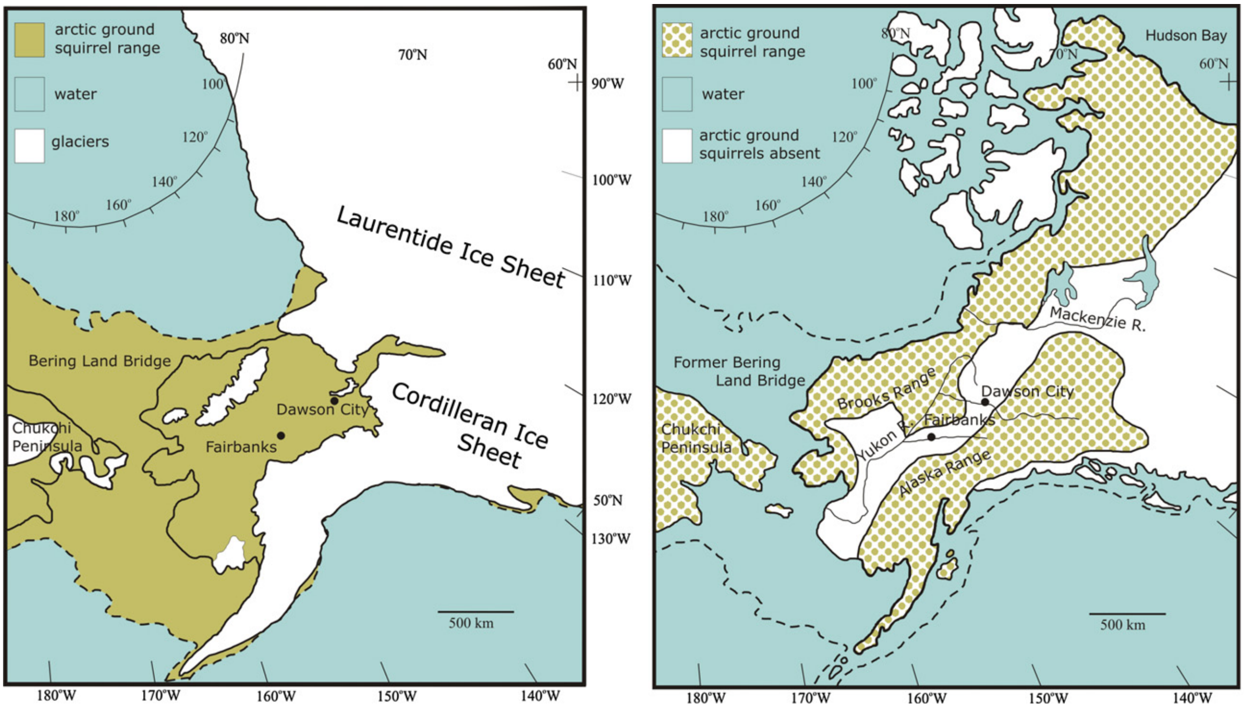

Fig. 9. Maps of Beringia demonstrating glacial vs. interglacial ranges for arctic ground squirrels in Beringia. A) Glacial Beringia. The green area is the ice free landscape that may have served as habitat for arctic ground squirrels during Pleistocene glacial conditions. Note the presence of Pleistocene arctic ground squirrels at sites near Dawson City (Klondike) and Fairbanks where they are absent at present. B) Interglacial range for arctic ground squirrels as demonstrated by their modern distribution in green (present distribution after Nadler and Hoffmann, 1977). Note the present-day absence of arctic ground squirrels in the interior of Alaska and Yukon, including Dawson City (Klondike) and Fairbanks.

a wide variety of cache food items in both boreal and tundra habitats and develop habitat or site specific cache foraging strategies (Gillis et al., 2005a,b; Zazula et al., 2006b).

5.4.1. *Arctic ground squirrels of the mammoth-steppe*

Arctic ground squirrels have a long history in Beringia and have persisted through repeated glacial—interglacial cycles (Eddingsaas et al., 2004). Fossil evidence (Storer, 2003) indicates that arctic ground squirrels have been present in Yukon since the Early Pleistocene (>740 000 yr), arriving in Eastern Beringia after divergence from ancestral Siberian populations (Nadler and Hoffmann, 1977). Divergence estimates based on mitochondrial DNA mutation rates (Eddingsaas et al., 2004) suggest a split occurred in North America between the northern and southern subspecies between 940 000 and 790 000 yr ago. Further divergence into the four geographically distinct clades occurred at the onset of major cold stages of the Middle and Late Pleistocene. Since ~80% of the Quaternary can be characterized by glacial, or at least interstadial conditions, environmental conditions of the mammoth-steppe can be considered the ecological “norm” for arctic ground squirrels.

The fossil midden record provides clear evidence for the association of arctic ground squirrels, steppe-tundra vegetation, well-drained loessal soils, and cryoxeric climates — all key ecological characteristics of the mammoth-steppe biome as envisioned by Guthrie (1990, 2001). Analysis of middens from two time periods indicate that the mammoth-steppe was successfully established during the last two major cold stages of the Late Pleistocene. Based on these data, we can reasonably extrapolate that the mammoth-steppe, complete with loess deposition, steppe-tundra expansion, widespread colonization of arctic ground squirrels, and establishment of megafaunal grazing communities also accompanied earlier Pleistocene cold stages in Beringia.

