Quaternary Research (2024), **119**, 118–128
doi:10.1017/qua.2024.1

Research Article

The Enmynveem mammoth and vegetation changes in arctic Chukotka during the Late Quaternary

Anatoly V. Lozhkin[a] and P.M. Anderson[b]

[a]North East Interdisciplinary Science Research Institute N.A. Shilo, Far East Branch Russian Academy of Sciences, Magadan, 685000, Russia and [b]Earth and Space Sciences and Quaternary Research Center, University of Washington, Seattle, Washington 98195, USA

Abstract

Mining operations in the Enmynveem valley, northeastern Siberia, exposed a well-preserved right hind leg of *Mammuthus primigenius* (woolly mammoth), dated to ca. 37,500 cal yr BP. The leg had a fracture that crosscut the midsections of the tibia and fibula. Additional skeletal and soft tissue remains, including two mummified adults (Berezovka, ca. 47,200 cal yr BP; Bolshoi Lyakhovsky, ca. 37,000 cal yr BP), document the presence of mammoths in interior mountain valleys and across both northern and southern coasts of far northeastern Siberia during Marine Isotope Stage (MIS) 3. A mosaic of herb-dominated tundra communities characterized the vegetation of the Enmynveem site during late to middle MIS 3 and MIS 2 (ca. 37,000–17,000 cal yr BP). Shrubs were limited to *Salix* during the late Pleistocene, whereas *Betula* also may have been present in sheltered sites during MIS 3. Herb communities remained dominant during the late Pleistocene–Early Holocene transition, although shrub *Betula* increased during this interval. By ca. 10,200 cal yr BP, the vegetation was *Betula–Alnus* shrub tundra. *Larix* and *Pinus pumila* were established in the valley by ca. 8700 cal yr BP and ca. 5700 cal yr BP, respectively.

Keywords: *Mammuthus*, paleovegetation, Holocene, Late Pleistocene, Western Beringia

(Received 22 August 2023; accepted 5 January 2024)

Introduction

Western Beringia (northeast Siberia) is a region that is known for its late Pleistocene deposits, which are rich in late Pleistocene faunal remains (referred to as the mammoth [*Mammuthus primigenius*] or mammoth-steppe fauna; Guthrie 1982, 1990). These finds range from the well-preserved baby mammoth "Dima" (Shilo et al., 1983; Lozhkin and Anderson, 2016; Fig. 1, site 4) to the Holocene-aged dwarf mammoths of Wrangel Island (Vartanyan et al., 1993). Of course, all mammoth sites, not only spectacular ones such as these, are of interest. They present not only paleontological information, but also provide excellent opportunities for a spectrum of studies, ranging from paleoecological to cryological. Most of the initial finds of the glacial-age fauna in western Beringia were discovered in the Yana-Kolyma lowland and the present-day islands of the East Siberian Sea, which during the cool stages of the late Pleistocene and the earliest Holocene formed an extensive coastal lowland (Fig. 1). The remains of Pleistocene mammals from this area are confined mainly to ice-rich, silty sediments, known as *yedoma* (Tomirdiaro, 1982), which underlie the elevated surfaces of the modern tundra. The thermal erosion processes common in this region result in the active destruction of these unconsolidated deposits. Bones and the remains of soft tissues, which have thawed from the frozen sediments, collect in the bottoms of thermokarst ravines found at the bases of cliffs, beside the banks of rivers and lakes, and along sea beaches. Accumulations of mammoth remains can reach an impressive scale, such as the mammoth "graveyard" discovered on the banks of the Berelyokh River (Fig. 1, site 2) in the lower reaches of the Indigirka drainage, where 8431 mammoth bones were unearthed (Nikolskiy et al., 2010, 2011; Pitulko, 2011; Pitulko et al., 2014; Lozhkin and Anderson, 2018). The early finds of Pleistocene fauna were fewer in the mountainous interior, which encompasses the basins of the upper Kolyma, Indigirka, and Yana drainages, and were almost exclusively the result of mining operations. Perhaps this geographic discrepancy was one of the reasons that Shilo et al. (1983) suggested a seasonal movement of mammoths, with populations congregating in the coastal lowlands during the winter and dispersing into smaller groups within the interior valleys during summer.

Mining activity increased in western Beringia during the latter half of the twentieth century, often resulting in the opening of large quarries in the central Indigirka-Kolyma region and in Chukotka. These excavations uncovered Late Quaternary strata associated with ancient alluvial terraces and infill of intermontane tectonic depressions. Such activity resulted in the unearthing of the Kirgilyakh mammoth (Shilo et al., 1983; Lozhkin and Anderson, 2016) in the upper reaches of the Kolyma River, as well as generally increasing the numbers of mammoth sites

Corresponding author: P.M. Anderson; Email: pata@uw.edu
Cite this article: Lozhkin AV, Anderson PM (2024). The Enmynveem mammoth and vegetation changes in arctic Chukotka during the Late Quaternary. *Quaternary Research* **119**, 118–128. https://doi.org/10.1017/qua.2024.1

Figure 1. Map of western Beringia showing the coast lines during MIS 2 (solid line, sea level of −100 m below present level) and MIS 3 (dashed line, sea level of −50 m below present level; Hopkins, 1973; Lozhkin, 2002). Locations of select mammoth and palynological sites in western Beringia indicated by black circles: 1, Enmynveem mammoth (leg); 2, Berelyokh mammoth, Indigirka Lowland (leg); 3, Bolshoy Lyakhovsky Island (skin); 4, Kirgilyakh River, Kolyma basin (body of baby mammoth “Dima”); 5, Tanon River, northern Okhotsk region (tusks); 6, El’gygytgyn Lake; 7, Ilirney Lake; 8, Rauchuagytgyn Lake; 9, Maly Krechet Lake, Sunset Lake, Melkoye Lake; 10, Gytgytkai Lake; 11, Ledovyi Obryv Exposure. Note that the specific location for the Berezovka mammoth is not shown, because precise coordinates were not taken when the carcass was excavated in the early 1900s.

found outside the northern lowland. It became apparent that mammoths occupied a wider geography in far northeastern Asia than was originally thought, including throughout the interior valleys, and extending to the northern coast of the Okhotsk Sea (Lozhkin et al., 2019; Fig. 1, site 5), the latter representing the southernmost mammoth population in western Beringia.

In this paper, we report on another mammoth find from a northern area of western Beringia. The site is in the mountainous region of northern Chukotka, a region less well known than the coastal lowland. In 1989, mining operations exposed a well-preserved right hind mammoth leg on the bank of the Enmynveem River (68°10′N, 165°56′E; Figs. 1, site 1, and 2). In addition to a description of the leg, we examine the Late Quaternary vegetation of the Enmynveem valley. Palynological data collected at the mammoth locale and from a nearby slope exposure supplement continuous pollen records obtained from Chukotkan lakes (Matrosova et al., 2004; Lozhkin et al., 2007; Lozhkin and Anderson, 2013a; Anderson and Lozhkin, 2015; Andreev et al., 2021; Fig. 1, sites 6–10; see also Andreev et al., 2012, site 6; Lozhkin et al., 2000, site 11). The Enmynveem site, in particular, provides much-needed information about the late Pleistocene and Holocene vegetation in the river valleys of northern Chukotka and insights into the mammoth habitats during the latter half of marine isotope stage (MIS) 3.

Study Area and Background

The study area is on the eastern edge of a vast coastal lowland that borders the East Siberian Sea in northeastern-most Siberia. The Enmynveem River, part of the Maly Anyui River basin (Fig. 1), joins the Bolshoy Anyui River, which in turn flows into the Kolyma River. Individual peaks near the study site are 1450–1500 m above sea level (m asl) and rise to ∼300–350 m above the valley floor. On the lower mountain slopes, open *Larix cajanderi* forests with a shrub understory of *Betula*, *Salix*, *Duschekia fruticosa* (*Alnus fruticosa*), and *Pinus pumila* are common. Graminoid–forb meadows are present within openings in the forest. Shrub tundra dominates the valley slopes at mid- and higher elevations. Continuous and discontinuous herb tundra occurs at the highest elevations within the Enmynveem basin.

