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The Mammoth fauna as a paleontological characteristic of the Yedoma Ice Complex of Bol'shoy Lyakhovsky Island (New Siberian Islands, Eastern Arctic Siberia)

Tatiana V. Kuznetsova[a], Sebastian Wetterich [ID][b,c], Vladimir E. Tumskoy[d], Heidrun Matthes[e], and Lutz Schirrmeister [ID][b]

[a]Department of Paleontology, Faculty of Geology, Lomonosov Moscow State University, Moscow, Russia; [b]Permafrost Research, Alfred Wegener Institute Helmholtz Center for Polar and Marine Research, Potsdam, Germany; [c]Institute of Geography, Technische Universität Dresden, Germany; [d]Laboratory of General Geocryology, Melnikov Permafrost Institute SB RAS, Yakutsk, Russia; [e]Atmospheric Physics, Alfred Wegener Institute Helmholtz Center for Polar and Marine Research, Potsdam, Germany

ABSTRACT

This article focuses on paleozoological characteristics of Yedoma Ice Complex deposits. It provides a comprehensive and detailed description of the mammoth fauna collection assembled by the Russian–German expedition for the "Laptev Sea System" project from the famous Western Beringia locality Zimov'e River (southern coast of Bol'shoy Lyakhovsky Island, the New Siberian Islands). Our goal is to present the factual material and the conclusions that can be drawn from it. The overall collection (>1,000 specimens) comprises eleven species, of which *Mammuthus primigenius, Bison priscus, Equus* ex gr. *caballus, Rangifer tarandus*, and *Ovibos moschatus* predominate. There are as many mammoth remains in the collection as horses. The number of ungulates exceeded that of mammoths. One hundred and six radiocarbon dates obtained from bone collagen were analyzed. The fifty-six finite ages from our collection span from 53.3 to 2.2 ka BP. The largest number falls within the interval from 45.5 to 20 ka BP, the most favorable period for mammoth fauna in the region. We propose a methodology for describing specimens based on their preservation. This work is part of an article series dedicated to a comprehensive description of paleozoological material collected from Yedoma Ice Complex deposits of Eastern Arctic Siberia.

Introduction

Herds of woolly mammoths trudged across the treeless tundra steppe, largely determining our imagination of the last ice age. These giants mainly lived in Beringia, the vast, unglaciated area between the Fenno-Scandinavian ice sheet to the west and the Laurentide ice sheet to the east, including the now-inundated East Siberian shelf (Lister and Sher 2001; Kahlke 2015). Here, the harsh, cold, and dry glacial climate favored the persistence of the Late Pleistocene mammoth fauna. Their faunal remains accumulated in permafrost deposits of the Yedoma Ice Complex, where they were preserved in a frozen state, together with numerous other floral and faunal fossils, all of which are traces of the unique ecosystem of Beringia (Schirrmeister et al. 2025a).

Insights into the paleoenvironments of West Beringia have been obtained from the study of floral fossils such

as pollen (e.g., Andreev et al. 2011), plant macro remains (e.g., Kienast et al. 2005), sedimentary ancient DNA (e.g., Zimmermann et al. 2017), faunal fossils such as aquatic invertebrates (e.g., Wetterich, Schirrmeister, and Pietrzeniuk 2005; Neretina et al. 2020), and terrestrial invertebrates (e.g., Kuzmina 2023). However, to fully understand this paleoenvironment, the most promising studies are those that combine multiple paleo proxy data to comprehensively characterize past environmental and climate conditions (Andreev et al. 2004, 2009; Wetterich et al. 2008; Wetterich, Rudaya et al. 2021; Monteath et al. 2023). In this context, fossil records of the mammoth fauna are of special value because they provide multiple opportunities to gain insights into the structure and functioning of the Beringian ecosystem (Nikolskiy, Sulerzhitsky, and Pitulko 2011; Boeskorov et al. 2021). The study of adjacent tissue remains or gut contents of

well-preserved carcasses provides information on the local environments, diets, and living conditions of the respective individuals (e.g., Rudaya et al. 2015). Studies using permafrost-preserved environmental DNA help unravel questions on phylogeny, taxonomy, and biogeography of the mammoth fauna (e.g., Enk et al. 2016), and better understanding of the spatiotemporal pattern of Late Pleistocene extinctions is revealed from DNA extractions of, for example, woolly mammoth bone, tooth, and ivory (Barnes et al. 2007).

Because Paleolithic humans exploited woolly mammoths and other large herbivores, traces of human presence and expansion are left behind; for example, at mammoth kill sites, where bone material exhibits signs of weapon-inflicted injuries (e.g., Pitulko et al. 2004, 2014; Pitulko 2023). Likewise, some mass assemblages of woolly mammoth bones indicate human occupation, such as in the lower reaches of the Yana River (Basilyan et al. 2011) and in the lower reaches of the Indigirka River (Berelekh and Achchagyi–Allaikha; Nikolskiy et al. 2010). Finally, bone and tissue fossils of the mammoth fauna are valuable sources of direct age information, as determined by radiocarbon dating (e.g., Kuzmin and Orlova 2004).

The variability of species distribution reflects, on the one hand, different climate and landscape conditions (e.g., warm or cool tundra steppe, shrub or forest tundra) over time and, on the other hand, local or regional differences in the landscape (e.g., soil moisture, plant food) that may have caused better or worse living conditions for the mammoth fauna (Sher et al. 2005). Therefore, comprehensive mammal bone collections are valuable and have been obtained during the last decades due to intense field sampling in the Laptev Sea coastal region, including Bykovsky Peninsula (Schirrmeister, Siegert et al. 2002; Sher et al. 2005; Kuznetsova et al. 2019), the Lena River Delta (Schirrmeister et al. 2003; Wetterich et al. 2008, 2020; Wetterich, Rudaya et al. 2021), and the Oyogos Yar mainland coast (Kuznetsova et al. 2022).

In this article, we focus on the most complete and representative mammoth fauna bone collection of the Russian–German expedition (Kuznetsova 2009) as well as historical collections from Bol'shoy Lyakhovsky Island (Chersky 1891; Vangenheim 1963) and Yana River (Pitulko et al. 2016).

Here, we present a comprehensive data set of mammal fossils from permafrost deposits collected during several sampling campaigns on the southern coast of Bol'shoy Lyakhovsky Island in 1999, 2007, and 2014 (Figure 1). The study aims to (1) characterize the local Late Pleistocene and Holocene mammal fossil record, (2) relate the fossil bones to the exposed cryostratigraphy by dating and systematic interpretation of the finding locations, and (3) deduce the local distribution
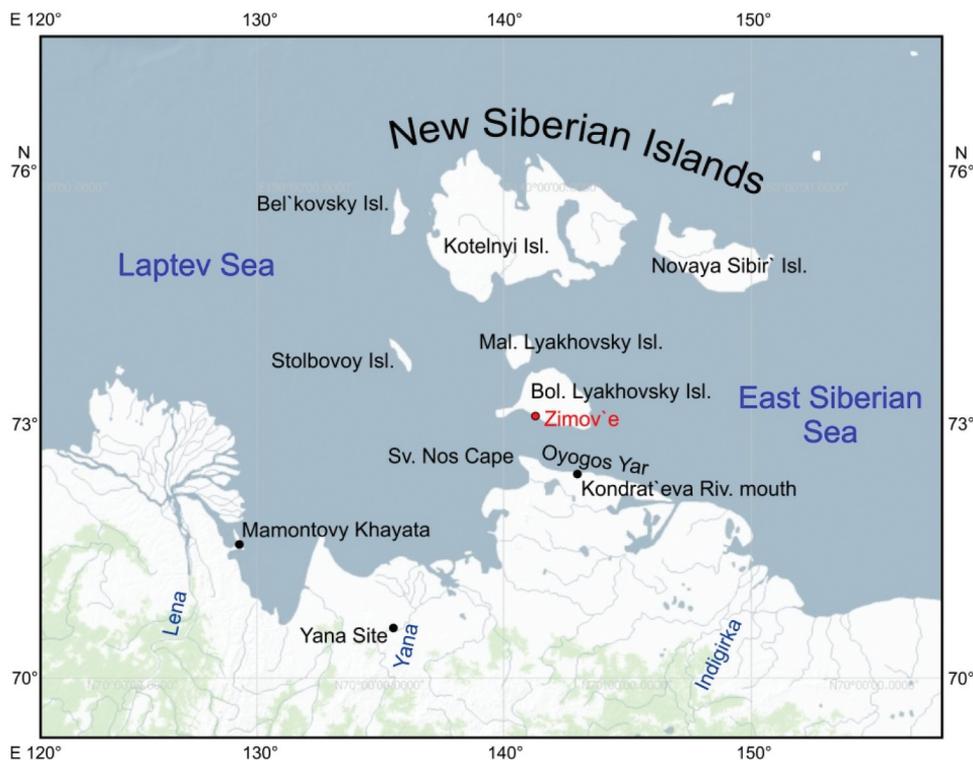

Figure 1. Study region in the East Siberian Arctic, showing the study site (Zimov'e), the New Siberian Islands, and further relevant study sites (Oyogos Yar, Yana Site, Mamontovy Khayata) mentioned in the study (redrawn after Kuznetsova et al. 2022).

pattern of mammal bones on the Bol'shoy Lyakhovsky coast including historical collection in comparison to neighboring prominent localities to deduce the regional pattern.

