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Research Article

Latest Pleistocene (17,500–13,500 cal yr BP) Arctic ground squirrel (Sciuridae: *Urocitellus parryii*) middens record late persistence of steppe-tundra in central Yukon Territory

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Abstract

This paper presents the palaeoecological analysis of five latest Pleistocene (17,500–13,500 cal yr BP) Arctic ground squirrel (*Urocitellus parryii*) middens from three sites in the Klondike goldfields of central Yukon Territory. Plant and invertebrate macrofossil records were represented by 24 and 20 taxa, respectively, providing a record of the local environment and the earliest known occurrences in Yukon Territory for several taxa (e.g., the robber fly [*Lasiopogon* sp.] and marsh yellowcress [*Rorippa* cf. *palustris*]). The plant and invertebrate assemblages indicate the persistence of steppe-tundra to at least 13,680 cal yr BP by the preservation of taxa typically occupying dry sites, many of which remain components of grasslands and south-facing azonal steppe communities in present-day Yukon Territory. In the context of shrub expansion that is documented to have occurred by 14,000 cal yr BP in interior Alaska, we consider the taphonomic biases associated with Arctic ground squirrel middens that may lead to the lack of shrub macrofossils preserved at the sites. Our study provides an ecologically unique and chronologically constrained perspective on the local persistence of steppe-tundra in easternmost Beringia despite the regional expansion of shrubs.

Introduction

Arctic ground squirrel (*Urocitellus parryii* Richardson) nests and caches (middens) from Pleistocene deposits are important palaeoenvironmental archives in Beringia. Early observations of fossil burrows and nesting sites were reported from Siberia, Alaska, and the Yukon (Porsild et al., 1967; Kaplina et al., 1978; Pirozynski et al., 1984; Harington, 1984, 2003; Guthrie, 1990; Gubin and Khasanov, 1996), but their palaeoecological value remained largely undetermined until recently. Systematic research on middens and caches intensified in the early 2000s. Zazula et al. (2005, 2007, 2011), working in the Klondike region of Yukon Territory, conducted detailed analyses of more than 100 fossil middens associated with dated tephra deposits, primarily from Marine Isotope Stage (MIS) 4 (~80 ka) and early MIS 2 (~30,000–24,000 ^{14}C yr BP). These studies revealed that the middens contain well-preserved remains of plants, insects, arvicoline rodents, and even mummified Arctic ground squirrels that detail the ecology of full-glacial ecosystems from the region.

There is a consensus on the regional geography (spanning western Europe to Yukon Territory), timing (125–15 ka; Guthrie 2001), and zonal ecology of the mammoth steppe biome (as a cold, arid grassland-forb ecosystem). However, there are considerably fewer data from plant and invertebrate macrofossil records, which currently limits our understanding of local-scale ecosystems across Beringia. These middens provide palaeoenvironmental records with strong taxonomic resolution of local-scale ecosystems during cold stages of the Pleistocene.

Our study focuses on the record of latest Pleistocene environments preserved in Arctic ground squirrel middens. We report palaeoecological data from five middens dating from ~17,500 to 13,500 cal. yr BP, from near the height of the last glacial maximum (LGM) through the amelioration of the late glacial. These middens are ~10,000 yr younger than the youngest analysed nests and middens in Zazula et al. (2007), and ~4000 yr younger than those in Gaglioti et al. (2011). These middens present the last records of Pleistocene Beringia through the lens of Arctic ground squirrels.

Study area

We collected five middens from three sites in the Klondike goldfields of central Yukon Territory and on the traditional territories of the Tr'ondëk Hwëchin First Nation (Fig. 1). This region has remained ice-free during periods of continental glaciation and was the easternmost portion of a widespread steppe-tundra ecosystem that covered an area of land from western Eurasia to northwest North America. This steppe-tundra ecosystem was dominated by herbaceous vegetation, had a cold and arid climate, and deep permafrost active layers (Guthrie 2001). Comparatively,

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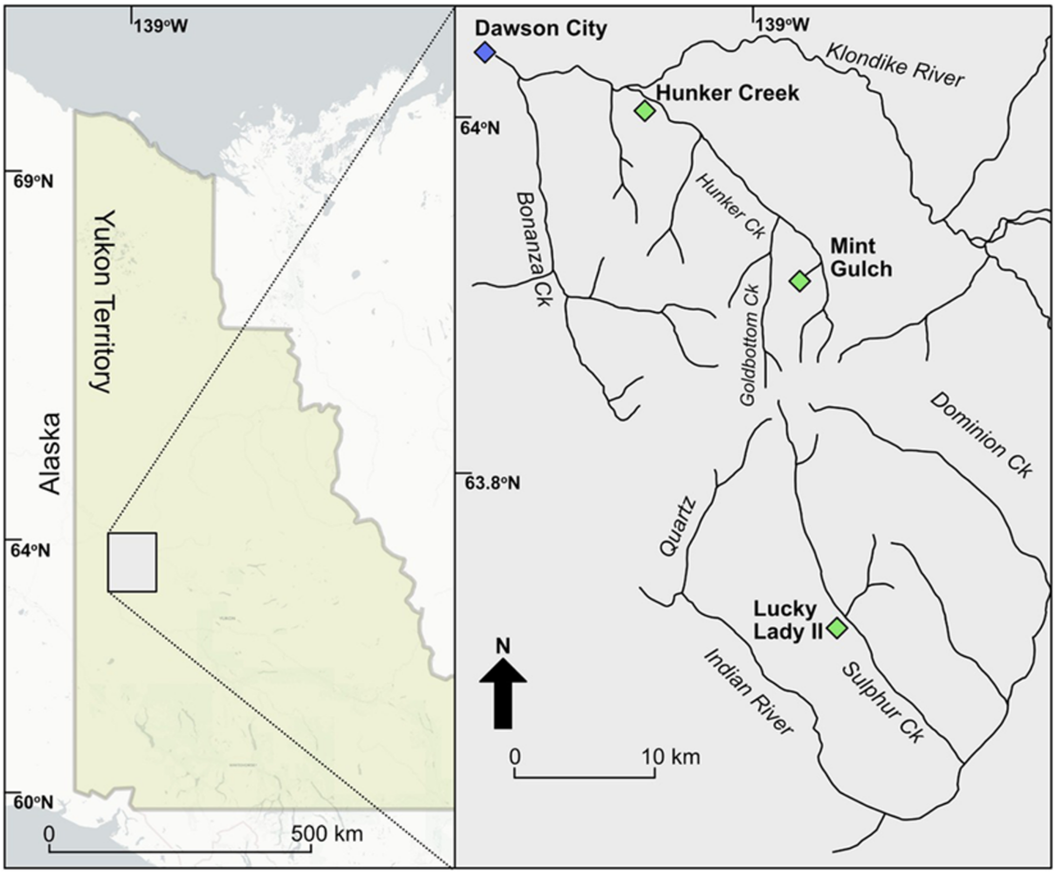

Figure 1. Map of Klondike goldfields with the Hunker Creek, Mint Gulch, and Lucky Lady II study sites indicated.

the Klondike goldfields are now characterised by shallow permafrost active layers covered in black spruce (*Picea mariana*), ericaceous shrubs, and mosses and are not presently inhabited by Arctic ground squirrels. All three study sites fall within the extensive discontinuous permafrost zone (Heginbottom et al., 1995) and the Northern Cordilleran High Boreal ecoclimatic region (Strong 2013). Our sites are located on active placer gold mines with ice-rich loess deposits on east- and/or north-facing exposures. The Hunker Creek site (64.015°N, 139.15°W) is located ∼14.5 km east-southeast of Dawson City, the Mint Gulch site (63.56°N, 139.542°W) is ∼29 km southeast of Dawson City, and the Lucky Lady II site (63.729°N, 139.121°W) is located ∼46 km south-southeast of Dawson City (Fig. 1).

Prior studies of Arctic ground squirrels across Pleistocene Beringia

Arctic ground squirrel middens are a rich source of plant (Lopatina and Zanina 2006; Gaglioti et al., 2011; Zanina et al., 2011; Langeveld et al., 2018), small mammal (Cocker et al., 2024), and invertebrate remains (Zazula et al., 2007; Cocker et al., 2025a, 2025b). They are composed of leaves and stems of graminoids (grass-like material including grasses, sedges, and rushes) that were used as nesting material, along with caches of seeds and fruits that are found in between the nest and the hibernaculum wall. Some middens are almost entirely composed of seeds and fruits and probably represent separate food caches without associated nests. Caches commonly contain thousands or tens of thousands of individual fruits and seeds from a variety of plants. Ancient midden plant assemblages contain graminoids (*Poa, Elymus, Festuca, Carex*, and *Carex myosuroides*), forbs (e.g., *Bistorta vivipara, Artemisia frigida, Ranunculus* spp., *Phlox hoodii*), dwarf shrubs (e.g., *Salix* cf. *arctica, S.* cf. *polaris*), and rare tree remains (*Picea* spp.), indicating the squirrels foraged within a local mosaic ecosystem dominated by steppe-tundra (Zazula et al., 2007). Other middens contain invertebrate remains that are dominated by common Pleistocene steppe-tundra taxa such as the weevils *Lepidophorus lineaticollis* and *Connatichela artemisiae* that support the palaeoecological interpretations based on plant macrofossils.