In the Enmynveem valley, the relatively gentle slopes formed by colluvial sediments have covered the underlying alluvial terraces. On the right bank of the Enmynveem, the width of such slopes reaches 1–2 km. The flat surfaces of the slopes gradually rise toward the mountains, and soils are usually wet. Ice-wedge polygons are clearly visible. The thickness of these unconsolidated deposits varies between 15 and 23 m and increases toward the foot of the mountains due to the downslope movement of clastic material. Alluvial pebbles lie at the base of these slope deposits. The coarse-grained deposits are overlain by layers of silt, often containing angular pebbles, and by peat horizons.

The study site includes two exposures within the Enmynveem valley: the mammoth exposure (68°10′N, 165°56′E; 400 m asl) and the slope exposure (68°15′N, 166°00′E; 500 m asl) (Fig. 1, site 1). Approximately 700 m from the bed of the river, ca. 830 cm of unconsolidated sediments were uncovered during mining operations, with the upper ca. 420 cm having been removed with explosives. The mammoth remains were found here, and we informally refer to this locality as the "mammoth exposure." The uppermost part of the deposits had been destroyed by the miners, but these sediments were preserved in another section (informally called the "slope exposure"), located 100 m downstream from the mammoth exposure.

Methods

The mammoth leg was uncovered in December 1989 during mining operations and reported to the North East Interdisciplinary Science Research Institute (NEISRI) in Magadan. Conditions for the preservation of the mammoth leg were ideal. December air temperatures were near −40°C, and because of the long polar nights, when the sun is above the horizon only for a short time, sunlight did not warm the exposed sediments. Fieldwork was done with artificial lighting. The leg was kept in subzero temperatures and then transported to Magadan, where it was stored in a cold room. The leg was subsequently thawed and dissected. The reconstructed leg is currently on display in Magadan at the Natural History Museum at NEISRI (note: there is no unique accession number, but the find has been catalogued as the Enmynveem mammoth leg). Upon notification of the discovery, AVL traveled to the site, recovered the leg, and described the site's lithology (Table 1).

Table 1. Lithology, Enmynveem sites, western Beringia.

Site name	Depth (cm)	Sediment description
Mammoth exposure	450–465	Silt mixed with pebbles and gravel; unit 1
	465–510	Peat; unit 6
	510–630	Silt mixed with sand, pebbles, and gravel; unit 2
	630–660	Peat mixed with silt; unit 5
	660–720	Silt with plant remains; unit 3
	720–755	Silt mixed with sand, pebbles, and gravel; unit 2
	755–805	Gravel and pebbles; unit 4
Slope exposure	0–30	Modern soil and surface vegetation; unit 1
	30–40	Peat; unit 2
	40–100	Silt with plant remains; unit 3
	100–180	Peat; unit 2
	180–225	Silt with plant remains; unit 3
	225–240	Peat; unit 2
	240–270	Silt with plant remains; unit 3
	270–280	Peat; unit 2
	280–315	Silt with plant remains; unit 3
	315–330	Peat; unit 2
	330–360	Silt with plant remains; unit 3
	360–380	Peat; unit 2
	380–410	Silt with plant remains; unit 3
	410–440	Peat; unit 2

Samples for palynological analysis were taken from the mammoth and slope exposures and the sediments coating the leg. In addition to the fossil samples, modern pollen samples were collected from surface soils in the Enmynveem River valley. Chemical preparation of these samples followed methods recommended for sediments collected from arctic lakes and estuaries (PALE Steering Committee, 1994).

The pollen and spore percentages were calculated using TILIA, and the diagrams were plotted with TILIAGRAPH (http://www.neotomab.org/apps/tilia). The pollen taxa are shown as a percentage of the sum of all terrestrial arboreal and nonarboreal pollen; spores and aquatics are shown as a percentage of the pollen sum. Percentages of the subsum groups (Trees & Shrubs; Herbs; Spores) are based on a sum of arboreal and nonarboreal pollen and spores. Plant taxonomy follows Czerepanov (1995), except for *D. fruticosa.* To avoid confusion, this taxon is referred to in the text as shrub *Alnus/Alnus fruticosa* following standard palynological rather than botanical nomenclature. *Pinus* subgen. Haploxylon pollen represents *P. pumila.* Radiocarbon dates from the mammoth leg and bulk peat samples (Table 2) were obtained in the radiocarbon lab at NEISRI using a benzene liquid scintillation method. The dates were converted to calibrated ages using the IntCal20 calibration curve in CALIB 8.2 (Reimer et al., 2020; Stuiver et al., 2020).

Results

Enmynveem exposures

The mammoth exposure consisted of peat, silt, gravel, and pebbles (Table 1), with the leg found in the basal sediments. Radiocarbon dates of 8315 ± 60 yr BP (9330 cal yr BP) and 9070 ± 65 yr BP (10,230 cal yr BP) were obtained from a peat layer (465–510 cm; Tables 1 and 2), indicating an Early Holocene age for the uppermost deposits. The lack of radiocarbon dates between ca. 500 and 800 cm prevents clear age assignments to the pollen zones. Nonetheless, the regional pollen stratigraphy suggests that upper zone ME2 probably is from the late glaciation (Anderson and Lozhkin, 2015). Zones dominated by herb taxa most likely reflect the full glacial vegetation of MIS 2. The site's lithology indicates the site experienced intervals of stable substrates with peat accumulation. However, the dominance of silt and coarse-grained sediments indicates that most of the site formed under less stable environments related to slope slippage and floodplain disturbances. Although it is not possible to conclude definitively from the available data, the lithology suggests that hiatuses are likely present at the Enmynveem exposure.

The slope exposure was dominated by silt and peat. The thickness of the active layer was ca. 45 cm. Seven radiocarbon dates were obtained from the peats (Table 2). Although dating reversals are present, the dates and pollen stratigraphy are consistent with a Middle to Late Holocene age for the exposure.

Both sections contained ice wedges that formed surficial polygons up to 15–25 m in width. These permafrost features are characteristic of the unconsolidated deposits in this region. The upper widths of the ice wedges at the Enmynveem locale reach 5–6 m. Vertically, the ice wedges completely span the entire thickness of the unconsolidated deposits. The radiocarbon dates indicate that the active growth of the ice wedges, which in western Beringia generally formed during MIS 2, continued to develop in arctic Chukotka into the Early and Middle Holocene, despite regional climatic warming (Lozhkin and Vazhenina, 1987; Lozhkin et al., 2011).

https://doi.org/10.1017/qua.2024.1 Published online by Cambridge University Press

Table 2. Radiocarbon and calibrated ages, Enmynveem sites, western Beringia.

Depth (cm)	^{14}C age (yr BP)	Median calibrated age; 2-sigma age range (cal yr BP)	Laboratory number	Material dated
		Mammoth exposure		
465	8315 ± 60	9330; 9470–9130	MAG-1070	Peat
500	9070 ± 65	10,230; 10,430–10,130	MAG-1069	Peat
800	32,850 ± 800	37,540; 39,480–35,680	MAG-1001A	Mammoth skin
800	32,890 ± 1200	37,630; 40,420–35,080	MAG-1001B	Mammoth skin and muscle
		Slope exposure		
145	4725 ± 390 BP	5380; 6300–4410	MAG-1068	Peat
175	5260 ± 60 BP	6050; 6190–5910	MAG-1067	Peat
235	7810 ± 80 BP	8600; 8790–8410	MAG-1066	Peat
275	7830 ± 170 BP	8680; 9130–8330	MAG-1064	Peat
325	7965 ± 140 BP	8820; 9140–8450	MAG-1062	Peat
365	7680 ± 200 BP	8510; 9000–8160	MAG-1060	Peat
425	7530 ± 35 BP	8360; 8410–8300	MAG-1059	Peat

Figure 2. Enmynveem mammoth leg in NEISRI laboratory after arrival from Chukotka. The length of the leg is 1.05 m.