Study region and research history

Study region

The southernmost island of the New Siberian Archipelago, Bol'shoy Lyakhovsky, is located on the northern shore of the Dmitry Laptev Strait (Figure 1). Here, at the southern coast of the island near the Maly Zimov'e River mouth (73°19′ N, 141°21′ E), coastal exposures up to 35 m.a.s.l. of late Quaternary permafrost have long been intensively studied (e.g., Tumskoy 2022).

The coastal sequences discontinuously preserve permafrost accumulations dating back to the last approximately 200 ka (e.g., Schirrmeister, Oezen, and Geyh 2002). Distinct ice complex generations formed during Marine Isotope Stage (MIS) 7 (Yukagir Suite; Andreev et al. 2009; Wetterich et al. 2019), MIS 5 (Buchchagy Suite; Tumskoy 2022; Wetterich et al. 2016), MIS 4 and 3 (Oyogos Suite; Andreev et al. 2004; Wetterich et al. 2014), and MIS 2 (Yana Suite; Tumskoy 2022; Wetterich et al. 2016). Subaerial deposits of MIS 6 (Kuchchugui Suite; Romanovsky, 1958b) and MIS 5 thermokarst deposits (Krest-Yuryakh Suite; Andreev et al. 2004; Ilyashuk et al. 2006; Wetterich et al. 2009; Schirrmeister et al. 2025b) stratigraphically divide the ice complex sequences. Holocene deposits occur on top and in vast thermokarst basins (Romanovsky 1958a; Wetterich et al. 2009).

Research history

The earliest references to Siberian fossil bones and the frozen carcasses of woolly mammoths are found in ancient Chinese writings dating back to the fifth century B.C. (Chersky 1891). In European literature, the earliest recorded mention of mammoth tusks dates to the first century A.D. (Smirnov 2003). Since the seventeenth century, the history of exploration and study of the arctic regions of eastern Siberia by Russian pioneers have been closely linked to the search for and extraction of woolly mammoth bone fossils. In addition, "information about finding tusks similar to those of an elephant in cold Siberia, and in general, the bones of large mammals not currently living in the north entered Western Europe already in the 17th century and aroused the attention of scientists" (Obruchev 1931, 127).

In 1690, Maxim Mukhoplev and Yakov A. Permyakov discovered Stolbovoy Island and Middle Island (today

known as Bol'shoy Lyakhovsky Island) of the New Siberian Archipelago in the eastern Siberian Arctic. In 1711, a detachment of ten Cossacks, led by Merkury Vagin, was dispatched to search for new islands. In 1712, the commercial collection of woolly mammoth tusks started on the island, which was later named Bol'shoy Lyakhovsky (Magidovich and Magidovich 1985). By the middle of the eighteenth century, fossil woolly mammoth bones were already being significantly traded in northern Yakutia. In the 1760s, the Yakutian merchant Eterikan discovered abundant occurrences of woolly mammoth bone on the Middle Island, and, moving further north, he was the first to reach Maly Island. Ivan Lyakhov explored both islands in 1770, which were later named Bol'shoy and Maly Lyakhovsky, by order of Empress Catherine II. Lyakhov furthermore discovered the largest island of the New Siberian Archipelago, Kotelny Island. Reports from most of the first scientific expeditions noted the abundance of woolly mammoth tusks and bones, as well as the remains of woolly rhinoceroses, bison, and musk oxen on arctic coasts and the New Siberian Islands (Chersky 1891).

In 1809, Matvey M. Gedenstrom was sent to inventory the discovered islands. He published his impressions in 1830 in his book *Passages About Siberia*. He pointed out that the steep banks of streams and lakes here consist of horizontally interlaced (Gedenstrom 1830, 119). The layers of earth always overlap the ice, and the ice veins crossing them "are of the newest origin, from the rupture of the whole mass by snow water." Gedenstrom described his observations as "an incomprehensible mystery of nature" (Gedenstrom 1830, 119) and noted that the north of Siberia hides "innumerable corpses of a huge animal called Mammoth" (Gedenstrom 1830, 121). According to his observations, the size of woolly mammoth tusks decreases to the north, and on the islands, they are not found to weigh more than five poods (80 kg) but their number increases. On Bol'shoy Lyakhovsky Island, where "mammoth bone has been sought for about 80 years, the main area for collectors has always been the shoal on the western side of the island." In addition to woolly mammoth remains, Gedenstrom noted finds of musk ox and woolly rhinoceros skulls. Even though he could not determine which animals these skulls belonged to, he gave such precise descriptions that the identification of these finds is not in doubt.

The first expedition to study permafrost and "animal kingdom of Siberia" (von Middendorff 1867, 270) took place in 1843 to 1845 under the leadership of Alexander T. von Middendorff. Based on his research, he published a work in which one chapter is devoted to the mammoth fauna (von Middendorff 1867). Middendorff concluded

that "the mammoths found in Siberia did not all at one time found their end from some general upheaval" (von Middendorff 1867, 270). Instead, they inhabited Siberia, died, and "were covered with earth for a long period, of course, for thousands of years" (von Middendorff 1867, 270).

The first collections of fossil remains of the mammoth fauna from the Novosibirsk Islands and their study

From 1885 to 1886, the New Siberian Polar Expedition, led by Alexander von Bunge, studied the New Siberian Archipelago. Eduard Gustav von Toll was invited as a geologist to this expedition. Bol'shoy Lyakhovsky Island turned out to be interesting both geologically and paleontologically "due to the richness of remains of prehistoric mammalian animals, observations on which occupied almost the first place in our program" (Bunge 1887, 579).

Representative collections of mammal fossils collected during this expedition were studied and described by Ivan Dementevich Chersky (Chersky 1891). He studied and described more than 2,500 different parts of mammal skeletons, which he classified into twenty-five species. "The most considerable number of both species (21) and remains (2082) belongs to the island of Bol'shoy Lyakhov" (Chersky 1891, 69). Part of the studied bones, as noted by Chersky, belonged to modern animals. The remains of horses, bison, and musk ox were numerous among fossil species. Reindeer fossils (794 specimens) included bones of both fossil and modern animals (Figure 2a).

The mammal remains from Bol'shoy Lyakhovsky Island, obtained during Bunge's expedition in 1886 and processed by Chersky, are still one of the most extensive collections in terms of the number of specimens and, undoubtedly, the most representative in terms of the number of species described. Most of the species were described for the first time in this territory. The findings of cave lion, saiga antelope, and red deer remains were the most unexpected and even unique (Table 1).

Chersky's (1891) work "Description of the Collection of Post-tertiary Mammals Collected by the New Siberian Expedition in 1885–86" is an important reference for all subsequent researchers of the mammoth fauna. It includes not only a description of the material collected by the expedition but also a summary of all previously known fossil mammal remains from Siberia, many of which have not been published before. Chersky discusses in detail the views of previous researchers on the "character of post-tertiary sediments of Siberia" and, based on his extensive experience in studying sediments in various

regions of Siberia, rejects the theories that a glacier or sea covered the entire territory of Siberia (Chersky 1891). However, he admits the presence of many freshwater lakes (Chersky 1891).

Eduard von Toll continued his explorations of the New Siberian Islands in 1893 and 1894. On Bol'shoy Lyakhovsky Island, he examined "ice outcrops." In one of them, near the Maly Zimov'e River, in frozen, loamy deposits below a peat layer and above the fossil ice, he discovered well-preserved plant remains, mainly represented by alder (*Alnus fruticosa*). He saw whole trunks with roots and noted that the leaves on the branches are firmly attached, even with clusters of flower buds. These findings indicate that on Bol'shoy Lyakhovsky Island, "at 74° N, at that time dominated a vegetation, the northern boundary of which is now four degrees further south on the mainland" (Toll 1897, 92). During the expeditions of 1885 and 1886 and 1893 and 1894, Toll noted that the animal corpses "never lay in ice, but always in frozen clay or sand layers, but often, however, above the ice masses" (Toll 1897, 132).