Arctic ground squirrel middens have also been recovered from permafrost deposits in Siberia. Gubin et al. (2001, 2003) and Lopatina and Zanina (2006) examined the composition and palaeoecological significance of fossil rodent burrows in late Pleistocene ice-rich deposits. Middens from west Beringia (Siberia) contain graminoid-rich nests, seed/fruit caches, fertile plants capable of regeneration, insects, and the mummified remains of Arctic ground squirrels (e.g., Gubin et al., 2001; Lopatina and Zanina, 2006; Zanina et al., 2011; Yashina et al., 2012; Faerman et al., 2017). These middens, primarily from northeast Siberia, record late Pleistocene environments during the MIS 3-2 transitional period. Middens dating to MIS 3 cryopedoliths provide a unique insight into the local environment due to the syngenetic nature of permafrost preservation. Plant macrofossil records from these middens indicate a vegetation mosaic of open larch woodlands with steppe-tundra meadows. In addition to larch (*Larix cajanderi*) seeds, an open woodland environment is inferred by the shrub birch (*Betula fruticosa*; syn. *B. divaricata*), procumbent shrubs (e.g., *Arctous alpina*), and alpine tundra grasses (e.g., *Poa pratensis* subsp. *alpigena*; syn. *Poa alpigena*). Steppe environments are also preserved by the presence of taxa like *Silene stenophylla, S. orientalimongolica* (syn. *Lychnis sibirica*), and *Poa attenuata* (Lopatina and Zanina 2006; Zanina et al., 2011). Zanina et al. (2011) also reports subfossil beetles from the middens that are dominated by dung beetles (*Aphodius* sp.), but also yield specimens of steppe-tundra taxa such as pill beetles (*Morychus viridis*) and weevils (*Stephanocleonus eruditus*) in addition to tundra species of ground beetles (e.g., *Dicheirotrichus mannerheimi*) and leaf beetles (e.g., *Chrysolina septentrionalis*).

Arctic ground squirrels can provide insight into changes in underlying permafrost conditions in the region (Buck and Barnes, 1999; Zazula et al., 2005, 2007, 2011). Permafrost active-layer depths can vary in response to several factors, including vegetation cover, air temperature, aspect, and snow cover (e.g., Zhang et al., 1997; Fisher et al., 2016). The widespread steppe-tundra vegetation of Pleistocene Beringia, dominated by graminoids and forbs, likely promoted deeper active layers through increased summer insolation and winter heat loss (Guthrie, 2001; Zazula et al., 2005). Modern Arctic ground squirrels require active layers at least 1 m deep or absence of permafrost for burrowing and hibernation (Buck and Barnes, 1999). In Yukon Territory, their current distribution reflects these requirements, occurring in open meadows, north-facing slopes, and alpine areas (Hik et al., 2001; Gillis et al., 2005a, 2005b; McLean, 2018). Arctic ground squirrels are now regionally extinct (extirpated) from the Klondike goldfields due to poorly drained soils with shallow active layers that prevent burrow construction (Zazula et al., 2005, 2007).

Although there are rich records of middens from MIS 4 and MIS 3/2 deposits, only two middens from Alaska have been analysed (Gaglioti et al., 2011) from MIS 2 sensu stricto, at the height of the LGM, when global sea levels and Northern Hemisphere temperatures were at a minimum (Clark et al., 2009; Porter et al., 2016; Farmer et al., 2023). Additionally, no middens or their contents have been reported from post-LGM sites in Beringia.

Latest Pleistocene shrub expansion in eastern Beringia

The transition from steppe-tundra to shrub tundra in east Beringia initiated around 15,000 cal yr BP. A regional expansion of mesic taxa occurred in response to rising sea levels, reduced sea-ice cover, and enhanced precipitation in response to a shift in atmospheric circulation. The emergent shrub tundra was characterized predominantly by woody shrubs, particularly willow (*Salix*) and birch (*Betula*), which are indicative of increased moisture availability (Monteath et al., 2021). These woody shrubs would have been accompanied by a diverse understory of herbaceous taxa. The establishment of shrub tundra reflects a fundamental reorganisation and extinction of the mammoth steppe ecosystem, marking a shift towards a more structurally complex and thermophilous vegetation community. Even though we understand the nature of this transition, establishing reliable chronologies for latest Pleistocene palaeoenvironmental records remains the most consistent barrier to detailed reconstructions of steppe-tundra collapse and the expansion of shrubs. Monteath et al. (2021) reanalysed 15 lacustrine sediment records from eastern Beringia that were deemed to have chronologies reliable enough to constrain the timing of late Pleistocene shrub expansion. The study concluded that by 14,000 cal yr BP, shrub birch (*Betula*) had expanded across and covered most of Alaska except for a delayed arrival at higher-elevation sites and the eastern regions more proximal to the continental glaciers in Yukon Territory (Murchie et al., 2021b; Monteath et al., 2023).

In interior Alaska, shrub expansion is expected to have occurred by at least 14,000 cal yr BP. Clarke et al. (2024) report a sedaDNA (sedimentary ancient DNA) analysis of plants from Chisholm Lake (also known as Lost Lake), which demonstrates that birch shrub tundra had arrived by 14,500 cal yr BP, about 500 yr earlier than what was suggested by the lacustrine records based on pollen and plant macrofossils. They argue that this early arrival of birch was likely in response to an increase in effective moisture, with the greatest floral turnover at ∼11,000 cal yr BP with the expansion of poplar (*Populus*) and the arrival of additional shrub taxa. The study reveals that between 14,500 and 11,000 cal yr BP, graminoids were in decline, but open-ground forb taxa persisted despite changes to regional moisture regimes. Palynological records from this site reported by Tinner et al. (2006) correspond with the shifts in floral composition reported by Clarke et al. (2024) but vary slightly in the timing. Pollen data suggest an expansion of birch approximately 1000 yr later (ca. 13,500 cal yr BP) than reported by sedaDNA data, but this difference might best be attributed to difficulties in establishing robust chronologies at Chisholm Lake. These temporal mismatches highlight the difficult task of developing chronologies from lacustrine sedimentary records.

Permafrost deposits are playing an increasingly important role in reconstructing Pleistocene environments of Beringia, thanks to the combination of an increasing number of sedaDNA records and strong chronological control (Froese et al., 2009; Haile et al., 2009; Murchie et al., 2021a, 2021b, 2022; Wang et al., 2021). Murchie et al. (2021b) provided the most regional reconstruction of latest Pleistocene shrub expansion/steppe-tundra collapse from permafrost in central Yukon Territory using sedaDNA spanning the last ca. 30,000 yr. The study highlights the decline of megafaunal grazing mammals and the appearance of woody shrubs and boreal taxa to replace the forb- and graminoid-dominated mammoth steppe across the Pleistocene–Holocene boundary between 13,500 and 10,000 cal yr BP. A subsequent study by Monteath et al. (2023) based on the Lucky Lady site, provides the most comprehensive insight into local-scale ecosystem dynamics during the latest Pleistocene in central Yukon Territory by combining sedaDNA data with pollen, plant macrofossils, invertebrates, and pore-ice stable isotopes. This multiproxy record reveals rapid changes in faunal and floral communities across the Pleistocene–Holocene transition. The site preserves a prominent palaeosol at ca. 13,480 cal yr BP that demonstrates the slowing of loess accumulation, increased landscape stability, and the subsequent expansion of shrubs. Before this environmental transition, the invertebrate fauna around ca. 16,500 cal yr BP is dominated by the cold-adapted, steppe-tundra indicator, and Beringian endemic weevil *C. artemisiae* (∼88% of the assemblage). A slight shift in habitat is recorded by the dominance of a dry tundra weevil species, *L. lineaticollis* (74% of the assemblage), sampled directly within the palaeosol (ca. 13,480 cal yr BP). Samples collected above the palaeosol indicate a rapid shift to mesic-dominated taxa (e.g., the ground beetle *Pterostichus brevicornis*) and the appearance of aquatic and riparian taxa (e.g., the rove beetle *Olophrum latum*) by 13,200 cal yr BP. In addition to the invertebrates, plant and animal sedaDNA (from Murchie et al., 2021b) from Lucky Lady generally agrees with the interpretation of steppe-tundra conditions before formation of the prominent palaeosol through the dominance of herbs and graminoids and grazing species such as mammoth and horse. Like the invertebrate fauna, a biotic shift occurs in samples taken directly from the palaeosol and is reflected by sedaDNA

Table 1. Chronology for Arctic ground squirrel (Urocitellus parryii) middens analysed in this study.[a]

YG no.#[b]	Midden ID	Site	Lab ID (UCIAMS)[c]	Material dated	^{14}C Age	Age (cal yr BP)	Median (cal yr BP)
760.101	DF18−37	Mint Gulch	215600	Grass nesting material	11,810 ± 25	13,762–13,533	13,679
528.4	DF13−05	Lucky Lady II	131092	Grass nesting material	11,875 ± 35	13,796–13,606	13,706
490.3	DF12−61b	Lucky Lady II	114721	Grass nesting material	13,300 ± 30	16,128–15,827	15,983
428.5	BJ11-LLII−63	Lucky Lady II	292564	*Phlox* cf. *hoodii* capsule	13,665 ± 35	16,664–16,351	16,509
456.2	DF09-HC−29	Hunker Creek	67157	Grass nesting material	14,100 ± 40	17,335–17,039	17,174

[a] All calibrated age ranges are reported at 2σ uncertainty.
[b] YG no., Yukon Government accession number.
[c] UCIAMS, – University of California Irvine Accelerated Mass Spectrometer.
YG# - Yukon Government accession number

records recording a transition in the plant community from herbs and graminoids to shrubs and, simultaneously, the appearance of ground-nesting birds, like willow ptarmigan (*Lagopus*), that generally inhabit thickets of shrubs (Wilson and Martin 2008). These studies illustrate the importance of establishing robust chronologies to accurately record the timing of latest Pleistocene shrub expansion in east Beringia.