Mammoth leg

The well-preserved mammoth remains from the Enmynveem site include a femur, patella, tibia, fibula, and small bones from the foot, in total measuring 105 cm in length (Fig. 2). The soft tissue included the surrounding muscles and skin. A sharp break with no displacement of the bones crosscuts the midsections of the tibia and the femur. The length from the bottom of the leg to the knee joint (i.e., top of the tibia, patella, and bottom of the femur) is 88 cm. The circumference of the leg around the knee joint is 105 cm, and at the level of the middle third of the lower leg, it is 84 cm. Foot size is 33 × 36 cm, and the foot circumference is 116 cm. Near the knee joint, a 20-cm-long piece of thigh skin is missing. A mass of coagulated blood was found near the breakage.

The skin of the mammoth was yellowish gray, with dark brown patches. Near the knee and in the lower part of the leg, fragments of guard hairs (0.5–3 cm long) have been preserved. In general, the hair cover is sparse, varying between single hairs to 15–20 hairs/cm^2. The thickness of the skin at the top of the leg is 3 cm and decreases at the level of the knee to 1.1 cm. The thickness of the skin of the lower leg is 1.2–2 cm. Ragged edges of the skin and muscles may indicate separation of the lower leg from the thigh. A deep, 30-cm-long linear tear on the outer lateral surface of the leg, extending from the base of the leg, was apparently formed by deep freezing of the soft tissues after the animal's death. There is a fracture in the midsection of the tibia and a double fracture of the fibula. A large hematoma was present at the fracture sites.

Two radiocarbon dates were obtained, one from the skin alone and one from the skin with attached muscle of the mammoth thigh (Table 2). The dates of ca. 37,470 cal yr BP and 37,630 cal yr BP indicate that the animal lived during the most recent MIS 3 cool period (ca. 38,900–29,000 cal yr BP; Lozhkin and Anderson, 2011).

Palynological data

Palynological samples were collected from the modern soils (Figs. 3, samples 1–3, and 4, 0 cm) and from two sections exposed

https://doi.org/10.1017/qua.2024.1 Published online by Cambridge University Press

during the mining operation (Figs. 3 and 4). Two additional samples were taken from the sediments coating the mammoth leg (Fig. 3, samples 4 and 5).

The modern pollen spectra from the soil samples are dominated by woody taxa, reaching up to 65% of total pollen and spores (note: given the importance of shrub tundra in northern Chukotka and the lack of tree species of *Betula* or *Alnus* in the Enmynveem valley, the trees and shrubs subsum essentially represents shrub taxa). In two of the four samples, *Betula* percentages exceed *Alnus*, whereas in the other two samples, the percentages are approximately equal. Ericales pollen is generally between 20% and 30% (note: following traditional Russian classification, Ericales is considered an herb and is part of the herb subsum group). The herb subsum group varies between ca. 25% and 45% and is characterized by numerous minor taxa, indicative of a variety of microhabitats. The spore subsum group has low percentages (up to ca. 15%) but like the herb group, represents differing ecologies.

Samples from sediments adhering to the mammoth leg are dominated by herb pollen (ca. 75–85% of total pollen and spores), with spores at 10–15% and trees and shrubs at <10%. As with the modern samples, a variety of minor herb taxa occur, but both percentages of Poaceae and *Artemisia* pollen are markedly higher than in the modern spectra.

Results from the undisturbed section associated with the mammoth leg (Fig. 4) indicate the presence of four pollen zones (ME1, 800–720 cm; ME2, 720–655 cm; ME3, 655–520 cm; ME4, 520–450 cm). All zones have high values of Poaceae pollen. The highest percentages occur in zone ME1 and lower zone ME2 (ca. 45–65%) with percentages in the other zones of <45%. Zone ME3 is distinguished by its high percentages of *Artemisia* pollen (up to 40%), in contrast to the other zones, where values are <10%. As in the modern samples, minor herbs represent various microhabitats. Arboreal taxa are low in zones ME1–ME3 (<10% of total pollen and spores), although *Salix* pollen is 7–10% in zone ME2. Samples in zone ME4 have 30–35% *Betula* pollen and 8–10% *Alnus* pollen. Bryales, the most common spore, is generally <10%, except in zone ME3, where it is 10–20%.

The palynological data from the slope exposure (Fig. 5) also fall into four zones (EN1, 430–255 cm; EN2, 255–195 cm; EN3, 195–80 cm; EN4, 80–0 cm), which represent the Middle to Late Holocene. The pollen assemblages in all the EN zones are dominated by *Betula* (up to 65%) and *Alnus* (up to 34%). Taxa that occur in more moderate percentages include *Salix* (up to 25%), Ericales (up to 35%), Poaceae (up to 22%), and Cyperaceae (up to 10%). *Salix* pollen is slightly higher in zone EN1. Maximum Ericales percentages occur in zones EN2 and EN4. *Pinus* subgen. Haploxylon pollen occurs consistently in zones EN3 and EN4, although it is <10%. Trace amounts of pollen of the deciduous conifer *Larix* appear consistently in the upper three zones, whereas only the uppermost sample in zone EN1 records *Larix*. Of the herb taxa, Poaceae has the highest percentages with the greatest values in zone EN1. *Sphagnum*, while showing variable percentages, is the dominant spore. As in the mammoth exposure, a variety of minor herb taxa are found in all zones.

Discussion

MIS 3 mammoths in western Beringia

Lozhkin and Anderson (2016) described the MIS 3 environments associated with seven juvenile mammoth sites within western Beringia. They concluded that unstable landscapes both in the lowlands and in mountain valleys were key factors in the deaths of the mammoth calves. Their synthesis of the paleobotanical data further indicated that mesic tundra and forests dominated the MIS 3 landscapes and that the association of mammoths with steppe or steppe tundra, first suggested by Guthrie (1982, 1990), albeit focused primarily on MIS 2, is incorrect, at least for western Beringia. Two additional finds of adults (described later), when combined with other mummified remains, show that mammoth populations were present across western Beringia during MIS 3, stretching from the islands of the East Siberian Sea southward to the Okhotsk Sea coast and from the Indigirka basin eastward to central Chukotka (Lozhkin and Anderson, 2016; Lozhkin et al., 2019; for distribution of mammoth sites in MIS 2, see Dehasque et al., 2021).

A large hematoma at the fracture sites in the tibia and fibula indicates that the Enmynveem mammoth was injured while still alive. Such a deep leg injury, which almost certainly caused circulatory disorder and tissue necrosis, could have instigated the death of the animal. The subsequent rapid freezing contributed to the preservation of the soft tissues, perhaps suggesting the animal was buried in water-rich sediments. The leg injury may have been indirectly caused by the mammoth's interaction with predators (e.g., being chased to a cliff edge where it fell and sustained injury, or ultimately perished) or, as suggested earlier, by accident in an unstable landscape (e.g., melting of an ice wedge exposed in the riverbank, which saturated and weakened the sediment, causing the cliffside to give way under the animal's weight). While predators probably would have focused on calves, the relative abundance of fossil finds of young mammoths in western Beringia suggest that they also faced danger from the landscape itself.