Toll's work confirms Chersky's conclusions that the remains of animals of the Ice Age, "in the vast majority of cases, were not subjected to the grinding action of flowing waters and thus exclude the idea of the possibility of their transfer by this route from other areas. In the present case, the proposal about the possibility of transferring at least some part of the bones from more distant localities, and, most importantly, from more southern latitudes is rejected" (Chersky 1891, 72). Toll rightly believed that "the mammoth and animals contemporary to it lived where their remains are found now," their extinction was not connected with any catastrophic phenomena but was a consequence of "changes in physical and geographical conditions." The corpses of these animals "were deposited at low temperatures, partly on river terraces, partly on the banks of lakes, partly on glaciers (ground ice) and were there covered with silt; their mummies could be preserved until now, as well as the ice masses forming the base of their graves, thanks to the constant or even increasing cold" (Toll 1897, 125). The living conditions of the woolly mammoth and other animals were, according to Toll, favorable. They lived in the north of Siberia, where they "roamed in a vast free space, which, connecting with the present continent, reached, perhaps, through the pole to the American archipelago and, despite the glaciers, was not poor in pastures" (Toll 1897, 126). Toll explained the reasons for the extinction of the mammoth fauna by writing: "The fragmentation of the continent and the appearance of cold sea currents changed the climate. Simultaneously with the lowering of the land, the accumulation of snow
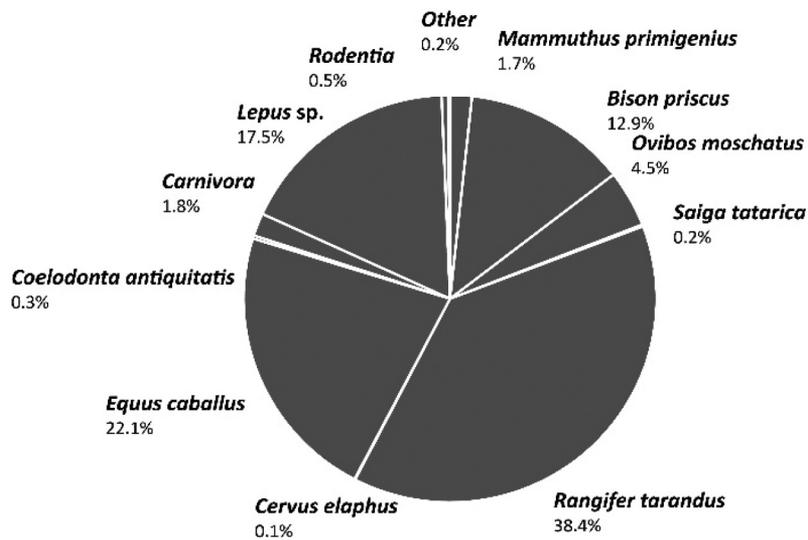
(a) Mammal bone collection of 1885-1886 (Chersky, 1891); n = 2034
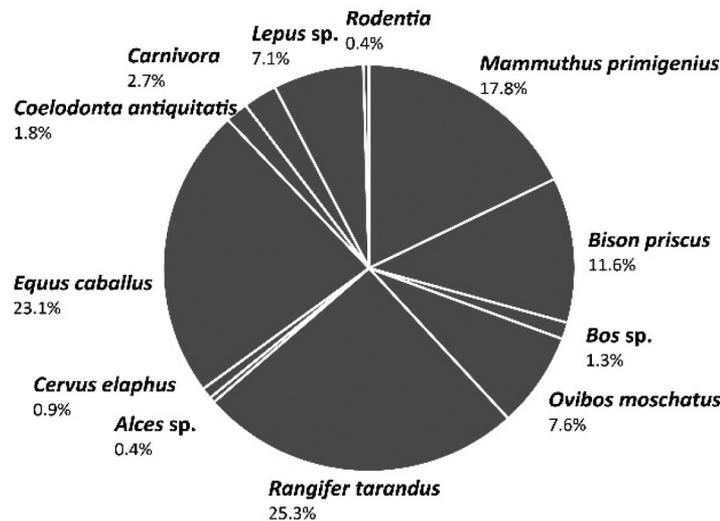
(b) Mammal bone collection of 1956 (Vangenheim, 1963); n = 225

Figure 2. Species composition of historical mammal bone collections on Bol'shoy Lyakhovsky Island published by (a) Chersky (1891) and (b) Vangenheim (1963). Note that the collection of Chersky (1891) includes several modern specimens (Table 1).

masses decreased while the cold increased. Flora perished, and from animals was taken away the possibility to roam freely over vast spaces" (Toll 1897, 126). This explanation of the disappearance of the mammoth fauna, with some refinements, is the most accepted version at present.

In 1908, an exceptionally well-preserved tusk was discovered on Bol'shoy Lyakhovsky Island, which had been taken from a skull lying at the bottom of an almost waterless river. In addition, the head, covered in some places by skin with dark hairs, was cut off about 2.1 m long part, also like the head skin, with

dark, almost black hair, from below and from the sides longer than on its upper part (Vollosovich 1915, 307). In 1910, Vollosovich organized excavations of the Lyakhovsky woolly mammoth corpse. They found:

(a) The skull with the left tusk, upper lip and left eye;
(b) The main parts of the torso skeleton;
(c) A piece of skin of the head and back with the left ear, a piece of skin of the croup with the tail and several pieces of skin from different parts of the torso;

Table 1. Historical findings of fossil (and modern) mammal remains on B. Lyakhovsky Isl. were collected by Bunge in 1885-1886 and published by Chersky (1891), and were subsequently collected by Lebedev and Romanovsky in 1956 and published by Vangenheim (1963). The number of findings interpreted by Chersky (1891) as modern are given in brackets. The terminology used by Chersky (1891) is transferred to the modern species names.

Order	Family	Taxon	B. Lyakhovsky Isl.	
			Chersky (1891)	Vangenheim (1963)
Proboscidea		*Elephas primigenius* [= *Mammuthus primigenius*]	34	40
Artiodactyla	Bovidae	*Bison priscus*	257	26
		Bos sp.		3
		Ovibos moschatus	90	17
		Colus saiga [= *Saiga tatarica*]	3	0
	Cervidae	*Rangifer tarandus*	767	57
		Alces sp.		1
		Cervus canadensis	1	2
Perissodactyla	Equidae	*Equus caballus*	442	52
	Rhinocerotidae	*Rhinoceros tichorhinus* [= *Coelodonta antiquitatis*]	5	4
Carnivora	Felidae	*Felis tigris* [= *Panthera spelaea*]	4	2
	Canidae	*Canis lupus*	22	1
		Canis familiaris	(11)	0
		Vulpes lagopus	8(+11)	3
	Mustelidae	*Gulo luscus* [= *Gulo gulo*]	1	
	Ursidae	*Ursus arctos*	1	
		Ursus maritimus	(1)	
Lagomorpha	Lagomorpha	*Lepus variabilis* [= *Lepus timidus*]	350	16
Rodentia	Cricetidae	*Arvicola* sp. 1?	2	
		Arvicola sp. 2?	3	
		Lemmus obensis [= *Lemmus sibiricus*]	2	1
		Cuniculus torquatus [= *Dicrostonyx torquatus*]	3(+1)	
Pinnipedia	Phocidae	*Phoca foetida* [= *Pusa hispida*]	3(+12)	
		Total	2034	225

(d) The male sex organ and several pieces of already decomposed meat with fat;

(e) Four legs, of which the left one is present entirely from the knee, the others only with skin and feet, and the whole skin is preserved only on the left front and right hind legs, and on the right front leg there is skin only down from the knees, as well as on the left hind leg (Vollosovich 1915, 327).

Today, the skeleton of this woolly mammoth is exhibited in the National Museum of Natural History in Paris, France.

In 1929, Innokentii Pavlovich Tolmachoff summarized all available data on finds of woolly mammoth and woolly rhinoceros carcasses, as well as the history of woolly mammoth tusk collection in Siberia. In his work, he characterized the climate and vegetation during the woolly mammoth's existence and sought to explain its extinction (Tolmachoff 1929).

Since the 1930s, a systematic study of the geological structure of the New Siberian Islands has been carried out. In 1956, Vladimir D. Lebedev and Nikolay N. Romanovsky (Romanovsky 1958a, 1958b) collected Quaternary mammal remains from twelve species in the southern part of Bol'shoy Lyakhovsky Island (Figure 2b; (Table 1). According to Vangenheim (1963), "this fauna is typical of the upper half of the Quaternary period of Siberia and indicates the close connection of the island with the mainland that existed at that time." Vangenheim confirmed Toll's conclusions that the New Siberian Islands were part of the mainland and represented an area with developed open landscapes. She suggested that during the second half of the

Pleistocene, there were small climatic fluctuations, resulting in the taiga moving northward during warming and retreating southward during cooling and tundra prevailing in the study area.

Finds and collections from the late twentieth and twenty-first centuries

At the end of the twentieth century, the number of found carcass fragments and soft tissues of the mammoth fauna increased sharply throughout northern Siberia and on Bol'shoy Lyakhovsky Island. This is due to the resumption of active tusk collection and the appearance of collectors in previously inaccessible areas. In 1993, on Bol'shoy Lyakhovsky Island, near the Bol'shoy Eterikan River, a partial skin with an eye socket and an ear, a portion of a leg, and a fragment of a woolly mammoth's head were discovered. In 1995, a fragment of a woolly mammoth hide with remnants of a hind leg was found near the site of previous finds (Lazarev, Boeskorov, and Tikhonov 2001). At this time, a part of a woolly mammoth skeleton with remains of soft tissues was found near the mouth of the Zimov'e River on the southern coast of Bol'shoy Lyakhovsky Island (Saige et al. 1995).