Materials and methods

We collected samples from permafrost exposures associated with placer gold mining at Hunker Creek in 2009 (n = 1); Lucky Lady II in 2011, 2012, and 2013 (n = 3); and Mint Gulch in 2018 (n = 1) (Fig. 1). All specimens have associated field numbers and have been assigned Yukon Government accession numbers (Table 1). All material has been deposited in the Yukon Palaeontology collections in Whitehorse, Yukon Territory.

Macrofossil preparation and identification

We processed the middens at the Permafrost Archives Science Laboratory at the University of Alberta. Middens were washed through 500 and 150 μm sieves, and the resulting fractions were examined individually. To standardise processing for botanical remains, midden fractions were hand sorted until the sample was exhausted or 3 hours had passed, whichever came first, similar to what has been done with fossil packrat middens (Latorre et al., 2002). For the invertebrate remains, we collected many of the specimens during the standardised method described; however, given the sparse nature of invertebrates compared with botanical remains, all samples were analysed to exhaustion to account for all invertebrate fossils present in the sample.

Plant identifications were made with reference to keys (Cody, 2000; Kershaw and Allen, 2020; Flora of North America Editorial Committee, 1993+), to reference collections housed in the Quaternary Environments and Botany programs at the Royal Alberta Museum, and to collections in the ALTA Vascular Plant Herbarium at the University of Alberta. Plant macrofossils were quantified using a relative abundance index (RAI) (e.g., Spaulding et al., 1990; Latorre et al., 2002; Zazula et al., 2007). RAI categories reflect an estimated abundance and are bound by the following limits: 0 = absence, 1 ≤ 1%, 2 = 1–5%, 3 = 6–25%, 4 = 26–50%, 5 = 51–75% and 6 ≥ 75%. Invertebrate specimens were identified using fossil collections (curated by SK) and modern specimens from the E.H. Strickland Entomological Museum at the University of Alberta. Invertebrate data are presented as the minimum number of individuals (MNI). Nomenclature for vascular plants is based on the Database of Vascular Plants of Canada online database (Brouillet et al., 2010) and various resources (see Table 3) for invertebrates.

Radiocarbon dating

Five samples of midden plant material were pretreated at the University of Alberta using a standard acid–base–acid methodology (e.g., Reyes et al., 2010). Samples were then frozen, freeze-dried, overnight, and stored in airtight sterilised vials. CO_2 production, graphitisation, and measurement of radiocarbon abundance of all samples were completed at the Keck-Carbon Cycle AMS facility (UCIAMS). Radiocarbon ages (^{14}C) in Table 1 were calibrated using OxCal v. 4.4 (Bronk Ramsey, 2009) and the IntCal20 calibration curve (Reimer et al., 2020). All calibrated ages are presented at 2σ uncertainty.

Results

Plant macrofossils

Identified plant macrofossils represent at least 24 taxa from 12 families (Table 2; Fig. 2A). The assemblage is dominated by forbs (18 taxa) and includes at least one species of dwarf shrub (*Salix* cf. *arctica*), three members of Poaceae (*Deschampsia* sp., *Elymus* sp., and *Anthoxanthum hirtum* [syn. *Hierochloë hirta*]), at least one species of Cyperaceae (*Carex* cf. *myosauroides* [syn. *Kobresia myosauroides*]), and one species of Selaginellaceae (*Selaginella* cf. *sibirica*; Fig. 3, no. 8). The forbs are dominated, in terms of species diversity, by members of Brassicaceae and Asteraceae, although taxon abundance between middens varies. Of abundance from midden DF09-HC-29 (Hunker Creek) are remains of *Draba* sp. (RAI = 3), of which many specimens preserve their inflorescence (Fig. 3, no. 2), and the cypselae of *Taraxacum* cf. *ceratophorum* (RAI = 3) (Fig. 4, no. 23). This midden is dominated by a singular member of *Plantago* cf. *canescens* (RAI = 4), and several specimens preserve capsule inflorescence (Fig. 4, no. 11a) and delicate floral calyx structures (Fig. 4, no. 11b and c). Present in three middens, *Phlox* cf. *hoodi* (Polemoniaceae) is the dominant

Table 2. Plant macrofossils from five middens recovered from the Klondike goldfields.[a]

Plants	Hunker Creek—DF09-HC-29 17,170 cal yr BP	Lucky Lady—BJ11-LLII-63 16,510 cal yr BP	Lucky Lady—DF12-61b 15,980 cal yr BP	Lucky Lady—DF13-05 13,710 cal yr BP	Mint Gulch—DF18-37 13,680 cal yr BP	Habitat—Yukon (Cody, 2000)	Habitat—North America (Flora of North America Editorial Committee, eds., 1993+; Douglas et al., 1998–2002)	Distributed in present-day Beringia (Siberia, Alaska, and the Yukon) (POWO, 2024) (✔ = yes; X = no/unknown)
Shrubs and trees								
Salicaceae								
Salix sp. Linnaeus					1		Arctic, boreal, temperate	✔
Salix cf. *arctica* Pallas		2		2	2	Mesic to dry meadows, slopes, ridges, heaths, and thickets in subalpine and alpine areas	Arctic and alpine areas, open wet to dry habitats such as meadows and wetlands, tundra, patterned permafrost polygons, snow beds, slopes and cliffs, moraine/till, and calcareous substrates	✔
Grasses								
Poaceae								
Deschampsia sp. Palisot de Beauvois		2				Wet meadows, lakeshores, gravel bars, moist alpine meadows, tundra, and rocky slopes	Cool, damp environments, Genus is comprised of about 20–40 species globally, with most occurring in the Americas and Eurasia.	✔
Elymus sp. Linnaeus			2	2		Mesic to dry grasslands, meadows, forest openings, rocky ridges, and slopes in all vegetation zones	Temperate (to subtropical)	✔
Anthoxanthum cf. *hirtum* (Schrank) Y. Schouten & Veldkamp (syn. *Hierochloë hirta* [Schrank] Borbás)		2	2			Sandy stream banks, lakeshores, and meadows	Occurs in (freshwater) wet meadows and marshes Widely distributed globally	✔
Indet. Poaceae		2			2			
Cyperaceae								
Carex cf. *myosuroides* Villars (syn. *Kobresia myosuroides* [Villars] Fiori])					2	Dry, usually calcareous sandy heaths and windswept ridges	Dry (to wet) areas, including tundra, grassland, heathland, and bare and rocky areas	✔

(*Continued*)

Table 2. (*Continued.*)

Carex spp. Linnaeus			4	2		Occurs worldwide in diverse habitats	✔
Forbs							
Caryophyllaceae							
Silene cf. involucrata subsp. *tenella* (Tolmachew) Bocquet (syn. *Silene taimyrensis* [Tolmachew] Bocquet)			1		Sandy and rocky open slopes and cliffs	Arctic, gravelly. and grassy areas, short-lived species	✔
Ranunculaceae							
Ranunculus sp. Linnaeus			3			Worldwide, excluding lowland tropics	✔
Anemone sp. Linnaeus		1				Cool temperate biome and arctic areas Mostly worldwide	✔
Boraginaceae							
Lappula sp. Moench	3						✔
Brassicaceae							
Draba sp. Linnaeus	3				Dry to mesic tundra, often calcareous.	Typical taxa of higher elevation including subalpine, subarctic and boreal areas Rarely occurs at low elevations in North America and Eurasia	✔
Erysimum sp. Linnaeus	2	2				Mostly occurs in the Northern Hemisphere	✔
cf. *Lepidium* sp. Linnaeus				3	Dry disturbed areas and waste places in steppe and montane zones	Mucilaginous seeds are suggested to contribute to long-distance transcontinental dispersal.	✔
Rorippa cf. *palustris* (Linnaeus) Besser	1				Wet areas including lakeshores and meadows, disturbance areas.	Variable and taxonomically challenging species with two subspecies (*R. palustris* subsp. *hispida* [Desvaux] Jonsell; *R. palustris* [Linnaeus] Besser subsp. *palustris*) in Yukon today. Both subspecies occur in mesic areas, including wetlands, meadows, lakeshores, and flats, with *R. palustris* subsp. *palustris* having broader habitat, including depressions, ditches, grasslands, thickets, and prairies/pastures.	✔

(*Continued*)

Table 2. (*Continued.*)