The earliest discovery of a mummified mammoth in western Beringia dates to August 1900, when an adult male (estimated to be 45–50 yr old) was discovered by Even hunter Semyon Tarabykin on the banks of the Berezovka River, a tributary to the Kolyma River (Komarov, 1930; Ukraintseva et al., 1993; Ukraintseva, 2013). The frozen corpse was lying in an unusual position, on his stomach, with legs stretched forward and slightly bent. The upper part of the head and the back had thawed and were extensively gnawed by predators. Most of the trunk was also missing. The mammoth had suffered a broken pelvis and shoulder. Apparently, the animal either fell into a deep gully or tumbled off a cliff. The age of the Berezovsky mammoth is estimated to be ca. 44,000 ^{14}C yr BP (ca. 47,200 cal yr BP; http://www.atlasobscura.com/places/berezovsky-mammoth; note that this age is near the limit of radiocarbon dating).

Unchewed pieces of vegetation were found in the animal's mouth. The plant remains were identified as *Carex* sp., *Thymus serpillum*, *Ranunculus acer*, *Gentiana* sp., *Cypripedium* sp., and *Papaver alpinum*. Seeds were attached in many of these plants, so it is believed that the mammoth died at the end of summer. Unfortunately, no additional paleovegetation data are available from the site. However, the plant macrofossils indicate the presence of tundra, consistent with paleoenvironments associated with other mammoth mummies. Although the plant remains represent only local vegetation eaten just before the mammoth's death, the macrofossils indicate the presence of both xeric (*T. serpillum*, *P. alpinum*) and mesic (*R. acer*) tundra sites on the landscape.

Another key mammoth site is from Bolshoi Lyakhovsky Island, discovered in 1990 (Lozhkin 1990; Fig. 1 site 3). The mammoth was discovered 57 km west of Shalaurov Cape in a 33- to

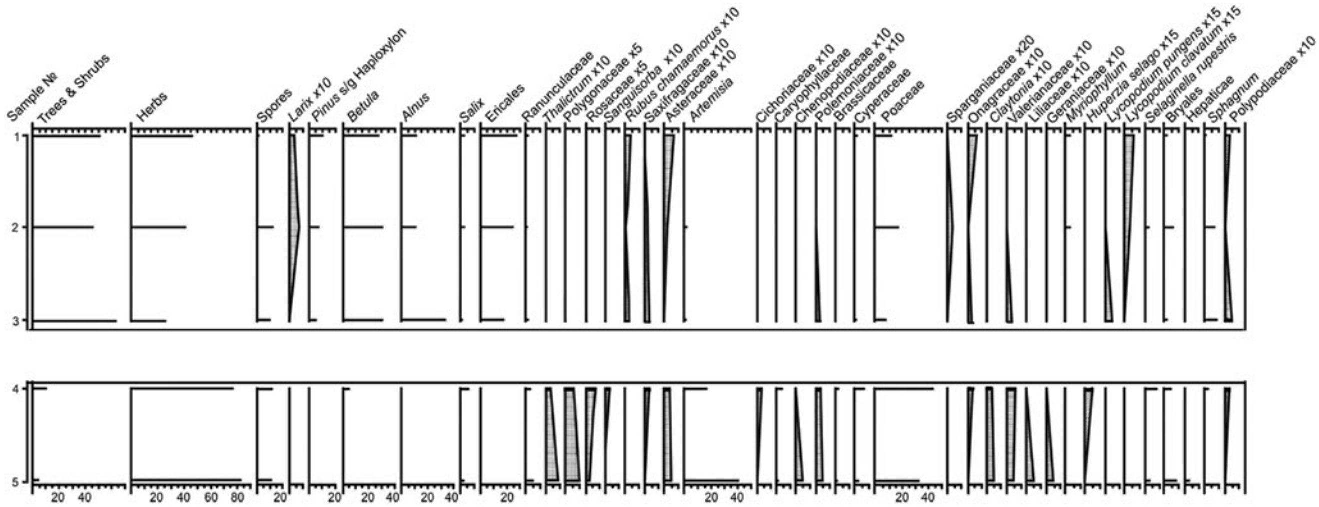

Figure 3. Percentages of modern pollen and spores taken from soils on the valley slopes bordering the Enmynveem River (1–3) and palynological spectra from sediments that surrounded the foot of the Enmynveem mammoth (sample 4 from the foot cavity; sample 5 from the foot surface).

35-m-high coastal cliff, which consists of ice wedges within yedoma deposits. Near the island's coast, the yedoma has been dissected by thermokarst processes, resulting in the formation of ravines and pillar-like remnants of interior sediments of ice-wedge polygons, the latter referred to as *baydzharaks*. A partial mammoth skeleton along with preserved soft tissues and skin with attached fur was uncovered in a 6-m-high baydzharak. The structure consists of sand and sandy loam; the latter included abundant plant remains. The 70-cm-thick layer containing the mammoth was a mix of sandy loam and fine-grained sand. This layer was at a height of 1.2 m asl. The site's lithology indicates a fluvial origin, including a streambed and bordering floodplain.

The mammoth skin was radiocarbon dated to 32,100 ± 900 BP (MAG-316; ca. 36,600 cal yr BP) and 32,030 ± 1170 BP (MAG-316A; ca. 37,800 cal yr BP).

Unlike today, the mammoth site was at that time considerably removed from the coast of the East Siberian Sea (Fig. 1). The vegetation at the site was dominated by herbaceous tundra (main taxa of Poaceae, Cyperaceae, Caryophyllaceae, Brassicaceae, *Artemisia*) but included modest percentages of shrub taxa (*Betula exilis*, *Betula middendorffii*, *A. fruticosa*, and *P. pumila*). Peat deposits of MIS 3 age from the island were also dominated by tundra, but with *Salix* being the only woody species present (Andreev et al., 2008). As with the Enmynveem mammoth, these sites both indicate that steppe or a steppe–tundra biome did not characterize northern Chukotka during this portion of MIS 3.

Modern pollen and vegetation, Enmynveem sites

The modern pollen spectra from the Enmynveem valley are dominated by woody taxa, indicating the importance of shrub tundra and the shrub understory within the local forest. *Betula* (e.g., *B. exilis*, *B. middendorffii*) is the most common shrub in the modern landscape, with *A. fruticosa*, and *P. pumila* playing secondary roles. Shrub thickets, particularly of *Betula*, are common on the slopes of the river valley. One of the most noticeable features of these modern spectra is the underrepresentation of *Larix*, the pollen of which either occurs in trace amounts (<2%) or is absent. The poor pollen preservation of *L. cajanderi*, the only forest-forming coniferous tree species in northeast Siberia, has long been noted in both modern and fossil samples (Vaskovsky, 1957). Thus, the extremely low amounts of *Larix* pollen do not reflect its dominant role in the regional forests.

The prominence of herb tundra and within-forest meadows in the Enmynveem valley is shown by the high percentages of herb pollen (up to 45%), with Poaceae (up to 15%) being the most abundant taxon. The importance of mesic, ericaceous communities is indicated by the high percentages of Ericales pollen (up to 30%) and to a lesser extent by the modest amounts of green moss spores. The former taxa perhaps indicate the presence of *Ledum palustrum*, *Ledum decumbens*, *Vaccinium vitis-idaea*, and *Vaccinium uliginosum*, which are common on the modern landscape.

Holocene and late Pleistocene vegetation of the Enmynveem valley

Both the mammoth and slope exposures reflect several different depositional environments. The mammoth exposure is dominated by silts and coarse sediments with gradational boundaries between lithological units. This lithology is typical of riverine settings in northern Chukotka. The coarse sediments (unit 1; for brevity, the lithologies are referred to as "units"; Fig. 4A) immediately associated with the mammoth leg originated as either floodplain deposits or colluvium from the nearby slopes. Other alluvial deposits (units 2–4) indicate the dominance of an active floodplain during much of the latest Pleistocene. Intervals with peaty deposits (units 5, 6) indicate less disturbed settings, where organic deposits could accumulate. In contrast, the alternating layers of peat and silt in the slope exposure (Fig. 5), which have sharp lithological boundaries, reflect shifts between stabilized (peat) and less stable (silt) surfaces in the valley bottom.