Throughout the twentieth century, museum collections were replenished with material collected during geological and zoological expeditions by the staff of the Yakutsk Commission of the Academy of Sciences and Polar Research, expeditions of the Research Institute of Arctic, Arctic and Antarctic Research Institute, the Geological Institute of the Russian Academy of Sciences (GIN RAS), the Lomonosov Moscow State University (MSU), and many other organizations. Paleontological collections and individual unique specimens collected on Bol'shoy Lyakhovsky Island are stored in many museums in Russia and around the world. The most representative collections are stored in museums in Yakutsk, St. Petersburg, and Moscow (Kuznetsova, Schirrmeister, and Noskova 2004). Unique collections, stored in the Zoological Institute of the Russian Academy of Sciences (ZIN RAS) and the Paleontological Institute of the Russian Academy of Sciences (PIN RAS) for over a hundred years, comprise those gathered by expeditions led by Bunge and Toll.

Paleontological samples of fossil mammals from Bol'shoy Lyakhovsky Island collected by our Russian–German expeditions were used to reconstruct environmental temperature changes during the Late Pleistocene and Holocene using data from stable isotope analysis of C, N, and O from fossil mammal bones (Nikolaev et al. 2005, 2006, 2010, 2012; Iacumin et al. 2010; Nikolaev, Kuznetsova, Alekseev et al. 2011; Nikolaev, Kuznetsova, Iacumin, and Di Matteo 2011). The carbon isotopic

composition of the carbonate ($\delta^{13}C_{carb}$) and collagen ($\delta^{13}C_{coll}$) from the bones of the woolly mammoth and bison was investigated to reconstruct the main climatic events in the interval 50 to 10 ka BP (Nikolaev, Kuznetsova, Iacumin, and Di Matteo 2011). The tibia of *M. primigenius* was taken for isotopic and geochemical studies (Nikolaev, Kuznetsova, Alekseev et al. 2011). A mammoth wool sample was taken from Bol'shoy Lyakhovsky Island to reconstruct the change in ambient temperature during the growth period of the wool. The studied samples represented segments of four hairs (Yakumin et al. 2004).

Based on bones of the mammoth fauna, an attempt was made to trace the migration routes of woolly mammoths in the arctic regions of Siberia during the Late Pleistocene. Strontium isotopes were isolated from woolly mammoth and bison samples from Bol'shoy Lyakhovsky Island (Barbieri et al. 2008). Geochemical studies of woolly mammoth tusks have been conducted, and a geochemical explanation of their structural abnormalities has been proposed (Nikolaev et al. 2015, 2017).

Genetic studies of large mammals from the mammoth fauna were also conducted using samples from our collection on Bol'shoy Lyakhovsky Island (Lorenzen et al. 2011). Bones of woolly rhinoceros (Willerslev et al. 2009), cave lion (Barnett et al. 2009), musk ox (Campos et al. 2010), woolly mammoth (Römpler et al. 2006; Barnes et al. 2007; Gilbert et al. 2008), bison (Shapiro et al. 2004), and mammoth wool (Gilbert et al. 2007) were studied.

Material and methods

Fieldwork

Fieldwork, including bone sampling, took place on the south coast of B. Lyakhovsy Island in 1999 (Kuznetsova and Kuzmina 2000), 2007 (Kuznetsova 2008), and 2014 (Fuchs et al. 2015). Thorough study and collection of fossil remains of Mammoth fauna at the modern level was one of the objectives of the Russian–German System Laptev Sea collaboration in the study of Pleistocene–Holocene permafrost deposits in the western part of the southern coast of Bol'shoy Lyakhovsky Island in the area of the Zimov'e River mouth (Figure 3). The longest and most detailed paleontological collection took place in 1999 and formed the main part of the mammoth fauna collection with 1,082 specimens. Small additions of specimens occurred in 2007 (13 specimens) and 2014 (3 specimens).

The bones were collected using the "total material collection" technique (Kuznetsova et al. 2019, 2022).
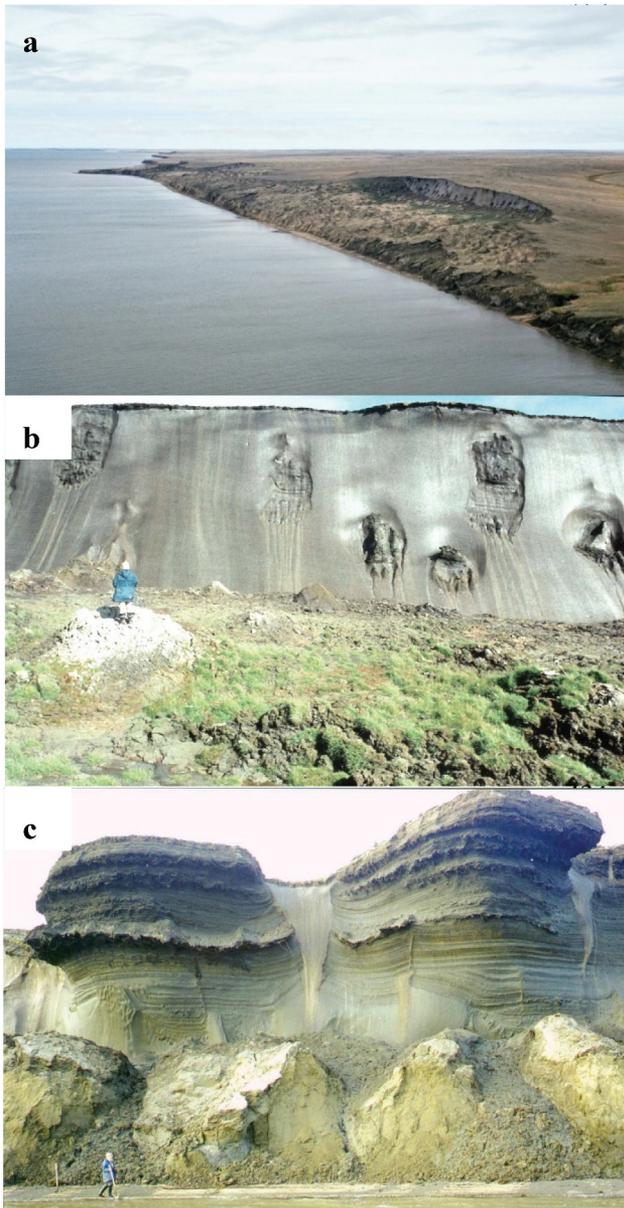
Figure 3. Permafrost exposures at the southern coast of Bol'shoy Lyakhovsky Island: (a) third thaw slump (third thaw slum in Figure 4) in section R, west of the Zimov'e River mouth in aerial view (July 2007; credit: V. Tumskoy), (b) view on the headwall of the first thaw slump (first thaw slump in Figure 4) in section R, west of the Zimov'e River mouth (August 1999; credit: V. Tumskoy), and (c) view on the coastal outcrop in section L, east of the Zimov'e River mouth (August 1999; credit: V. Tumskoy). Note persons for scale in (b) and (c).

All, even small and poorly preserved, remains of fossil mammals and birds were collected from the outcrop and on the shore below it. Each bone directly on the outcrop was assigned a number, and the specimen collection site was noted on the plan. This collection-based approach to paleontological material allows the reconstruction of species ratios in the mammoth fauna of the described region at the end of the Pleistocene as realistically as possible, while accounting for the incompleteness of the paleontological record. Each bone in the collection belongs to one species, depending on the location where the specimen was collected.

Group A includes samples taken directly from the frozen layer (i.e., in situ). The sample's height above sea level is specified. The samples in group B were already thawed but had not moved far from their initial location. The upper and lower boundaries of the sample in the section can be identified to determine the so-called bone field. The upper boundary of the bone field is the upper boundary of the outcrop, and the lower boundary is the location where the specimen was found, usually directly beneath the ice wall of the outcrop (Figures 4a and 4b). Group C consists of specimens collected in debris on a transect. These are bones that were thawed out of this outcrop not so long ago. Sea currents, waves, or ice cannot have transported them. The transects on which the material was collected were divided into two sections during the study: Section R, comprising transects west of the mouth of the Zimov'e River, and section L, comprising transects east of the mouth of the Zimov'e River (Figures 4 and 5). Bones and their fragments, classified into groups A, B, and C, could be collected in both sections R and L.

Bones collected along the shore transects were divided into two groups. Group D unites the bones collected on the shore under the outcrops of section R with those of group E, which are also located on the shore under the outcrops of section L. The different geological structures of the outcrops in both sections caused the bones to be divided into groups D and E. The shore profiles were horizontally divided into 100-m sections. However, it made no sense to mark exactly where each specimen was found on the shore, because wave transport of bones along the shore is present. Although water transport of bone remains that fell on the shore under sections R and L is possible, the mouth of the Zimov'e River separates the shores under the profiles.