Indet. Brassicaceae		1						
Asteraceae								
Artemisia sp. Linnaeus					4	Dry southerly slopes, sandy banks, grasslands, and open forests in montane to subalpine areas	Most occur in North America and Eurasia. Diverse habitats Taxonomically challenging taxa	✔
Artemisia cf. *frigida* Willdenow			1			Steep open slopes, dry, disturbed	Dry, well-drained, and open habitat, including grasslands, meadows, fields, and steppes.	✔
Aster-Erigeron Linnaeus type	3	1	2			Slopes, meadows River flats, open areas	Mostly in temperate areas in North America and Eurasia (*Aster*) to nearly worldwide (*Erigeron*)	✔
Solidago sp. Linnaeus					3		Mostly in North America, with some occurrence in South America and diverse habitats Often in open canopy to closed forests, wetlands, meadows, and thickets	✔
Taraxacum cf. *ceratophorum* (Ledebour) de Candolle	3		2			Woodland and heath to tundra	Widespread temperate species Broad distribution from arctic, montane-alpine, to boreal areas Wet habitats, including meadows, shorelines, seepage slopes, and snow beds Calcareous, igneous rock, gravels, sands and clay substrates	✔
cf. *Anntenaria* sp. Gaertner	2						Temperate, arctic, and alpine areas	✔
Polemoniaceae								
Phlox cf. *hoodii* Richardson	2	5	2			Dry prairies and foothills	Dry open areas including steppe, subalpine, and rocky outcrops.[b]	**X** (Not in Siberia)
Plantaginaceae								
Plantago cf. *canescens* Adams	4		1			Dry open slopes, disturbed areas	Dry open areas including grasslands, gravels, rocky slopes, and cliffs.	✔
Penstemon cf. *gormanii* Greene					3	Dry rocky slopes, dunes, and sandy or gravelly river terraces	Dry open areas including rocky slopes, dunes, gravelly stream/river terraces, and forest clearings	✔

(*Continued*)

Table 2. (*Continued.*)

Rosaceae								
Dryas cf. *integrifolia* Vahl				2		Dry to moist tundra, heath, rocky ridges, talus slopes, and gravel bars in the montane to alpine zones	Taxonomically challenging taxa (hybridizes) Dry to wet areas including tundra, heaths, alpine slopes, grasslands, and sandy /gravelly beaches Subspecies *D. integrifolia* subsp. *sylvatica* (Hultén) Hultén *sylvatica* also occurs in mesic spruce-birch forests and bogs.	✔
Potentilla cf. *glaucophylla* Lehmann					4	Mesic to dry meadows, tundra, rocky slopes, gravel bars, grasslands, and open forests in montane to alpine zones	Two subspecies with *P. glaucophylla* var. *glaucophylla* occurring in Yukon and western North American in higher-elevation mesic to dry areas, including meadows, gravelly flats, slopes, grasslands, and tundra *P. glaucophylla* var. *perdissecta* (Rydberg) Soják is excluded from Yukon today.	**X** (not in Siberia)
Fabaceae								
Oxytropis-Astragalus type					1		Habitats vary, with *Oxytropis* occurring mostly in the Northern Hemisphere and subarctic, and *Astragalus* more widely distributed including the Southern Hemisphere.	✔
Selaginellaceae								
Selaginella cf. *sibirica* (Milde) Hieronymus		1				Dry rocks or rocky soil in the alpine zone	Dry and open habitats, including grassland, tundra, alpine areas, and rocky slopes	✔
Miscellaneous vegetation (nesting material)	6	6	6	6	6			

[a] Data are presented using relative abundance index (RAI) values. RAI categories reflect an estimated abundance and are bound by the following limits: 0 = absence; 1 ≤ 1%; 2 = 1–5%; 3 = 6–25%; 4 = 26–50%; 5 = 51–75%; and 6 ≥ 75%.

[b] Bennett (2017); Klinkenberg (2023).

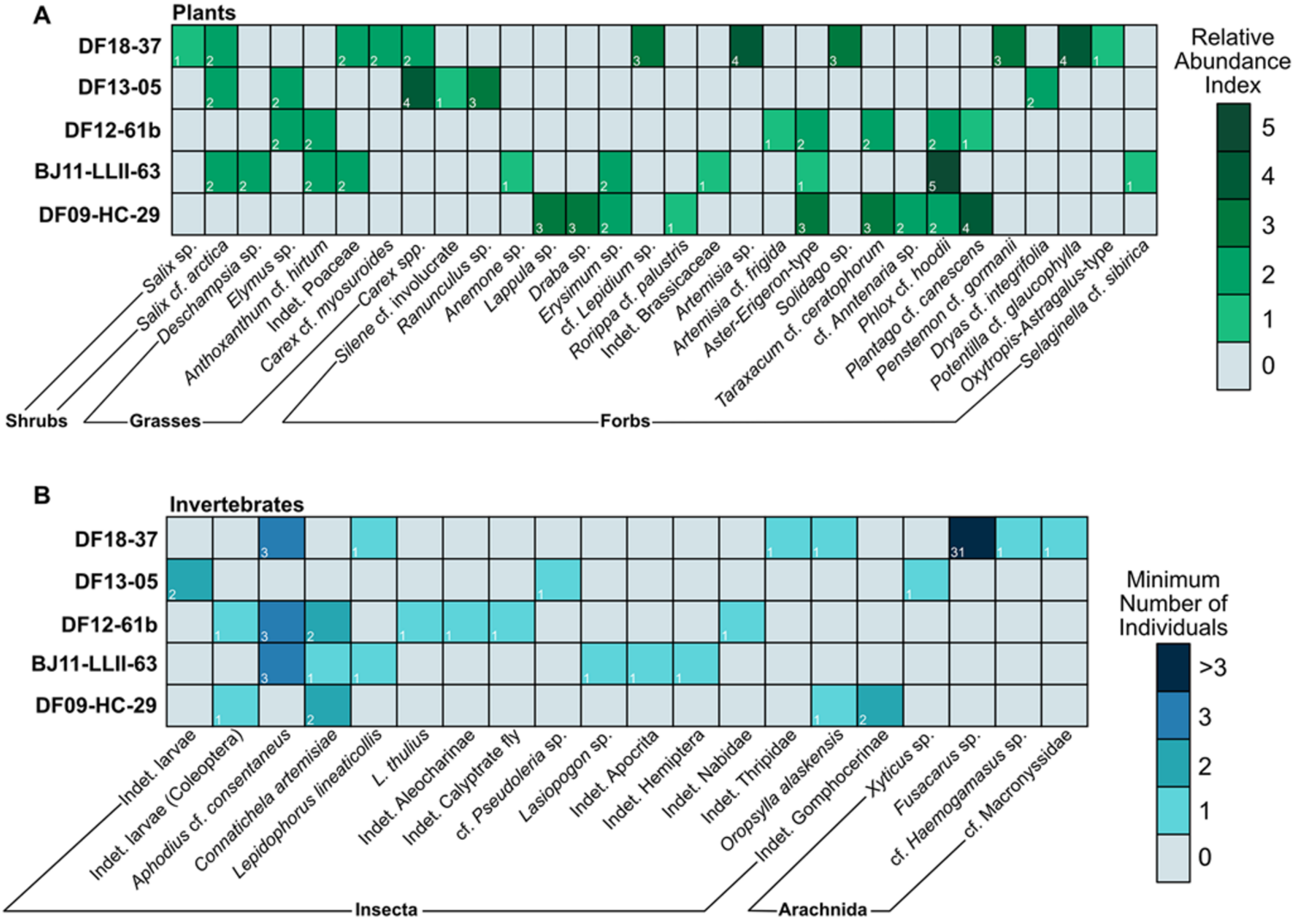

Figure 2. Heat map showing plant (**A**) and invertebrate (**B**) records from the five middens analysed in this study. Plant data (**A**) are represented by their assigned relative abundance index (RAI) value and invertebrate data (**B**) are presented as minimum number of individuals (MNI).

taxon from BJ11-LLII-63 (RAI = 5) (Lucky Lady II) and preserves both capsules and seeds (Fig. 3, no. 1a–c). At the Mint Gulch site, midden DF18-37 is dominated by *Potentilla* cf. *glaucophylla* and *Artemisia* sp. (RAI = 4) and, in lesser abundance, *Penstemon* cf. *gormanii, Solidago* sp., and cf. *Lepidium* sp. (RAI = 3). From various middens and present in lesser abundance are taxa such as marsh yellowcress (*Rorippa* cf. *palustris*) (Fig. 3, no. 6a-c, DF09-HC-29, ~17,170 cal yr BP, Hunker Creek), *Anemone* sp. (BJ11-LLII-63; ~16,510 cal yr BP, Lucky Lady II), *Silene* cf. *involucrate* subsp. *tenella* (syn. *Silene taimyrensis*) (Fig. 3, no. 4, DF13-05, ~13,710 cal yr BP, Lucky Lady II), and *S.* cf. *sibirica* (Fig. 3, no. 8, BJ11-LLII-63, ~16,510 cal yr BP, Lucky Lady II). All middens are dominated (RAI = 6) by indeterminate graminoid vegetation that represents nesting material.