Palynological samples associated with the mammoth leg (Fig. 3, samples 4 and 5) and from zone ME1 (Fig. 4) reflect a vegetation that differed from the modern, with the fossil assemblage showing higher percentages of herb pollen and reduced amounts of arboreal pollen. These spectra are reminiscent of the herb pollen zone initially described for MIS 2 (i.e., high percentages of graminoid and *Artemisia* pollen; Hopkins, 1982; Lozhkin et al.,

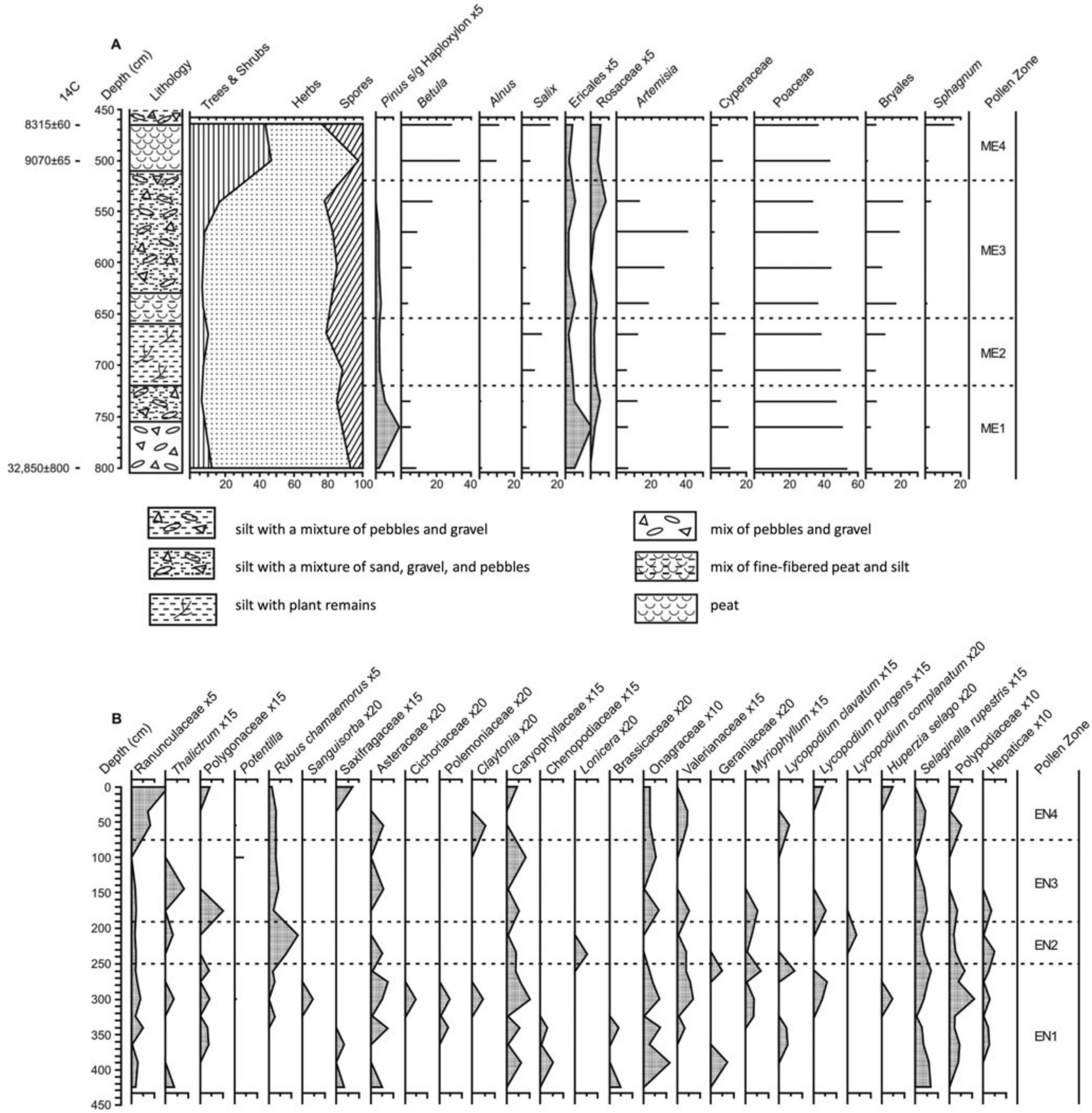

Figure 4. Palynological results from the mining exposure that contained the Enmynveem mammoth leg: (**A**) percentages of subsum vegetation groups (left side of the diagram), individual percentages of major taxa; (**B**) minor pollen and spore taxa. The mammoth leg was found at the bottom of the exposure. See Table 1 for more details on site lithology.

2007; Lozhkin and Anderson, 2013b), but are also characteristic of MIS 4 in western Beringia (Lozhkin at al., 1998; Lozhkin and Anderson, 2013b). In the Enmynveem samples, the high percentages of total herb pollen, dominated by Poaceae, indicate the prevalence of Poaceae and Poaceae–forb associations in the local and probably the regional vegetation. Cyperaceae and Poaceae–Cyperaceae communities with Ranunculaceae, *Polygonum*, *Sanguisorba*, *Rubus chamaemorus*, Caryophyllaceae, Polemoniaceae, and Gentianaceae likely occupied mesic habitats along shores bordering rivers, streams, and lakes. The presence of well-drained substrates is indicated by pollen of *Artemisia*, Rosaceae, Saxifragaceae, Asteraceae, Cichoriaceae, and Chenopodiaceae, as well as *Selaginella rupestris* spores.

In terms of woody taxa, *A. fruticosa* and *P. pumila*, shrubs that today grow in northern Chukotka, were absent in the Enmynveem valley ca. 37,660–36,370 cal yr BP. *Betula* pollen percentages also are noticeably lower than in modern samples. Perhaps the shrubs were limited to low-growth forms, such as *B. exilis*. *Salix* was present in protected places along stream sides and as part of snow bed communities, as seen today, for example, in the tundra of

https://doi.org/10.1017/qua.2024.1 Published online by Cambridge University Press