Group D was subdivided into three subgroups: bones collected under the first, second, and third thaw slumps; bones collected under thermokarst basins; and bones collected on Cape Kamennyi (Stone Cape) at the westernmost point of our work (Figure 4). Group E is subdivided into seven subgroups of bones collected on the eastern shore: near the camp (L-0–L-4 + 50), under the first thaw slump, under the first alas, under the second thaw slump, under the second alas (further L-14), on the shore about 5 to 6 km east of the mouth of the Zimov'e River (Figure 5), and on the shore 10 km east of the mouth of the Zimov'e River.
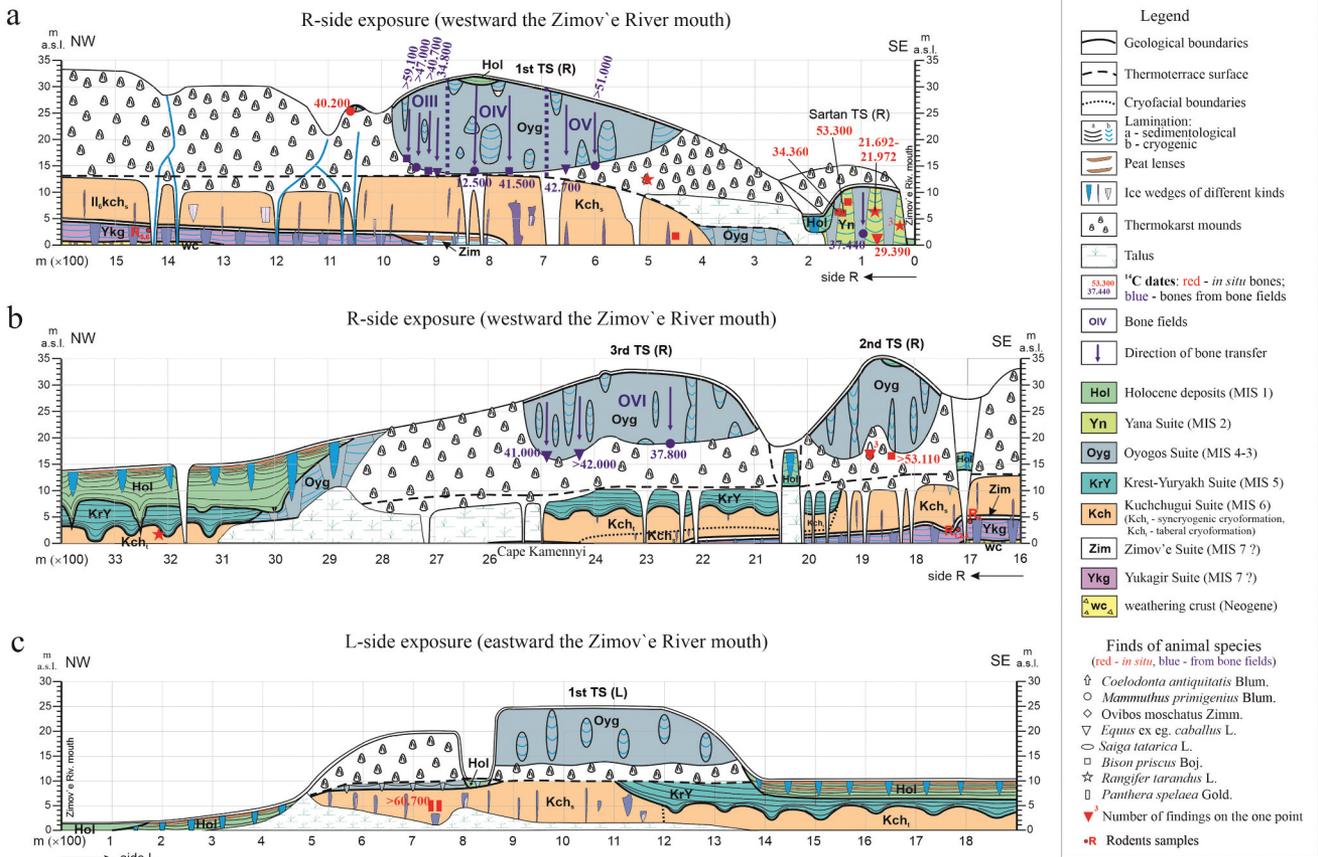
Figure 4. Geological profile near Zimov'e River mouth of the southern coast of Bol'shoy Lyakhovsky Island with fossils in situ, bone samples from the bone fields, rodent samples, and some radiocarbon bone dates. (a) Section R (R-side exposure) between 1,600 and 3,400 m west of the Zimov'e River mouth, (b) section R (R-side exposure) between 0 and 1,600 m west of the Zimov'e River mouth, and (c) section L (L-side exposure) between 0 and 1,900 m east of the Zimov'e River mouth.
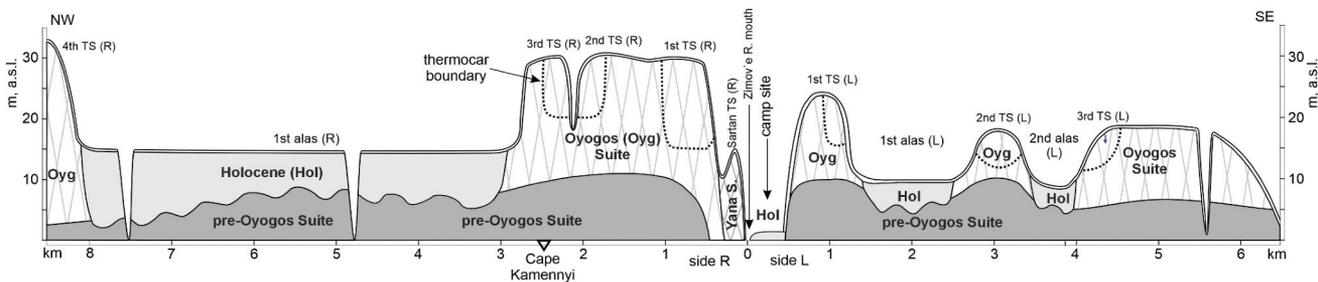
Figure 5. Generalized profile of the south coast of Bol'shoy Lyakhovsky Island near the Zimove River mouth, including sections R and L (see Figures 4a–4c, pre-Oyogos Suite, deposits older MIS 4).

Group F includes bones and their fragments collected on the floodplain of the Zimov'e River (one subgroup) and on the shoal (the second subgroup) formed at the river's confluence with the Dmitry Laptev Strait. On the shore, bones may be mixed with those carried by the river and those taken by the current or waves from the shores of both profiles.

Group G combines bone remains found by local tusk collectors in other areas of the island.

To collect small mammal remains, six sediment samples from the lowest frozen part of the exposure (Yukagir Formation, MIS 7) were collected and 50-80 kg were washed out each from three locations (R-14 + 30 m, R-17, R-17 + 30 m) at about 1,430,

1,700, and 1,730 m west of the Zimov'e River mouth (Figure 4). The washing was performed with a 1-mm hand sieve, using water supplied by a motor pump in a special sampling box. In addition, one sample (BL-O-1001-L) containing many fragments of skulls, mandibles, teeth, and bones of the postcranial skeleton of rodents was collected on the shore 10 km east of the mouth of the Zimov'e River.

The collection of mammal remains described in this article is stored at the Paleontological Institute of the Russian Academy of Sciences in Moscow. Each specimen is numbered, and lists of specimens have been published (Kuznetsova and Kuzmina 2000). Large limb bones and woolly mammoth tusks were only photographed but not collected due to weight limitations, because the expedition was transported by helicopter. However, a large fragment was sawed off from heavy bones; for limb bones, this is usually the proximal part.

In addition to bone remains of mammals and birds on Bol'shoy Lyakhovsky Island, in the floodplain of the Zimov'e River, in the place where a woolly mammoth leg was found in 1995 (Saige et al. 1995; Lazarev, Boeskorov, and Tikhonov 2001), woolly mammoth hair was collected and later studied by isotopic (Nikolaev et al. 2010) and genetic methods (Gilbert et al. 2007). Several samples of woolly mammoth hair stored in the Ust-Lensky Reserve Museum from various locations on Bol'shoy Lyakhovsky Island, including Cape Shalaurova and the Eterikan River area, were also studied (Gilbert et al. 2007). In 2004, Vladimir E. Tumskoy found a well-preserved fragment of a fossilized musk ox skin in the mouth of the Zimov'e River. To the best of our knowledge, this is the only fragment of a musk ox skin found, and isotopic and genetic studies (Campos et al. 2010) have been conducted on it. Five samples were collected in 1994 on Bol'shoy Lyakhovsky Island and are presented in the collection by the geocryologist Aleksey A. Arkhangelov.

Specimen identification and statistics

Most finds were identified to the species level using the Department of Osteology's collection at the Zoological Museum of the MSU as comparative material. All whole bones and 98.5 percent of bone fragments were identified. In addition, specimens and collections from the New Siberian Islands are stored in the PIN RAS and the GIN RAS in Moscow, in the ZIN RAS in St. Petersburg, in the Mammoth Museum, and in the Museum of the Institute of Geology of Diamonds and Noble Metals in Yakutsk. Specimens stored in the Museum of the Lena Delta Reserve in Tiksi were also identified and studied.

A total of 1,108 samples of fossil bone remains have been collected (Table 2). Statistical analyses were conducted to evaluate the degree of similarity in species distributions among the mammoth fauna from different collections (Table 1) and sampling sites (Bol'shoy Lyakhovsky Island, Yana site). First, Pearson correlation coefficients were calculated between the species distributions of the different collections. Second, to further explore those differences and similarities, an agglomerative hierarchical cluster analysis was performed on species counts for each sample site. Given that the numbers are actual counts of mammoth fauna bones, chi-squared distances were used in the analysis set to "average." The statistical significance of the clusters recovered by the analysis was assessed using a bootstrapping approach following Suzuki and Shimodaira (2006). The analysis was performed using R's Pvclust Package (Suzuki, Terada, and Shimodaira 2019; R Core Team 2021).