Invertebrate macrofossils

Invertebrate macrofossils were recovered from all five middens and include 20 taxa (Table 3; Fig 2B). Specimens are presented as MNI. The most numerous taxa recovered was the mite *Fusacarus* sp. represented by 31 individuals from midden DF18-37 (13,680 cal yr BP). Coleoptera (beetles) were represented by three families: Scarabaeidae (Fig. 5, no. 4a–c), Curculionidae (Fig. 5, nos. 6a and b and 10), and Staphylinidae (Fig. 5, no. 3). Individuals of the dung beetle *Aphodius* cf. *consentaneus* (Scarabaeidae; MNI = 9) (Fig. 5, no. 4a–c) are the most numerous beetles, followed by the weevil *Connatichela artemisiae* (Curculionidae; MNI = 5), both of which are present in three of the five middens analysed. Of additional interest is the preservation and identification of taxa that are typically unrepresented in publications of Pleistocene invertebrates. Our study includes individual invertebrates of flies (Diptera) (Fig. 5, no. 1, 2, and 5), true bugs (Hemiptera), thrips (Thysanoptera), fleas (Siphonaptera) (Fig. 5, no. 9), grasshoppers (Orthoptera), spiders (Araneae) (Fig. 5, no. 11), and mites (Astigmata and Mesostigmata). A single specimen of a robber fly (*Lasiopogon* sp.) from midden BJ11-LLII-63 has been studied in more detail in Cocker et al. (2025a). Specimens of thrips, fleas, grasshoppers, and mites are subjects of a more in-depth study by Cocker et al. (2025b).

Discussion

Evidence for the persistence of steppe-tundra in easternmost Beringia

The occurrence of late Pleistocene Arctic ground squirrel middens and associated macrofossil records at sites like Mint Gulch and Lucky Lady II suggests the persistence of steppe-tundra environments in easternmost Beringia for several hundred years longer than in interior Alaska. In comparison to lacustrine pollen records and/or permafrost pore-ice isotopes that typically provide more

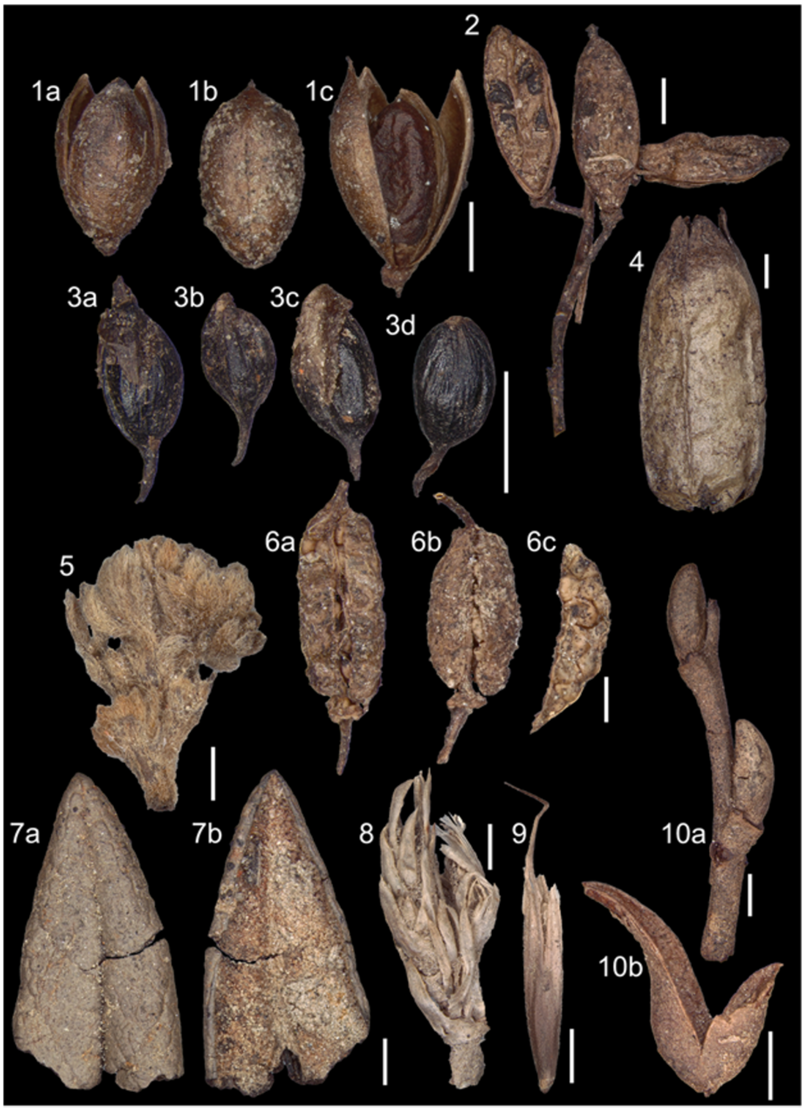

Figure 3. Vascular plant remains. (1) *Phlox* cf. *hoodi* capsules; (2) *Draba* sp. fruits; (3) *Carex* sp. achenes; (4) *Silene* cf. *involucrate* subsp. *tenella* (syn. *Silene taimyrensis*) capsule; (5) *Artemisia* cf. *frigida* leaves and stem; (6) *Rorippa* cf. *palustris* silicle; (7) *Dryas* cf. *integrifolia* leaf apex; (8) *Selaginella* cf. *sibirica* leaves and stem; (9) Indet. Poaceae floret; (10) *Salix* (a) twig and (b) capsule. Scale bars: 1 mm.

regional reconstructions of the environment and climate (e.g., Demske et al., 2005; Porter et al., 2016; Bandara et al., 2020), analyses of Arctic ground squirrel middens present an opportunity to reconstruct local-scale environments. These middens aid in our understanding of fundamental questions in Beringian palaeoecology. As previously discussed, one of the major barriers to understanding the timing of latest Pleistocene shrub expansion and/or the collapse of steppe-tundra environments in eastern Beringia is the uncertainty that surrounds the chronology of published palaeoecological data.

Monteath et al. (2021) concluded that shrub tundra expansion in east Beringia occurred around 14,000 cal yr BP in response to bottom-up processes that follow a climate-driven expansion rather than a top-down process that favours the keystone role of grazing megafauna. From Yukon Territory, the last-appearance dates of steppe tundra taxa like mammoth (*Mammuthus*) occur by ∼13,800 cal yr BP and by ∼15,400 cal yr BP for horses (*Equus*); and first-appearance dates of shrub tundra–associated browsers like moose (*Alces*) occur by ∼13,450 cal yr BP and by ∼14,800 cal yr BP for elk (*Cervus*). We agree that a bottom-up model is the best explanation to account for the loss of steppe-tundra; however, we think that there is still ambiguity surrounding the timing of subregional records of change across the eastern Beringian geographic gradient from western Alaska to central Yukon Territory.

Considering a regional shift in climate and vegetation by 14,000 cal yr BP reported by Monteath et al. (2021), our data indicate that Arctic ground squirrels are present in easternmost Beringia for at least another 300 yr based on the presence of our youngest nest, DF18-37 from Mint Gulch, that dates to 13,680 cal yr BP. These data indicate that the regional signal of change is not fully representative of local-scale ecosystem response and does not account for the local persistence of steppe-tundra. An additional consideration for the persistence of steppe-tundra is the proximity of these sites to the limit of the Cordilleran–Laurentide ice sheet complex. Monteath et al. (2023) discuss this in the context of the Lucky Lady II site, suggesting the potential influence on atmospheric dynamics, precipitation, and precipitation seasonality. Given the location of Mint Gulch, we may therefore consider the influence of the Cordilleran–Laurentide ice sheet complex when interpreting data that support the persistence of steppe-tundra.

Even when considering selective caching biases, plant, and invertebrate macrofossil records from the two youngest nests, DF18-37 (∼13,680 cal yr BP) and DF13-05 (∼13,700 cal yr BP), our results are still consistent with an interpretation of a steppe-tundra