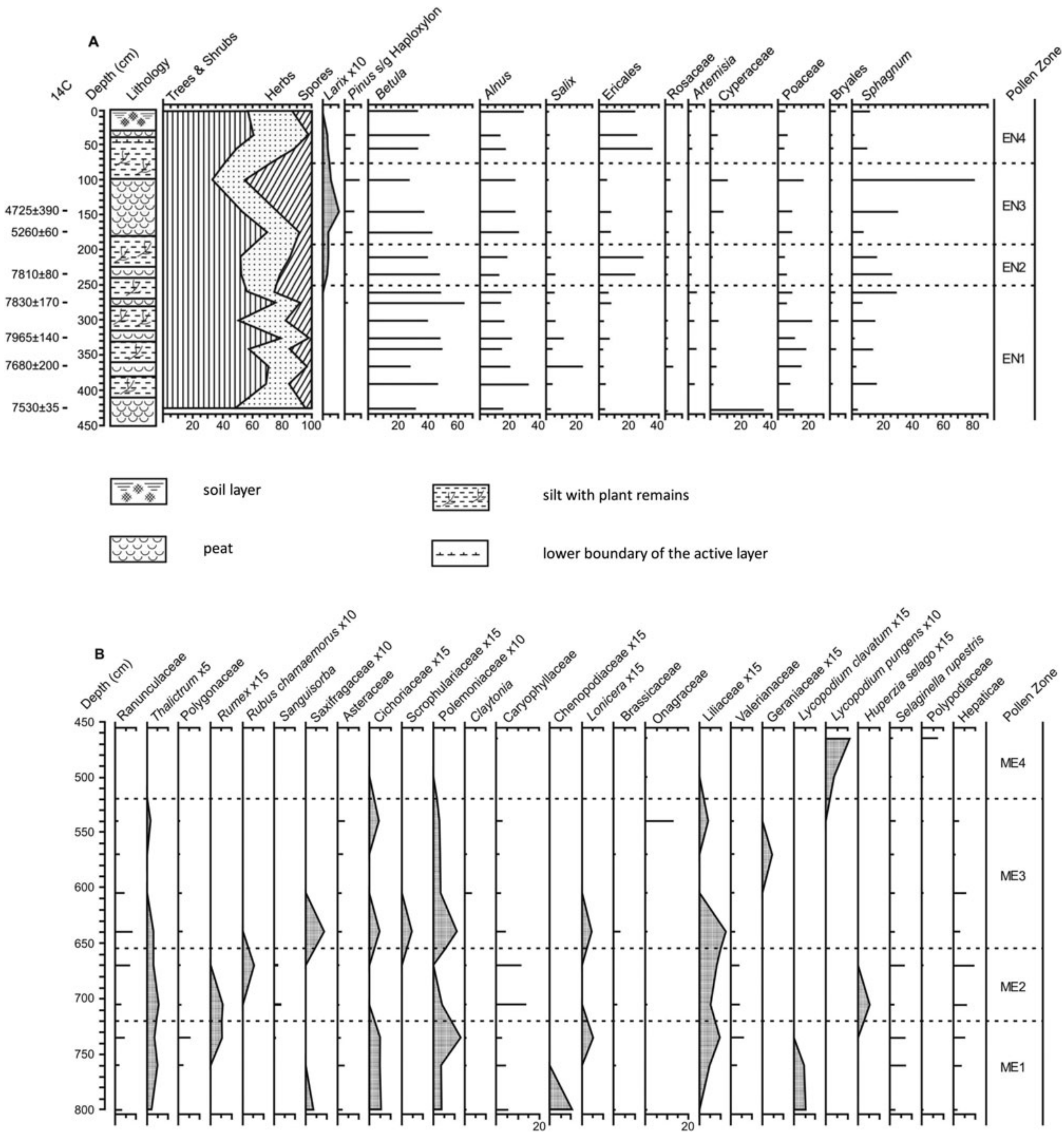

Figure 5. Palynological results from slope sediments of the Enmynveem River valley: (**A**) percentages of subsum vegetation groups (left side of the diagram), individual percentages of major taxa; (**B**) minor pollen and spore taxa. See Table 1 for more details on site lithology.

Wrangel Island (Anderson and Lozhkin, 2015; Lozhkin et al., 2001). The absence of *Larix* pollen, although not definitive given the taxon's underrepresentation, suggests that the deciduous conifer did not grow in the Enmynveem River basin during this portion of MIS 3. Data from El'gygytgyn Lake (Fig. 1, site 6) also indicate that *Larix* was absent or rare in the vegetation of northern Chukotka (Lozhkin et al., 2007).

Thus, the herb-dominated pollen spectra from the sediments that contained the mammoth's leg most likely represent a mosaic of various herb-dominated communities, varying from a discontinuous cover of graminoids and *S. rupestris* on dry slopes to mesic Cyperaceae–moss and Cyperaceae–Poaceae communities with low-growth *Salix* in stream and river valleys. The Enmynveem data, combining cryophilic and xerophilic floristic elements, suggest that the MIS 3 vegetation was probably similar to modern herb tundra.

The zone ME2 assemblage, while still dominated by herb pollen, particularly that from Poaceae, reflects a slight change from the zone ME1 vegetation. Shrub *Betula* is no longer present, whereas shrub *Salix* and to a lesser extent Bryales increase on the landscape. The ME2 assemblage suggests an expansion of *Salix*–*Dryas*–Bryales–Poaceae tundra. *Salix* probably was present in prostrate forms and as scattered thickets in protected lowland areas. In the river valleys, Cyperaceae–Poaceae communities with Ranunculaceae, Polygonaceae, *Sanguisorba*, Caryophyllaceae, Brassicaceae, Liliaceae, and Valerianaceae were established in seasonally wet areas. Similar tundra associations are characteristic of modern vegetation in the central regions of Wrangel Island (Lozhkin et al., 2002) as well as full-glacial pollen spectra within Beringia (Hopkins et al., 1982; Anderson and Lozhkin, 2002; Lozhkin and Anderson, 2013b). Such an assemblage suggests a slight cooling as compared with ME1 and probably reflects MIS 2 climate.

Zone ME3 marks a change in the vegetation associated with postglacial climatic amelioration. Although herb communities remain a major element in the vegetation, the increase in *Betula* pollen from zone ME3 to ME4 suggests the shrub's more widespread presence by the Early Holocene, a characteristic of Beringian pollen records (Hopkins et al., 1982). The minor but consistent appearance of pollen from *Salix*, Ranunculaceae, Asteraceae, Caryophyllaceae, and Valerianaceae and spores from *S. rupestris* and Hepaticae represents a mosaic of tundra types. Large areas of wet to mesic substrates were occupied by Cyperaceae–Poaceae communities with Polygonaceae, Polemoniaceae, Onagraceae, Liliaceae, Valerianaceae, Caryophyllaceae, shrub *Betula*, and shrub *Salix*. *Artemisia* communities with Asteraceae, Brassicaceae, and *S. rupestris* occurred on well-drained rocky slopes and in the uplands.

Zones ME4 and EN1–EN4 reflect the Early to Middle Holocene vegetation in the Enmynveem valley. By ca. 10,200 cal yr BP (ME4), shrub tundra was probably the main vegetation within the valley. *Betula* was the dominant shrub, occurring within valleys and extending up the nearby slopes. It perhaps occurred as scattered individuals across the landscape as well as growing in thickets. The high pollen percentages of Poaceae indicate the persistence of herb communities.

A possible alternative interpretation of the Early Holocene vegetation based on pollen and macrofossils was suggested by Edwards et al. (2005), who postulated the presence of deciduous forest or woodland across areas of Beringia between ca. 13,000 and 10,000 cal yr BP. In western Beringia, *Larix* was the dominant tree, whereas palynological data from eastern Beringia suggest *Populus* played a major role in the forest or woodlands. No data were available from northern Chukotka at the time of their analysis. While, ecologically, the presence of tree *Betula* would be reasonable, tree and shrub growth forms are not easily distinguishable by the pollen. Regardless of the species of *Betula* present at the time, climate had become warmer with greater effective moisture as compared with MIS 2. This interpretation is supported by palynological results from Ilirney Lake (Fig. 1, site 7) to the northeast of Enmynveem, which indicate that *Larix* had established, at least in some valleys of northern Chukotka, by ca. 11,500 cal yr BP (Andreev et al., 2021).

The palynological diagram from the slope sediments (Fig. 5) reflects only minor changes in the plant communities. Reversals in the radiocarbon dates in the lower two zones prevent the assignment of specific ages, but suggest that the sediments were deposited over the past ca. 8000 cal yr BP. The spectra are dominated by pollen from *Betula* and *Alnus*. However, changes in the subsum portion of the diagram can be used to distinguish four pollen zones.