Radiocarbon dating

Dating was carried out by bone's collagen using conventional radiocarbon age determination and accelerator mass spectrometry. Dating was performed at the Laboratory of Isotope Geochemistry and Geochronology of the Institute of Geology (GIN) RAS (lab code GIN); the Leibniz Laboratory for Radiometric Dating and Stable Isotope Research, University of Kiel, Germany (lab code KIA); the Center of Isotope Research, University of Groningen, the Netherlands (lab code GrA); and the Oxford Radiocarbon Accelerator Unit (lab code ORAU). Further ten dates were found in the literature for the remains of *M. primigenius* from Bol'shoy Lyakhovsky Island (Sulerzhitsky 1995; Kuzmin and Orlova 2004; Sher et al. 2005) employing laboratories of the GIN RAS, Tohoku University, Sendai, Japan (lab code TH), and the Northeastern Interdisciplinary Research Institute Magadan, Russia (lab code MAG). Age determination was carried out using the standard method for the Laboratory of Isotope Geochemistry and Geochronology of the GIN RAS, as described in the works of L.D. Sulerzhitsky (Romanenko 1997, 2004; Sulerzhitsky and Romanenko 1999). The Leibniz Laboratory prepares its samples for collagen dating according to the method described by Grootes, Nadeau, and Rieck (2004). The Oxford Laboratory prepares its samples according to the publications in Brock et al. (2013). In general, bone preparation follows the Longin (1971) method in all laboratories. All ages are reported as uncalibrated years before present (a BP). Uncalibrated dates younger than 50,000 years BP were calibrated using Calib 8.1.0 (Reimer et al. 2020).

Table 2. Collection of mammalian remains sampled at Bol'shoy Lyakhovsky Island in 1999, 2007, and 2014.[a]

Taxon	Total	Exposure (groups A, B, C)			Section R (group D)		Shore				Total		Zimov'e River (group F)	Other sites
		Section R	Section L	Total	At Cape Kamennyi	Total	Section L (group E)				Section R	Section L		
							Near the camp (L-0–L-4 +50)	Under thermokarst basins and thaw slumps	10 km from camp	Total				
Mammuthus primigenius (Blumenbach, 1799)	260+1	51	6	57	14	44	7	53	20	124	95	130	18+1	17
Bison priscus (Bojanus, 1827)	196+5	43	7	50	14	37	12	39+4	12+1	93+5	80	100+5	4	12
Ovibos moschatus (Zimmermann, 1780)	80+1	6	4	10	6	15	4	24	6	44	21	48	1+1	10
Saiga tatarica L., 1758	2				1	1			1	1	1	1		
Rangifer tarandus L., 1758	191+2	33+2	7	40+2	41	62	17	25	9	66	95+2	73	5	18
Equus ex gr. *caballus* L., 1758	255+1	51	15+1	66+1	16	45	11	37	15	93	96	108+1	10	41
Coelodonta antiquitatis Blumenbach, 1790	6				1	1		3		4	1	4		1
Panthera spelaea (Goldfuss, 1810)	5		2	2			1	1		3		5		
Canis lupus L., 1758	2				1	1					1			1
Other Carnivora	2						1		1	2		2		
Lepus sp.	29	5		5	5	14	2		5	8	19	8		2
Dicrostonyx ex gr. *simplicior-henseli*	20								20	20		20		
Lemmus ex gr. *sibiricus* Kerr, 1792	28								28	28		28		
Microtus middendorffii Poljakov, 1881	3								3	3		3		
Clethrionomys cf. *rufocanus* Sundevall, 1846–1847	1								1	1		1		
Avis	1											1		
Unidentified	17	5		5	5	7	3	1		5	12	5		
Total	1,108	196	42	238	103	227	58	187	122	501	423	543	40	102

Note. [a]Numbers after the + signs indicate remains of soft tissues, horns, hooves, or wool.

It is worth noting that one of the first radiocarbon-dated samples in Russia was a fragment of mammoth skin from Bol'shoy Lyakhovsky Island (Lozhkin 1977). In our study, we also dated a fragment of mammoth skin and several samples of mammoth wool. All samples were found to be older than 50,000 years (Table S1). A total of ninety-six radiocarbon dates were received from the samples during our work. Ninety-one specimens, including teeth, bones, and bone fragments of woolly mammoths, horses, bison, musk ox, woolly rhinoceroses, reindeer, and cave lions from the collection were dated, as well as one fragment of musk ox skin (Table S1). One specimen was dated twice, a tooth of *Coelodonta antiquitatis* (BL-O 919). It is likely that two samples of a proximal fragment of a reindeer metatarsal bone (L14-07-#1 and L14-07-#3) belong to one individual. Three samples of woolly mammoth hair from the museum collection of the Lena Delta Reserve were also dated (Table S1). Additionally, ten radiocarbon dates for bone material collected on Bol'shoy Lyakhovsky Island from the literature are presented in Table S1. Thus, a total of 106 age determinations are available.

Study of the fossil preservation

When working with paleontological collections, attention is drawn to the different ratios of whole and fragments of bones in different groups of bones, both by place of discovery (groups A, B, C, D, E, F) and by taxonomic affiliation. We developed a method for dividing bones into groups and analyzed the preservation of all collected material for the first time. In terms of morphology, some bones are almost always completely preserved, such as the small bones of the wrist or tarsus, and others are almost always found in fragments, including ribs, horns, and the pelvis. The large limb bones are among the strongest in the skeleton and are often preserved in the fossil record, either intact, damaged, or in fragments. The most fragile are the skull bones. Skulls and their fragments are rarely preserved; if preserved, the most durable skull fragments are the brain box, skull parts with horny outgrowths, and the occipital part. Teeth are generally well preserved in a fossil state. The cheek teeth of woolly mammoths, characterized by a lamellar structure, typically disintegrate into separate parts or even individual plates. Tusks are also well preserved as fossils. When splitting a tusk, many different pieces of one tusk can be preserved.

To describe and analyze the material in terms of preservation, we grouped the femur, tibia, humerus, ulna, and radius into the group of large limb bones.

The bones of the wrist and tarsus were classified as small bones of the limbs. We consider all other bones and teeth separately. The material is analyzed and described by both bone groups and animal species. When calculating the percentages, all bones and their fragments were included.

Results

The Bol'shoy Lyakhovsky mammal bone collections from 1999, 2007, and 2014

The collection of mammoth fauna remains on the southern coast of Bol'shoy Lyakhovsky Island comprises 1,108 specimens, of which 17 specimens (1.5 percent) could not be identified and 1,091 specimens were identified (Table 2). The overwhelming part of the collection (91.8 percent) consists of bones and bone fragments of large mammals, considerably fewer remains of hares and rodents (81 pieces, 7.3 percent), and 0.9 percent are fragments of soft tissues (fragments of sheep skin, hair of woolly mammoth and reindeer, horn hoofs of reindeer and horse, horn covers of bison). Only one specimen in the collection relates to birds, a damaged skull of *Clangula hyemalis* (long-tailed duck), probably modern, collected on the east-side shore. Only specimens that are certainly identified are considered when discussing percentages.

Many intact or slightly damaged large woolly mammoth limb bones contained bone marrow. It is most likely that most large ungulate limb bones also contained marrow inside, as indirectly indicated by findings of damaged limb bones with marrow.

The systematic composition of the collection is typical of the Mammoth fauna (Figure 6). The most numerous remains are those of woolly mammoth [*Mammuthus primigenius* (Blumenbach, 1799)] bones and fragments (24.9 percent), almost as many as horses [*Equus* ex gr. *caballus* L., 1758] (23.5 percent), bison [*Bison priscus* (Bojanus, 1827)] (18.4 percent), reindeer [*Rangifer tarandus* L., 1758] (17.7 percent), and fewer musk ox [*Ovibos moschatus* (Zimmermann, 1780)] (7.4 percent) and lagomorphs [*Lepus* sp.] (2.7 percent). Bones of other mammals, such as woolly rhinoceros [*Coeleodonta antiquitatis* (Blumenbach, 1790)], saiga antelope [*Saiga tatarica* L., 1758], and predators such as cave lions [*Panthera spelaea* (Goldfuss, 1810)] and wolves [*Canis lupus* L., 1758], are rare. Each represents less than 1 percent of the collection (Table 2). Rodent remains constitute 4.8 percent of the whole collection and are represented by four genera and four species: hoofed lemming [*Dicrostonyx* ex gr. *simplicior-henseli*], Siberian lemming [*Lemmus* ex gr. *sibiricus* Kerr, 1792],
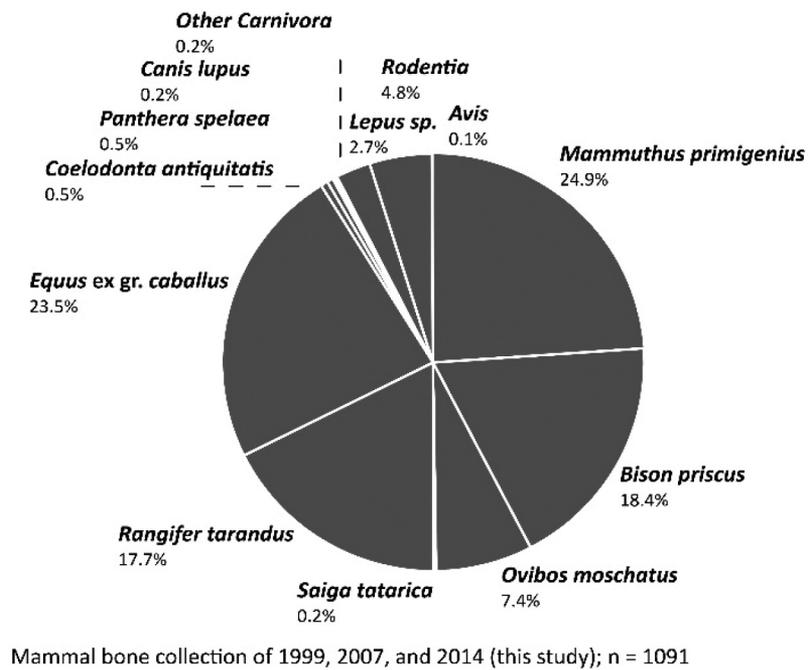
Figure 6. Composition of the bone collections from Bol'shoy Lyakhovsky Island showing the total collection from 1999, 2007, and 2014. The percentages are calculated based on the total number of identified samples, which is 1,091 (Table 2).