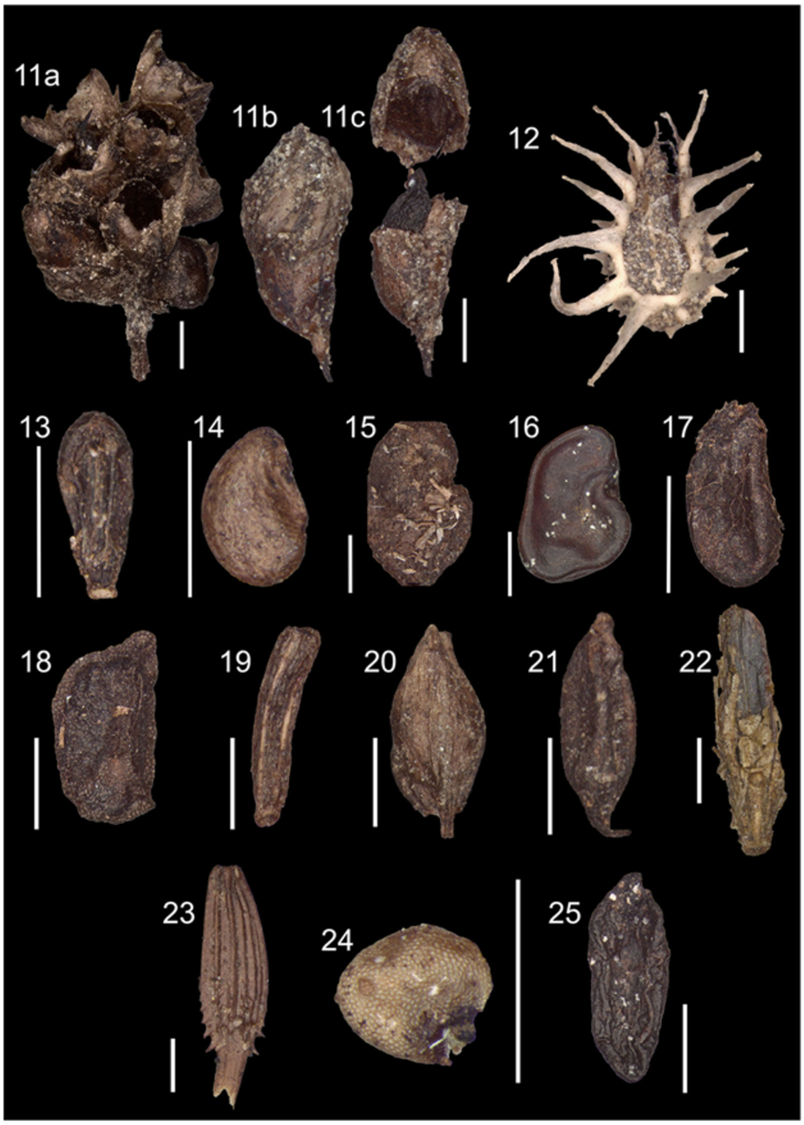

Figure 4. Vascular plant remains. (11) *Plantago* cf. *canascens* (a) capsule inflorescence, (b) capsule, and (c) separated capsule revealing dark seeds inside; (12) *Lappula* sp. nutlet; (13) *Artemisia* sp. achene; (14) *Potentilla* cf. *glaucophylla* achene; (15) *Oxytropis-Astragalus* type degraded seed; (16) *Oxytropis-Astragalus* type seed; (17) cf. *Lepidium* sp. seed; (18)*Penstemon* cf. *gormanii* seed; (19) *Solidago* cf. *missouriensis* achene; (20) *Carex* sp. achene; (21) *Carex* cf. *myosuroides* achene; (22) *Elymus* sp. floret with exposed caryopsis; (23) *Taraxacum* cf. *ceratophorum* cypsela; (24) *Rorippa* cf. *palustris* seed; (25) *Plantago* cf. *canascens* seed. Scale bars: 1 mm.

environment and do not immediately indicate the local presence of shrubs. DF13-05, from the Lucky Lady II site, contained the capsules of *S.* cf. *involucrate* subsp. *tenella*. This taxon has an amphiberingian distribution and has been recorded from sandy and rocky open slopes and cliffs in Yukon Territory (Cody 2000). Zazula et al. (2007, 2011) record this taxon in several Arctic ground squirrel middens from sites dating to MIS 2 and MIS 4. Of additional importance is *P.* cf. *gormanii* from DF18-37 from the Mint Gulch site, which has been previously discussed in the context of its ecological significance to both recognising steppe environments and its continued presence around modern Arctic ground squirrel habitats.

For the invertebrate record, one notable omission from the youngest nests is the characteristic steppe-tundra weevil, *C. artemisiae*, a species that is commonly found on host plants of *A. frigida* and is endemic to Yukon Territory (Anderson, 1984). It is difficult to identify whether the lack of this species represents its decreased presence on the landscape, or whether taphonomic factors have played a role in its lack of preservation. The Lucky Lady II data show a significant decline in the presence of *C. artemisiae*, likely a response to the arrival of shrubs and decline of steppe taxa such as *Artemisia* (Monteath et al., 2023). A decline in *Artemisia* would have impacted populations of *C. artemisiae*, as their larvae feed on the roots of *Artemisia* and adults have been observed copulating on this plant, typically *A. frigida* (Anderson, 1984).

Small Arctic willow species, likely *Salix arctica*, are present within three of the five middens. This taxon is recorded by Cody (2000) from a variety of habitats, including sedge meadows, heath, and dry sandy tundra. The occurrence of this species in the middens could be interpreted as evidence for the expansion of shrubs into the region; however, *S. arctica* is a prostrate to somewhat erect subshrub not exceeding about 25 cm in height (Flora of North America Editorial Committee, 1993+) and therefore is not considered as contributing to the canopy-forming willow species that have been reported to expand under a warming climate (e.g., Myers-Smith et al., 2011). This subshrub occupies the subalpine and subarctic, within open-canopy graminoid–forb-dominated ecosystems such as tundra. Zazula et al. (2007, 2011) record *S. arctica*, from ~30,000-yr-old middens and a buried vegetation surface (Zazula et al., 2006a) and *S. polaris* from both ~30,000- and ~80,000-yr-old middens. *Salix polaris*, snow-bed willow, has a low-lying growth form similar to *S. arctica*, and so both taxa

Table 3. Invertebrate macrofossils from five middens recovered from the Klondike goldfields.[a]

Invertebrates	Hunker Creek—DF09-HC-29 17,170 cal yr BP	Lucky Lady II—BJ11-LLII-63 16,510 cal yr BP	Lucky Lady II—DF12-61b 15,980 cal yr BP	Lucky Lady II—DF13-05 13,710 cal yr BP	Mint Gulch—DF18-37 13,680 cal yr BP	Habitat	Distributed in present day Beringia (Siberia, Alaska, and Yukon) (✔ = yes; **X** = no/unknown)
Class Insecta							
Indet. larvae				2			
Coleoptera							
Indet. larvae	1		1				
Scarabaeidae							
Aphodius cf. *consentaneus* LeConte		3	3		3	Coprophilous dung beetle found in grasslands[b]	**X** (*A. consentaneus* only known from continental United States of America)
Curculionidae							
Connatichela artemisiae Anderson	2	1	2			Found along dry river banks and dry south-facing slopes (steppe) in association with *Artemisia*[c]	✔
Lepidophorus lineaticollis Kirby		1			1	Wet to dry tundra, steppe, and river shorelines[c]	✔
L. thulius Kissinger (syn. *Vitavitus thulius*)			1			Found in dry tundra and south-facing slopes[c,d]	✔
Staphylinidae							
Indet. Aleocharinae			1			Widely distributed	✔
Diptera							
Indet. Calyptrate fly			1			Widely distributed	✔
Heleomyzidae							
cf. *Pseudoleria* sp. Garrett				1		Often associated with animal burrows[e]	**X** (Unknown – records are limited)
Asilidae							
Lasiopogon sp. Loew		1				Found in dune habitats, on south-facing slopes, and dry forest habitats[f]	✔
Hymenoptera							
Indet. Apocrita		1				Widely distributed	✔
Hemiptera							
Indet. Hemiptera		1				Widely distributed	✔
Indet. Nabidae			1			Widely distributed	✔

(*Continued*)

Table 3. (*Continued.*)

Thysanoptera					
Indet. Thripidae			1	Widely distributed	**X** (Unknown – records are limited)
Siphonaptera					
Ceratophyllidae					
Oropsylla alaskensis Baker	1		1	*Urocitellus parryii* hosts and burrows[g]	✔
Orthoptera					
Acrididae					
Indet. Gomphocerinae	2			Widely distributed	✔
Class Arachnida					
Araneae					
Thomisidae					
Xysticus sp. sensu lato		1		Ranging from dunes to tundra to moss in coniferous woodlands[h]	✔
Astigmata					
Glycyphagidae					
Fusacarus sp. Michael			31	Found in mammal and bird nests in North America[i]	**X** (modern specimens only recorded from Northwest Territories)
Mesostigmata					
Laelapidae: Haemogamasinae					
cf *Haemogamasus* sp. Berlese			1	Rodent parasite[j]	✔
cf. Macronyssidae			1	Parasitic mites, widely distributed[k]	✔

[a] Data are presented as minimum number of individuals (MNI).
[b] Krell (2024).
[c] Anderson (1997).
[d] Bright and Bouchard (2008).
[e] Gill (1962).
[f] Cannings (1997).
[g] Nadler and Hoffmann (1977).
[h] Dondale et al. (1997).
[i] Halliday and Walter (2006).
[j] Whitaker and Wilson (1974).
[k] Baulieu et al. (2019).