The zone EN1 assemblage is consistent with Early to Middle Holocene palynological data from western Beringia (Anderson and Lozhkin, 2002, 2015). These spectra probably reflect the dominance of *Betula*–*Alnus* shrub tundra, which had replaced the herb tundra that had characterized most of the region during the last glacial stage of the Pleistocene. As mentioned earlier, it is possible that *Betula* woodlands were present in northern Chukotka. Although occurring in lower percentages as compared with zones ME1 and ME2, herb pollen is sufficiently high in zone EN1 to suggest the presence of Cyperaceae–Poaceae–forb communities. The low percentages of Ericales pollen indicate the establishment of the subshrub, but it did not become common until zone EN2. These ericaceous communities also included *R. chamaemorus*, *Claytonia*, Caryophyllaceae, Polemoniaceae, and *Sphagnum*. Thickets of *Salix* shrubs probably were present along the riverbanks.

Larix pollen appears for the first time in the section in zone EN2 and indicates the spread of deciduous conifer forest into the Enmynveem valley during the Middle Holocene. Although not definitive from the pollen, tree *Betula* was probably part of the forest, as the tree and *Larix* have similar ecological requirements. Ericales communities perhaps dominated the ground cover in association with *R. chamaemorus*, *V. vitis-idaea*, *V. uliginosum*, *Andromeda polifolia*, *L. decumbens*, and *Sphagnum*. With the exception of low percentages of *Pinus* pollen, the EN2 palynological assemblage is similar to the modern pollen spectra, especially in terms of the importance of Ericales pollen.

Radiocarbon dating places zone EN3 in the Late Holocene. Lower elevations were occupied by open *Larix* forests. However, the main feature of this zone is the increase in *Pinus* subgen. Haploxylon pollen (up to 10%), representing the spread of *P. pumila* in the Enmynveem basin ca. 5700 cal yr BP. *Pinus pumila* was part of the shrub understory in the *Larix* forest and occurred with *A. fruticosa*, *B. middendorffii*, and *Salix* sp. in thickets at lower elevations within the river valley. The high percentages of *Sphagnum* spores suggest the presence of moist soils in forested areas and/or bogs in the valley lowlands.

The palynological spectra from zone EN4 are dominated by *Betula*, Ericales, and *Alnus* pollen, indicative of vegetation similar to that found today in the Enmynveem River basin. Low percentages of *Pinus* subgen. Haploxylon and *Larix* also reflect the continuing presence of these conifers. *Pinus pumila* is not abundant on the present-day landscape, and *Larix* is restricted to lower elevations within the valley.

Conclusions

The Enmynveem site includes two exposures, one containing the right hind leg of an adult mammoth, which was uncovered during mining operations, and a second from nearby slope deposits. The leg had two fracture sites and a large hematoma indicating that the mammoth was injured while still alive. A fall from riverside slopes or cliffs resulting in the broken leg and tissue necrosis was likely the cause of the animal's death.

In addition to the mammoth remains, the Enmynveem site provides a discontinuous record of vegetation change spanning the last ca. 37,600–37,440 cal yr BP. Herb-dominated tundra was present in the Enmynveem valley during MIS 3 and MIS 2. Populations of *Betula*, possibly including both shrub and tree forms, expanded during the late Pleistocene–Early Holocene transition. *Alnus*, *Larix*, and *P. pumila* were present in the valley by ca. 10,200 cal yr BP, 8700 cal yr BP, and 5700 cal yr BP, respectively.

The cause of death of the three adult mammoth mummies described in this paper and the associated interstadial vegetation

https://doi.org/10.1017/qua.2024.1 Published online by Cambridge University Press

are in accord with previous conclusions of Lozhkin and Anderson (2016): (1) mammoths were present in both coastal lowlands and interior mountain valleys during MIS 3; (2) unstable landscapes both in the lowlands and in mountain valleys were key factors in the deaths of mammoths in western Beringia; and (3) a mix of mesic tundra, forest–tundra, and deciduous forest characterized the western Beringian vegetation during MIS 3.

Acknowledgments. We are grateful to E.E. Schubert for his help with the description of the mammoth leg and morphometric measurements. We wish to thank Yu.A. Korzun for her assistance in preparing the manuscript. We also thank Mary Edwards and two unnamed reviewers for their helpful comments for improving the article.

References

Anderson P.M., Lozhkin A.V., 2002. Palynological and radiocarbon data from Late Quaternary deposits of northeast Siberia. In: *Late Quaternary Vegetation and Climate of Siberia and the Russian Far East (Palynological and Radiocarbon Database)*. North East Science Center Far East Branch Russian Academy of Sciences and U.S. National Oceanic and Atmospheric (NOAA) Paleoclimatology Program, Magadan, Russia, pp. 27–34.

Anderson P.M., Lozhkin A.V., 2015. Late Quaternary vegetation of Chukotka (Northeast Russia), implications for Glacial and Holocene environments of Beringia. *Quaternary Science Reviews* **107**, 112–128.

Andreev, A.A., Grosse, G., Schirrmeister, L., Kuznetsova, T.V., Kuzmina, S.A., Bobrov, A.A., Tarasov, P.E., *et al.*, 2008. Weichselian and Holocene palaeoenvironmental history of the Bol'shoy Lyakhovsky Island, New Siberian Archipelago, Arctic Siberia. *Boreas* **38**, 72–110.

Andreev, A.A., Morozova, E., Federov, G., Schirrmeister, L., Bobrov, A.A., Kienast, F., Schwamborn, G., 2012. Vegetation history of central Chukotka deduced from permafrost paleoenvironmental records of the El'gygytgyn impact crater. *Climate of the Past* **8**, 1287–1300.

Andreev, A.A., Raschke, E., Biskaborn, B.K., Vyse, S.A., Courtin, J., Bohmer, T., Stoof-Leichensenring, K., Kruse, S., Pestryakova, L.A., Herzschuch, U., 2021. Late Pleistocene to Holocene vegetation and climate changes in northwestern Chukotka (Far East Russia) deduced from lakes Ilirney and Rauchuagytgyn pollen records. *Boreas* **50**, 652–670.

Czerepanov, S.K., 1995. *Vascular Plants of Russia and Adjacent States (the Former USSR)*. Cambridge University Press, Cambridge.

Dehasque, M., Pečnerova, P., Muller, H., Tikhonov, A., Nikolskiy, P., Tsigankova, V., Danilov, G., *et al.*, 2021. Combining Bayesian age models and genetics to investigate population dynamics and extinction of the last mammoths in northern Siberia. *Quaternary Science Reviews* **259**, 106913.

Edwards, M.E., Brubaker, L.B., Anderson, P.M., Lozhkin, A.V., 2005. Functionally novel biomes: a response to past warming in Beringia. *Ecology* **86**, 1696–1703.

Guthrie, R.D., 1982. Mammals of the mammoth steppe as paleoenvironmental indicators. In: Hopkins, D.M., Matthews, J.V., Jr., Schweger, C.E., Young, S.B. (Eds.), *Paleoecology of Beringia*. Academic Press, New York, pp. 307–326.

Guthrie, R.D., 1990. *Frozen Fauna of the Mammoth Steppe*. University of Chicago Press, Chicago.

Hopkins, D.M., 1973. Sea level history in Beringia during the last 250,000 years. *Quaternary Research,* **3**, 520–540.

Hopkins D.M., 1982. Aspects of the paleogeography of Beringia during the Late Pleistocene. In: Hopkins, D.M., Matthews, J.V., Jr., Schweger, C.E., Young, S.B. (Eds.), *Paleoecology of Beringia*. Academic Press, New York, pp. 3–28.

Hopkins, D.M., Matthews, J.V., Jr., Schweger, C.E., Young, S.B. (Eds.), 1982. *Paleoecology of Beringia.* Academic Press, New York.

Komarov, V.L. (Ed.), 1930. *Proceedings of the Commission for the Study of the Yakut Autonomous Socialist Republic, volume XV, 1930. The Lena-Kolyma Expedition of 1909 under the Command of K.A. Vollosovich.* [In Russian.] Publishing House of the Academy of Sciences of the USSR, Leningrad.