Middendorff's vole [*Microtus middendorffii* Poljakov, 1881], and red-gray vole [*Clethrionomys* cf. *rufocanus* Sundervall, 1846–1847] (Kuznetsova and Tesakov 2003).

The collection was assembled in an area of Late Pleistocene Yedoma Ice Complex sediment with high ice content, sometimes reaching up to 90 volume percent. The ice in the sections actively melts at positive temperatures, and the thawed deposits, which host paleontological remains, flow down the section. Under such conditions, the number of bones collected from the in situ layer is generally low.

Description of the different finding locations

For each sample in the collection, there is information about the collection site. Because our article focuses on the characteristics of the Zimov'e section, the samples collected from the section (groups A, B, and C) will be described in detail. Data on samples from other groups are fully presented in Table 2 and are summarized briefly here.

Collection of in situ samples (group A)

Group A, which consists of bones collected in situ and comprises thirty-nine specimens (3.5 percent of the total number of bones), of which one specimen remains unidentified. This group, except for two specimens, consists of bones collected in section R, west

of the Zimov'e River mouth (Figures 4a and 4b). The largest number of samples (twenty-eight) was collected from the MIS 2 deposits (Yana Suite) of the Sartan thaw slump (SR TC). Most of them (twenty-two samples, height near 6 m), and possibly all, belong to a single skeleton of *B. priscus*. Remains of *R. tarandus* were also found in the same thaw slump: first and third phalanges and hair (height of 3.5 m asl; Schirrmeister et al. 2008; Wetterich et al. 2011) and fragments of metapodia (height of 7 m.a.s.l.; Fuchs et al. 2015; Wetterich, Meyer et al. 2021; Figures 4a and 4b).

Three horse bones, two of which may belong to the same individual; a fragment of a reindeer vertebra; and a humerus bone of *M. primigenius* were found in MIS 4 to 3 deposits (Oyogos Suite) at various outcrops. A tusk fragment of *M. primigenius* was found at the boundary of MIS 4 to 3 (Oyogos Suite) and the underlying MIS 6 (subaquatic Kuchchugui Suite) deposits at 8 m.a.s.l. A fragment of a discarded horn of *R. tarandus* from MIS 5a to 5d (Kuchchugui Suite) and an indeterminate fragment of a large mammal limb bone in deposits of the MIS 7 (Yukagir Suite; Figures 4a and 4b) stem from older sediments. Thus, the remains of *B. priscus*, *R. tarandus*, *E.* ex gr. *caballus*, and *M. primigenius* were found in situ in section R. Only two bones were found in situ in section L, which are a fragment of a mandible and a metapodia of a cave lion (identified

by M.V. Sotnikova, GIN RAS, Moscow, Russia) at a height of 5.6 m.a.s.l. in deposits of the MIS 5a to 5d (Kuchchugui Suite; Figure 4c).

Collection of bone-field samples from thaw slumps (group B)

A total of fifty-five specimens, which is 5.0 percent of the total number of bones, belong to group B. One specimen (rib fragment) was not identified. The remains of *E. ex gr. caballus*, with twenty-one specimens (38.9 percent), dominate group B, whereas *M. primigenius* was found with fifteen specimens (27.8 percent). Ten specimens (18.6 percent) belong to *R. tarandus*, seven specimens (13 percent) to *B. priscus*, and one to *O. moschatus*. The main part of fifty-three samples was found in outcrops of section R, of which twenty-one belong to *E. ex gr. caballus*, thirteen to *M. primigenius*, ten to *R. tarandus*, seven to *B. priscus*, and one to *O. moschatus*; one was not identified.

From the Sartan thaw slump (MIS 2, Yana Suite), three bones were found: one reindeer, one mammoth, and one horse. The first thaw slump, in which deposits of the MIS 4 to 3 (Oyogos Suite) are exposed (section R), is divided into three bone fields: bone field O III in the western part, bone field O IV in the central part, and bone field O V in the eastern part of the thaw slump (Figure 4a). Because the wall of the first thaw slump was almost vertical, exposed wedge ice prevailed, and sediments formed only windows in the ice wall (Figures 3b, 4a, and 4b), where fossil material could not be collected. Thawed material was relocated with mudflows to the base of the ice wall. The upper boundary of bone field O III was the upper edge of the western part of the first thaw slump (maximum height 31–32 m.a.s.l.), and the lower boundary was 14 to 15 m.a.s.l. The maximum height at which it was possible to search for and collect bones and their fragments for bone field O III was 18.6 m.a.s.l.; that is, the bottom of the ice wall in the western part of the first thaw slump. Nine specimens were collected from the bone field O III, belonging to *B. priscus* (four bones), *E. ex gr. caballus* (two bones and one fragment), and one bone fragment each of *R. tarandus* and *M. primigenius*. Bone field O IV has an upper boundary at the edge of the central part of the thaw slump at 32.5 m.a.s.l. The lower boundary was the bottom of the ice wall at 13.5 m.a.s.l. Eleven samples were collected from bone field O IV. These are only bone fragments: five fragments of *M. primigenius* bones, three fragments of *E. ex gr. caballus* limb bones, three fragments of *R. tarandus* bones, and a fragment of *B. priscus* sacrum. The upper boundary of bone field O V was located at the edge of the eastern part of the first thaw slump east of profile R 7 at 29 m.a.s.l. The lower

boundary was at 10.5 m.a.s.l. Eighteen bones and their fragments were collected from bone field O V. Bone fragments predominate. *E. ex gr. caballus* includes eleven specimens, among them the left branch of the mandible with severely obliterated teeth, P4-M3; four limb bones are whole. There are *R. tarandus* (one whole and three fragments), one fragment sample each of *M. primigenius, B. priscus,* and one whole *O. moschatus*. Bone field O VI (MIS 4–3, Oyogos Suite) covers the central part of the third thaw slump (Figure 4a); its upper boundary was the edge of the thaw slump at 30 m.a.s.l., and its lower boundary was 15 m.a.s.l. Eleven specimens were collected from bone field O VI; the rib fragment was not identified. *M. primigenius* includes five samples, of which three (lumbar vertebra, two fused thorax vertebras, and one thorax vertebra) most likely belonged to one animal. Three bone fragments belong to *E. ex gr. caballus* and two samples belong to *R. tarandus*. In the alas thermocircus 4 m above the upper boundary of the Krest–Yuryakh Suite, a bison bone was found.

Only two bones of *M. primigenius* belong to group B in section L: a humerus found in the debris at 15 m.a.s.l. in the third thaw slump and a fragment of a humerus found in the debris of MIS 4 to 3 (Oyogos Suite) sediments at 10 m.a.s.l. in an outcrop of the Yedoma Ice Complex.

Collection within the thawed debris at the base of exposures (group C)

A total of 144 specimens (13.0 percent of the entire collection), of which three were unidentified, were collected from the debris of the exposures and constitute group C. In species terms, remains of *E. ex gr. caballus* predominates with 43 specimens (30.5 percent) and *M. primigenius* with 42 specimens (29.8 percent). There are further remains of *R. tarandus* (25 specimens, 17.7 percent), *B. priscus* (20 specimens, 14.2 percent), *O. moschatus* (9 specimens, 6.4 percent), and *L. tanaiticus* (5 specimens, 3.5 percent). According to the place of collection, group C is divided into two parts: specimens collected under thaw slumps of section R and specimens collected under thaw slumps of section L.