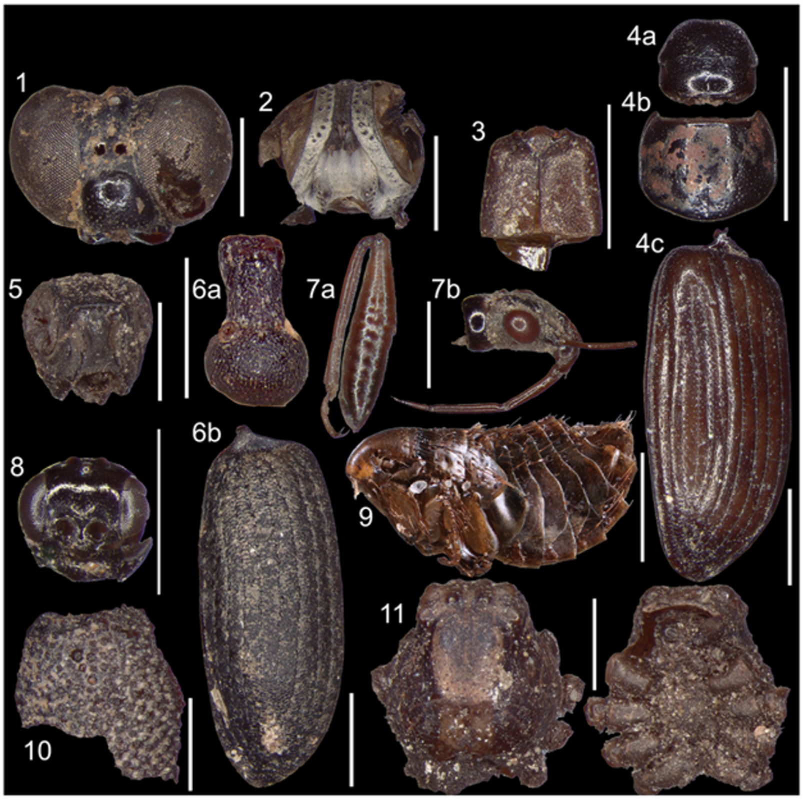

Figure 5. Invertebrate remains. (1) *Lasiopogon* sp.; (2) Indet. Calyptrate fly; (3) Indet. Aleocharinae; (4) *Aphodius* cf. *consentaneus* (a) head, (b) prothorax, and (c) left elytra; (5) Heleomyzidae, cf. *Pseudoleria* sp.; (6) *Lepidophorus lineaticollis* (a) head and (b) right elytra; (7) Indet. Nabidae (a) leg and (b) head; (8) Indet. Apocrita; (9) *Oropsylla alaskensis*; (10) *Lepidophorusthulius*; (11) *Xysticus* sp. sensu lato. Scale bars: 1 mm.

are presumably evidence for the occurrence of subshrub species within steppe-tundra environments rather than evidence for the expansion of shrubs towards the end of the Pleistocene. Overall, the preferred ecological interpretation of these midden assemblages indicates that steppe-tundra environments persist until at least 13,680 cal yr BP, or at a minimum that no significant shrub expansion has occurred in the central Yukon at this time. Macrofossils from shrub species, including *Betula* spp. and *Alnus* spp., can be preserved in sediments (e.g., Kaltenrieder et al., 2011) and have been recovered from older Arctic ground squirrel middens (e.g., Gaglioti et al., 2011). The omission of shrub taxa from our samples likely reflects the selective foraging behaviours of Arctic ground squirrels. Subsequently, the absence of shrub macrofossils in our study cannot simply be interpreted as a lack of these species on the landscape.

Plants of special interest

Although all the identified plant taxa provide habitat information to aid in palaeoecological interpretations, we highlight a selection of taxa that are of special interest.

The record from Hunker Creek, midden DF09-HC-29, represents the earliest known specimen of *Rorippa* cf. *palustris* from Yukon Territory and could play a considerable role in our understanding of *Rorippa* sp. biogeography. *Rorippa palustris* is a species of flowering plant that typically occurs in mesic sites (Flora of North America Editorial Committee, 1993+), including shorelines, meadows, wetlands, and disturbance sites in the Yukon (Cody, 2000) and has a circumpolar distribution (Klimešová et al., 2004). From the Hengduan Mountains of China, Han et al. (2022) report on the genetic history of *R. palustris*, suggesting Pleistocene glaciations played a significant role in the phylogeographic history of this taxon as it migrated north during interglacial periods and south during glacial periods. Kultti et al. (2003) report the presence of *R.* cf. *palustris* seeds in Early Holocene lake sediments in northeastern European Russia. Additional records have reported *Rorippa* spp. from the middle Pleistocene of Poland (Stachowicz-Rybka 2015), the mid-Wisconsin of the eastern Great Plains (Baker et al., 2009) and from late Pleistocene sites in the United Kingdom (e.g., Holyoak and Preece 1985). In northern Canada, records of *R. palustris* are limited. Ovenden (1982) reports the presence of seeds, similar to *Rorippa* sp. (cf. *Rorippa*), from a polygonal peatland in northern Yukon Territory. However, due to the uncertainty in identification, it is difficult to confidently use this site as a locality for the presence of *Rorippa* from the latest Pleistocene of Yukon Territory (ca. 11,800 cal yr BP). An additional species of *Rorippa* was reported by Dallimore et al. (1997) from mid-Wisconsin deposits of the Tuktoyaktuk Coastlands (Northwest Territories) and was conservatively identified by the authors as *R. islandica* type. However, *R. islandica* is not present in northern Canada and has previously been revised as misidentifications of *R. palustris* and/or *R. barbareifolia*. Additionally, the study does not report whether the taxon was identified using seeds and/or pods, so we can only speculate on which species it may represent. We do not contend the designation of genus and recognise this record as a valid representation of this taxon in the mid-Wisconsin of northern Canada. Of particular interest in our study is the quality of preservation of *R.* cf. *palustris*. All the Pleistocene records cited earlier only report this taxon as individual seeds (similar to Fig. 4, no. 24), but here we have the preservation of the fruit (silicles) and seed (Fig. 3, no. 6a–c).

Penstemon gormanii is a perennial herb with a distribution restricted to Yukon Territory, Northwest Territories, British Columbia, and Alaska (Flora of North America Editorial

Committee, 1993+), where it inhabits dry and often disturbed sites, including azonal steppe communities (Laxton et al., 1996) gravels, riverbanks, and terraces (Cody, 2000), and are restricted to areas with open canopy between 400 m to 1200 m asl (Flora of North America Editorial Committee, 1993+). This taxon has previously been reported from ~30,000-yr-old Arctic ground squirrel middens by Zazula et al. (2007), but has not been recorded from studies of older middens (~80,000 yr old) (Zazula et al., 2011). A relationship between *P. gormanii* and Arctic ground squirrels continues with modern populations from Yukon Territory, where it is regularly present on disturbed soils surrounding burrow entrances (Vetter, 2000) and remains an important cache resource (Zazula et al., 2006b).

Dryas integrifolia is a prostrate subshrub not exceeding 14 cm in height (Flora of North America Editorial Committee, 1993+) that is known to hybridise within the genus (Cody, 2000). In the Yukon, *D. integrifolia* is reported to occur in gravel sites and less commonly in tundra or heathlands and on calcareous soils (Cody, 2000). This species is regularly recorded from Yukon's arctic and alpine tundra communities (Scudder, 1997). On the Alaskan North Slope, *D. integrifolia* is most common on rocky slopes and on sandy or gravelly ridges and not in the dense vegetation of the flat tundra (Wiggins and Thomas, 1962). *Dryas integrifolia* has not been previously reported from Pleistocene middens from Yukon Territory (Zazula et al., 2007, 2011) or interior Alaska (Gaglioti et al., 2011). However, Gaglioti et al. (2011) record the presence of *D. octapetala* from a singular midden in interior Alaska, but the study does not record *D. integrifolia*, despite its growing in the surrounding study area.

Considering all of the middens, the recovered plant macrofossils indicate that the vegetation community spanned two distinct local habitat types: wet with freshwater sources, including shorelines, wetlands, and meadows; and dry with well-drained and open habitats, including rocky slopes, gravels, sandy sites, tundra, and alpine areas. Further, the taxa that can be identified to the species level mostly occur today in open to mostly open canopy sites without canopy-forming shrubs or trees present (Table 2). The three recovered grass taxa are typical of mesic to dry sites and are probably species inhabiting the late Pleistocene Beringia fine-grained lowland soils (Swanson, 2006). Strong (2021) divided eastern Beringian flora into two distinct groupings, with arctic/alpine taxa occurring in drier conditions, and subarctic taxa occurring in more mesic conditions. There does not appear to be a significant trend from dry to wet or wet to dry conditions throughout the samples. However, in all of our samples, there are more taxa present that inhabit dry habitats today for which the majority are still present in western Beringia (Siberia) and eastern Beringia (Alaska–Yukon Territory) (Table 2).

Invertebrates of particular interest

Beetles (Coleoptera) are routinely the most abundant invertebrate remains recovered from rodent middens: for example, packrats (e.g., Elias 1990; Elias et al., 1992) and Arctic ground squirrel (Zazula et al., 2005, 2007, 2011). Our middens are no exception and preserve the remains of beetles previously reported from Arctic ground squirrel middens from the region (Zazula et al., 2005, 2007, 2011). The abundance of aphodiine burrow dung beetles remains (*A.* cf. *consentaneus*) (MNI = 9) is not surprising given the presence of faecal pellet latrines within ground squirrel burrow complexes. The recovery of the Beringian endemic weevil, *C. artemisiae*, indicates the local presence of dry steppe-tundra habitats with the prairie sage *A. frigida* (Anderson, 1984; Zazula et al., 2007, 2011). Interestingly, the fossil record indicates that *C. artemisiae* was considerably more abundant and widespread during the Pleistocene and that the retraction of *Artemisia* to small, often south-facing meadows of azonal steppe vegetation was likely a driver for this range contraction (Matthews, 1982; Anderson, 1984). Of additional interest is the presence of a single pronotum of the weevil *Lepidophorus thulius* from midden DF12-61b (Lucky Lady II). This taxon is typically reported from dry tundra and southern steppe habitats (Anderson, 1997) and has been recorded from Pliocene (Matthews, 1977), Early Pleistocene (Matthews, 1974), late Pleistocene (Kuzmina et al., 2014), and Holocene (Morgan et al., 1983) deposits. Unlike, *C. artemisiae*, which is relatively common on present-day azonal steppe localities in Yukon Territory, *L. thulius* has remained a much rarer member of the present-day fauna (Matthews, 1975; Ashworth, 1980).