5.4.2. *Arctic ground squirrel responses to past environmental change*

Paleoecological records indicate that past interglacial boreal forests in central Alaska and Yukon were similar in composition and structure to those of today (e.g. MIS 5; Muhs et al., 2001, Hamilton and Brigham-Grette, 1991; Péwé et al., 1997; Schweger et al., in this volume). Closed boreal forests with shallow permafrost and visually obstructive vegetation are important factors that prevent the establishment of arctic ground squirrels in much of the interior today, and it is reasonable to assume that they were also locally rare or extirpated during the last interglacial (MIS 5). However, arctic ground squirrel populations were able to track the establishment of interglacial forests in the interior and migrate to disjunct interglacial microrefugia (Rull, 2009) that retained characteristics of the formerly widespread glacial mammoth-steppe (Fig. 8). Interglacial microrefugia for steppe-tundra organisms include dry alpine tundra (Edwards and Armbruster, 1989; Wesser and Armbruster, 1991; Lloyd et al., 1994; Gillis et al., 2005b), south-facing steppe-dominated slopes and meadows (Fig. 8; Laxton et al., 1996; Vetter, 2000; Guthrie, 2001) and well-drained sites in Arctic tundra (Carl, 1971; Walker and Everett, 1991; Walker et al., 2001). Given that only ~20% of Quaternary is characterized by non-glacial conditions (Ehlers and Gibbard, 2004), interglacials in Beringia can be seen as temporary disturbance intervals in the evolutionary history of arctic ground squirrels, steppe-tundra vegetation and other organisms that are adapted to cold, dry glacial environments.

Conversely, as climates cooled following the last interglacial (MIS 5/4 transition), ice sheets expanded and the continental interior of Alaska and Yukon became more arid with widespread, active loess deposition. The return to glacial conditions created nearly continuous, zonal habitat across much of Beringia for arctic ground squirrels and other glacial-adapted species in places such as

Fairbanks and the Klondike (Fig. 9). Our midden data suggests that the MIS 5 interglacial boreal forests in the interior were replaced by open steppe-tundra vegetation that expanded from disjunct interglacial microrefugia. Arctic ground squirrel populations tracked the expansion of steppe-tundra habitats from disjunct interglacial refugia back into the interior during the MIS 5/4 transition and established widespread populations on the mammoth-steppe. The expansion of arctic ground squirrel populations likely had important implications for genetic mixing and high rates of gene flow as formerly isolated interglacial populations became reunited during subsequent cold stages (Eddingsaas et al., 2004).

The widespread establishment of arctic ground squirrels during Quaternary cold stages in Beringia suggests they are ideally adapted to glacial conditions and have an evolutionary history linked to the mammoth-steppe (Eddingsaas et al., 2004). A hallmark characteristic of arctic ground squirrels has been their ability to endure the numerous climate driven expansions and retractions of the mammoth-steppe by tracking environmental changes and establishing populations in diffuse interglacial refugia during relatively brief Quaternary warm intervals. The ability to subsist on a wide variety of plants may be a key factor that enabled arctic ground squirrel populations to track these environmental fluctuations, disperse to new, sometimes sub-optimal, habitats, and maintain viable populations over glacial-interglacial time scales. Present-day interglacial microrefugia that include thriving arctic ground squirrel populations with well-drained soils, and steppe and/or herbaceous tundra vegetation should be considered at least partial relict habitats of the former glacial mammoth-steppe biome and further investigated to provide information on Pleistocene ecosystems of Beringia.

6. Conclusions

Data from arctic ground squirrel middens provides evidence for the expansion of steppe-tundra vegetation, loessal paleosols and arctic ground squirrel populations in the interior Yukon during both MIS 4 and MIS 2 glacial intervals. Their overall similarity with previously published MIS 2 middens suggests the repeated establishment of steppe-tundra and arctic ground squirrels in the Beringian interior during two successive cold stages of the Late Pleistocene. Together, this record supports Guthrie's (2001) notion that the mammoth-steppe biome responded synchronously to Quaternary climatic oscillations in the Northern Hemisphere.

This study marks another step in the use of permafrost preserved Pleistocene arctic ground squirrel middens as highly informative paleoecological archives. Here, we have extended their record back to the MIS 4 cold stage and demonstrated the local presence of steppe-tundra environments at that time. However, we believe that research on these fossil middens is truly in its infancy. Additional work should also be conducted within other regions of Beringia with well-developed loess sediment archives with aim to document additional fossil middens and expand this dataset to new areas. With the widespread application of molecular biological methods and the study of ancient DNA from permafrost preserved Pleistocene plants and animals (Shapiro and Cooper, 2003; Willerslev et al., 2003; Debruyne et al., 2008), these arctic ground squirrel middens will undoubtedly be a valuable resources to further our knowledge of Beringian paleoenvironments. DNA from the midden plant materials certainly will provide information on the evolution and phytogeographic changes for particular species that were important within Pleistocene Beringia. Furthermore, DNA extracted from skeletal and fecal remains from the arctic ground squirrels themselves may provide valuable insight to test models of their evolution and adaptations to Quaternary climate change.

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