Lozhkin A.V., 1990. An interdisciplinary approach to the study of mammoth localities in North-East USSR. *Bulletin of the Commission for the Study of the Quaternary* **59**, 156–159.

Lozhkin A.V., 2002. Boundaries of Beringia during the Late Pleistocene and Holocene. In: *Quaternary Paleogeography of Beringia*. [In Russian.] North East Interdisciplinary Scientific Research Institute Far East Branch Russian Academy of Sciences, Magadan, Russia, pp. 4–12.

Lozhkin, A.V., Anderson, P.M., 2011. Forest or no forest: implications of the vegetation for climatic stability in Western Beringia during Oxygen Isotope Stage 3. *Quaternary Science Reviews* **30**, 2160–2181.

Lozhkin, A.V., Anderson, P.M., 2013a. Late Quaternary Lake Records from the Anadyr Lowland, Central Chukotka (Russia). *Quaternary Science Reviews* **68**, 1–16.

Lozhkin, A.V., Anderson, P.M., 2013b. Northern Asia. *The Encyclopedia of Quaternary Sciences*. 2nd ed. Elsevier, Amsterdam. **4**, 2623–2632.

Lozhkin, A.V., Anderson, P.M., 2016. About the age and habitat of the Kirgilyakh mammoth (Dima), Western Beringia. *Quaternary Science Reviews* **145**, 104–116.

Lozhkin A.V., Anderson P. M., 2018. Another perspective on the age and origin of the Berelyokh mammoth site (northeast Siberia). *Quaternary Research* **89**, 459–477.

Lozhkin, A.V., Anderson, P.M., Belaya B.V., Stetsenko T.V., 2002. Reflections on modern pollen rain of Chukotka from bottom lake sediments. In: *Quaternary Paleogeography of Beringia*. [In Russian.] North East Interdisciplinary Scientific Research Institute Far East Branch Russian Academy of Sciences, Magadan, Russia, pp. 40–50.

Lozhkin, A.V., Anderson, P.M., Brubaker L.B., Kotov A.N., Kotova L.N., Prokhorova T.P., 1998. The herb pollen zone from sediments of glacial lakes, Chukotka. *Environmental Changes in Beringia during the Quaternary.* [In Russian.] North East Interdisciplinary Scientific Research Institute Far East Branch Russian Academy of Sciences, Magadan, Russia, pp. 96–111.

Lozhkin, A.V., Anderson, P.M., Glushkova, O.Yu., Vazhenina, L.N., 2019. Late Quaternary environments on the far southwestern edge of Beringia. *Quaternary Science Reviews* **203**, 21–37.

Lozhkin, A.V., Anderson, P.M., Matrosova, T.V., Minyuk, P.S., 2007. The pollen record from El'gygytgyn Lake: implications for vegetation and climate histories of northern Chukotka since the late middle Pleistocene. *Journal of Paleolimnology* **37**, 135–153.

Lozhkin, A.V., Anderson, P.M., Vartanyan, S.L., Brown, T.A., Belaya, B.V., Kotov, A.N., 2001. Late Quaternary paleoenvironments and modern pollen data from Wrangel Island (northern Chukotka). *Quaternary Science Reviews* **20**, 217–234.

Lozhkin A.V., Anderson P.M., Vazhenina L.N., 2011. Younger Dryas and Early Holocene peats from northern Far East Russia. *Quaternary International* **237**, 54–64.

Lozhkin, A.V., Kotov, A.N., Ryabchun, V.K., 2000. Palynological and radiocarbon data of the Ledovyi Obryv exposure (southeast Chukotka). *The Quaternary Period of Beringia.* [In Russian.] North East Interdisciplinary Scientific Research Institute Far East Branch Russian Academy of Sciences, Magadan, Russia, pp. 118–131.

Lozhkin, A.V., Vazhenina, L.N., 1987. Vegetation development in the Kolyma lowland during the Early Holocene. In: *Quaternary Period of the North-East of Asia.* [In Russian.] North East Interdisciplinary Scientific Research Institute Far East Branch Russian Academy of Sciences, Magadan, Russia, pp. 135–144.

Matrosova T.V., Anderson P.M., Lozhkin A.V., Minyuk P.S., 2004. Climate history of Chukotka during the last 300,000 years from the Lake El'gygytgyn Pollen Record. In: Onoprienko, Yu.I., Lozhkin, A.V. (Eds.), *Climate Records from Quaternary Sediments of Beringia.* [In Russian.] North East Interdisciplinary Scientific Research Institute Far East Branch Russian Academy of Sciences, Magadan, Russia, pp. 26–42.

Nikolskiy, P.A., Basilyan, A.E., Sulerzhitsky, L.D., Pitulko, V.V., 2010. Prelude to the extinction: revision of the Achchagyi-Allaikha and Berelekh mass accumulations of mammoth. *Quaternary International* **219**, 16–25.

Nikolskiy, P.A., Sulerzhitsky, L.D., Pitulko, V.V., 2011. Last straw vs. blitzkrieg overkill: climate-driven changes in the arctic Siberian mammoth population and the Late Pleistocene extinction problem. *Quaternary Science Reviews* **30**, 2309–2328.

PALE Steering Committee, 1994. *Research Protocols for PALE: Paleoclimates of Arctic Lakes and Estuaries*. PAGES Workshop Report Series 94-1. International Geosphere-Biosphere Past Global Change (PAGES) International Program Office, Bern, Switzerland.

Pitulko, V.V., 2011. The Berelekh quest: a review of research in the mammoth graveyard in northeast Siberia. *Geoarchaeology* **26**, 5–32.

Pitulko, V.V., Basilyan, A.E., Pavlova, E.Y., 2014. The Berelekh mammoth "graveyard": new chronological and stratigraphic data from the 2009 field season. *Geoarchaeology* **29**, 277–299.

Reimer, P., Austin, W.E.N., Bard, E., Bayliss, A., Blackwell, P.G., Bronk Ramsey, C., Butzin, M., *et al.*, 2020. The IntCal20 Northern Hemisphere radiocarbon age calibration curve (0–55 cal kBP). *Radiocarbon* **62**, 725–757.

Shilo, N.A., Lozhkin, A.V., Titov, E.E., Shumilov, Yu.V., 1983. *Kirgilyakh Mammoth (Paleogeographic Aspect).* [In Russian.] Nauka, Moscow.

Stuiver, M., Reimer, P.J., Reimer, R.W., 2020. Calib 8.2. http://calib.org, accessed June 2023.

Tomirdiaro, S.V., 1982. Evolution of lowland landscapes in northeastern Asia during Late Quaternary times. In: Hopkins, D.M., Matthews, J.V., Jr., Schweger, C.E., Young, S.B. (Eds.), *Paleoecology of Beringia*. Academic Press, New York, pp. 29–37.

Ukraintseva, V.V., 2013. *Mammoths and the Environment*. Cambridge University Press, New York.

Ukraintseva, V.V., Agenbroad, L.D., Mead, J.I., Hevly, R.H., 1993. *Vegetation Cover and Environments of the "Mammoth Epoch" Siberia*. Mammoth Site of Hot Springs, Rapid City, SD.

Vartanyan, S.L., Garutt, V.E., Sher, A.V., 1993. Holocene dwarf mammoths from Wrangel Island in the Siberian Arctic. *Nature* **362**, 337–340.

Vaskovsky A.P., 1957. Spore-pollen spectra of modern plant communities of the Far North-East of the USSR and their significance for the restoration of Quaternary vegetation. *Materials on Geology and Minerals of the North-East of the USSR* **11**, 130–178. [In Russian.]