The remains of flies (Diptera) from Pleistocene deposits in eastern Beringia are typically reported as indeterminate Diptera puparia due to a lack of diagnostic features required for identification or simply their limited presence, likely a function of preservation (e.g., Kuzmina et al., 2014). The most common dipteran subfossils are fly puparia and Tipulidae larvae heads. There is one exception, the non-biting midges (Chironomidae), that are commonly recovered from lake sediments (e.g., Bunbury and Gajewski, 2009; Kurek et al., 2009). Here we present two dipteran taxa that are unreported from Pleistocene deposits in east Beringia.

Midden BJ11-LLII-63 (16,510 cal yr BP; Lucky Lady II) preserves a single head of an asilid fly, *Lasiopogon* sp., studied in detail by Cocker et al. (2025a) (Fig. 5, no. 1). There are five known species of robber flies from Yukon Territory, of which at least three taxa are considered Beringian species: *Lasiopogon canus, L. prima*, and *L. hinei*. Additionally, *L. yukonensis*, is recorded from central and southern Yukon and therefore is eastern Beringian based on distribution alone (Cannings, 1997, 2014). Both *L. yukonensis* and *L. canus* are species that have had recent radiations in North America despite belonging to a basal clade originating in the Palearctic (McKnight and Cannings, 2020). Subsequently, the biogeographic history of these species is more complex than initially considered. All four taxa are present on Yukon's south-facing azonal steppe slopes, although not exclusively (Cannings, 2014). These relict azonal steppe habitats are particularly important when considering Pleistocene assemblages, as they are still home to Beringian endemic species, such as the weevil *C. artemisiae* (Anderson, 1984).

Midden DF13-05 (13,710 cal yr BP; Lucky Lady II) preserves a single head of a Heleomyzid fly, cf. *Pseudoleria* sp. (Fig. 5, no. 5). Heleomyzidae are a heterogeneous family that are considered to be paraphyletic (Roháček et al., 2001) and are represented by numerous species that are predominantly saproxylic. Although the specimen is not identified with certainty to the genus *Pseudoleria*, because of missing identifiable features, the ecology of several species in this genus would support this tentative identification. Larvae of this genus have been previously recorded to feed on rodent faeces, and adults have been recovered from the burrows of various rodents (e.g., Gill, 1962).

Members of the true bugs (Heteroptera) are common in Pleistocene deposits across Beringia and can often be identified to taxonomic family (e.g., Saldidae, Corixidae, and Pentatomidae). From Quaternary deposits in Yukon Territory, true bugs are predominantly represented by members of the family Saldidae, although a few others are present (see Matthews and Telka, 1997). Here we present what appears to be the first individual of a damsel bug (Heteroptera: Nabidae) (Fig. 5, no. 7a and b). In the present-day Yukon fauna, damsel bugs consist of one genus, *Nabis* (syn.: *Nabicula*), and five species: *N. americolimbata, N. nigrovittata nearctica, N. flavomarginata, N. americoferus*, and *N. inscriptus*. Apart from *N. americoferus*, all these species also have known distributions in Alaska (Scudder, 1997; Maw et al., 2000). Habitat tolerances within this genus vary from humid grasslands, to mixed conifer forests, to dry and often sandy fields of grass (Larivière, 1994).

The presence of unique and previously unreported invertebrate taxa demonstrates the optimal taphonomic conditions provided by Arctic ground squirrel middens. In many cases, these records represent the earliest known occurrences of individual taxa and can aid in our understanding of invertebrate biogeographic histories across eastern Beringia.

Fossil midden biases

Arctic ground squirrel middens may reflect biases due to cache selectivity (Gillis et al., 2005b; Zazula et al., 2006b). From modern Arctic ground squirrel populations in alpine meadows in southwest Yukon, Gillis et al. (2005b) report evidence for selective caching behaviours by recording cheek-pouch contents from both male and female individuals. Female Arctic ground squirrels do not cache seeds and fruits and were less likely to be carrying food when trapped in comparison to males. For those that did have cheek-pouch contents, female individuals were more likely to be transporting materials for nest building, including mosses and lichens. In contrast, males with cheek-pouch contents were almost always carrying seeds or fruits. Gillis et al. (2005b) identified the most abundant taxa recovered as *Bistorta vivipara* (syn. *Polygonum viviparum*), which grew at sites with a density similar to another species, *B. officinalis* (syn. *P. bistorta*), that was recovered from none of the males. This disparity is evidence of clear selective caching. As an important food source in northern ecosystems, due to high starch content in their roots, *B. vivipara* is preferentially consumed by other alpine herbivores (e.g., tundra vole [*Microtus oeconomus*], willow grouse [*Lagopus lagopus*], and snow geese [*Anser caerulescens*]). However, it is not clear why *B. officinalis*, which was growing at a similar density and forms a larger root mass, was not present in the cheek pouches. *Bistorta vivipara* primarily reproduces vegetatively through the production of bulbils (Diggle et al., 2002; Law et al., 1983) of varying morphotypes (Dormann et al., 2002) and is commonly recovered from Pleistocene-aged fossil middens from central Yukon territory (Zazula et al., 2007).

Although selective caching can introduce biases, Arctic ground squirrel middens have been shown to be resources of rare taxa on present-day landscapes. Zazula et al. (2006b) report on foraging behaviours by comparing the contents of present-day midden caches to the surrounding vegetation from steppe meadows in open boreal forests of southwest Yukon. From two study sites, the most commonly cached taxa reported were fruits from *Rosa acicularis* (prickly rose shrubs) and *Geocaulon lividum* (northern comandra) despite both taxa representing a small fraction of the vegetation community in the study area. This study demonstrates that the two most commonly cached taxa are not found directly on the steppe meadows where Arctic ground squirrels burrow, but rather on the edge or within the forest, indicating that the squirrels must therefore have increased their foraging distances to source them.

All palaeoecological records reflect the influence of biases, mostly driven by taphonomic processes (Behrensmeyer et al., 2000), secondarily by sampling (e.g., Carrasco, 2013), with a possible third source of bias due to ecological processes (e.g., Gillis et al., 2005b; Zazula et al., 2006b). Here we discussed the possible biases introduced by Arctic ground squirrel selective caching behaviours and their implications for interpreting our Pleistocene-aged middens. However, we contend that this does not detract from the palaeoecological value of middens as records of past environments and argue that because of cache selectivity, middens can provide valuable records of rare taxa on Pleistocene landscapes.

Conclusion

The analysis of the youngest cache-bearing Arctic ground squirrel middens from Yukon Territory provides evidence for the persistence of steppe-tundra in easternmost Beringia for several hundred yr longer than in interior Alaska. This study examined five middens dating from approximately 17,500 to 13,500 cal yr BP, spanning the LGM through the period of climatic warming of the latest Pleistocene. The plant and invertebrate macrofossil assemblages preserved in these middens offer a unique and well-dated perspective on the persistence of steppe-tundra environments in easternmost Beringia.

The middens preserve macrofossils that capture local-scale habitats in easternmost Beringia due to excellent preservation and high taxonomic resolution that is rarely replicated in lacustrine records of similar age. We present the earliest known records of several taxa from east Beringia (e.g., *R.* cf. *palustris*), which demonstrate the unique taphonomic setting provided by permafrost-preserved middens. The invertebrate assemblages are similarly diverse, with beetles dominating in both abundance and diversity. The preservation of taxa such as robber flies, grasshoppers, parasitic mites, fleas, and damsel bugs can further contribute to our understanding of invertebrate biogeographic histories in the region.

The complex interplay between regional vegetation shifts and local ecosystems in late Pleistocene Beringia reveals nuanced insights into megafaunal decline and climate change responses. Regional pollen records from Alaska suggest a shift towards shrub-tundra by 14,000 cal yr BP, marking the widespread expansion of shrubs and the decline of the mammoth steppe ecosystem. In contrast, the record of Arctic ground squirrel middens from the Lucky Lady II and Mint Gulch sites farther east in central Yukon provide evidence for the local persistence of steppe tundra for at least an additional several hundred years. In the context of shrub expansion and the loss of steppe-tundra, these data can provide additional insight into the role of vegetation change in the decline of megafauna by providing chronologically well-constrained evidence for the local persistence of steppe-tundra in easternmost Beringia. Whether such sites could have provided a late-persisting refugium for grazing megafauna before their extinction is unknown, but the premise that all steppe-tundra was lost in east Beringia by 14,000 cal yr BP is too generalised. These findings underscore the importance of local-scale records in understanding the spatial and temporal variability of ecosystem responses to climate change. While acknowledging potential biases introduced by selective caching behaviours, this study demonstrates the value of Arctic ground squirrel middens as archives of past biodiversity and environmental conditions. The persistence of steppe-tundra habitats in easternmost Beringia beyond the regional signal of vegetation change highlights the complex nature of ecosystem transitions and emphasises the need for high-resolution, local-scale studies to complement broader regional reconstructions.

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