On the thermal terrace and in the debris under section R, there were 106 specimens of thawed bones and their fragments, which constitute 73.6 percent of the entire group C. In the debris of the MIS 2 (Yana Suite, Sartan thaw slump) deposits, 7 specimens were found. Two samples, including a hoof fragment, belong to *R. tarandus*, and one sample each belong to *E. ex gr. caballus* and *M. primigenius*. Three bone fragments were not identified. On the thermoterrace, under and between the thaw slumps, 92 samples were found. Remains of

M. primigenius predominate with 30 samples, and *E.* ex gr. *caballus* was found with 26 samples; one specimen is a pelvic fragment with tendon remnants. Further findings include *R. tarandus* (14 samples), *B. priscus* (12 samples), *L. tanaiticus* (five samples), and *O. moschatus* (four samples). One specimen of each *B. priscus, O. moschatus, M. primigenius*, and *R. tarandus* was found in the sediment under the alas cut.

All thirty-eight specimens (26.4 percent) belonging to group C of section L (Figure 4c) were collected in the debris under the first thaw slump. Of these, sixteen specimens belong to *E.* ex gr. *caballus*, including hoof. Seven specimens each belong to *B. priscus* and *R. tarandus*. Four specimens, each belonging to *M. primigenius* and *O. moschatus*, including a fragment of the male skull.

A total of 238 specimens (21.8 percent) were collected within groups A, B, and C from both sections R and L. Bones from the western section R predominate, with 194 specimens and two additional specimens (wool and reindeer hoof fragment; 18.0 percent). From the eastern section L 41 bones and horse hoof were collected (3.8 percent; Table 2, Figure 7). Such significantly different numbers are explained by the different geological structures of these two sections. In the western part, the sediments of MIS 4 to 3 (Oyogos Suite) and MIS 2 (Yana Suite), which contain a much greater number of mammal fossils than the underlying sediments of older age, are represented in a much larger volume (Figure 4). This also accounts for the large amount of bone material collected in the western profile sections. In the eastern part, only one low-thaw slump, with a small width and extent of the thermal terrace, is well exposed. In contrast, the western part features three very high thaw slumps, each with a long and wide thermal terrace. Therefore, here the bones are expected to remain in the sediment below the outcrop or on the thermal terrace for a long time before reaching the shore.

Collection from the shore (groups D and E)

The largest number of bones and their fragments, as in other transects of the Yedoma Ice Complex, were collected on the shore. A total of 728 specimens were collected from the shores of sections R and L; that is, 65.7 percent of the entire collection, with 14 undetermined specimens. From the shore of section R (group D), 227 specimens were collected (20.5 percent), including 7 undetermined specimens; from the shore of section L (group E), 501 specimens were collected (45.1 percent), of which 52 specimens were rodent remains (4.7 percent); five bone fragments were undetermined (Table 2).

Most of group D was collected on the shore, and only one collection point, Cape Kamennyi, was separated from the others (Table 2). The separation of bones collected on the western shore (section R) under outcrops was not meaningful due to the active wave transport of the material. Ice transport was probably also present, as indicated by the preservation of individual bones (Table 2, Figure 7a). Seven samples were not identified. Among the rare finds at the cape was a distal fragment of the humerus of *S. tatarica* and a carpal bone (astragalus) of a wolf. A damaged skull of a hare, identified as *L. tanaiticus* (Averianov, Kuznetsova, and Nikol'sky 2003), was also found on the shore near profile R 1.

Group E bones, collected from the shore to the east of the Zimov'e River mouth (section L), are significantly larger than those from group D. This is primarily due to the greater distance from which the bone material was collected. The samples in this group are further divided into several subgroups, the most numerous of which are samples collected on the shore near the camp from the markers L-0 to L-4 + 50, samples under thermokarst basins and thaw slumps, and samples collected at a distance of about 10 km east of the camp (Figure 5). A total of five bone fragments out of 501 samples of group E were not identified. This is the only group that includes not only the remains of large and medium-sized animals from the mammoth fauna but also those of rodents (52 samples; Table 2). Among large mammals, 444 defined samples remain (Table 2, Figure 8b). Significantly fewer remains were attributed to *Lepus* sp. (8 samples), *C. antiquitatis* (four samples), *P. spelaea* (3 samples), Carnivora (2 samples), *S. tatarica* (1 sample), and a damaged bird skull of *Clangula hyemalis* (identified by V.N. Kalyakin, Faculty of Geography, MSU, Moscow, Russia). Rare finds include the metacarpal bone of *R. tarandus* from a sick animal. The lower part of the bone is missing, and it is safe to say that the animal could not step on the front foot; however, the proximal joint is incorporated into the diaphysis (Figure 9a). Among the specimens belonging to *B. priscus*, the following should be noted: four specimens are horn sheaths and their fragments and two skull fragments, one with horny outgrowths. A skull fragment of a female musk ox is a rare specimen in the collections, and also a left branch of the mandible with an incomplete tooth row of *P. spelaea*. The most remarkable find, approximately 5.6 km from the camp (Figure 4c), is a huge woolly mammoth tusk (3 m long, 10 cm in diameter), the end of which was broken off; in one piece it would have been even longer (Figure 10a).

The easternmost collection site was a shoreline approximately 10 km from the camp. At this location,
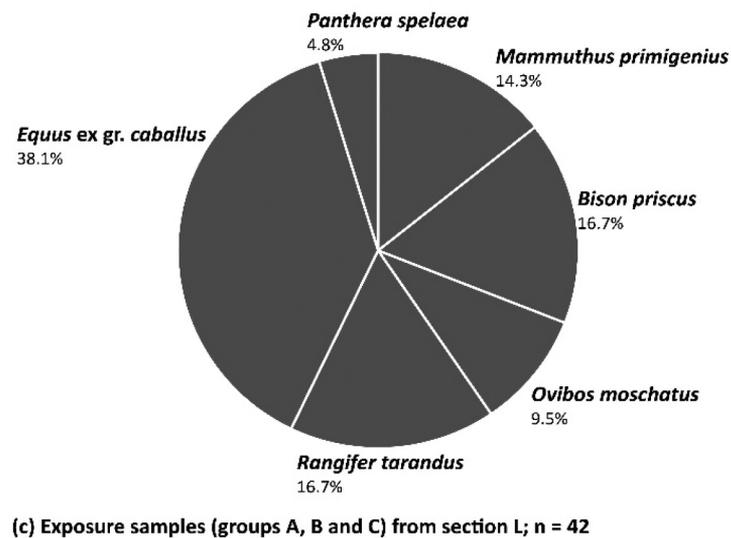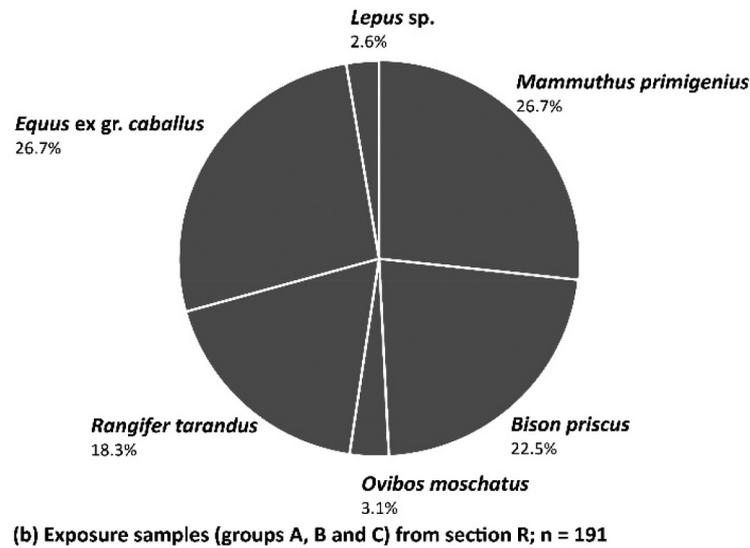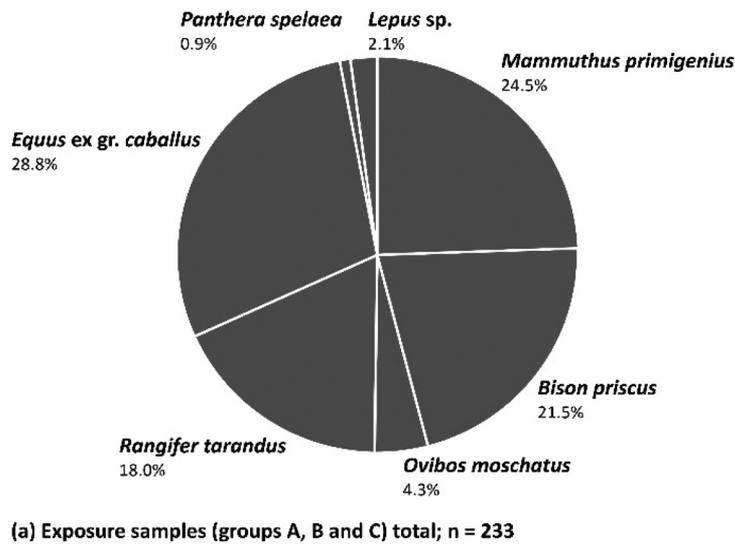
Figure 7. Composition of the mammal bone collections from in situ, in the bone fields, and at the base of the exposures (groups A, B, C). The percentages are calculated from the total number of identified samples: (a) finds from sections R-side and L-side together (n = 233), (b) finds from section R (n = 191), and (c) finds from section L (n = 42).
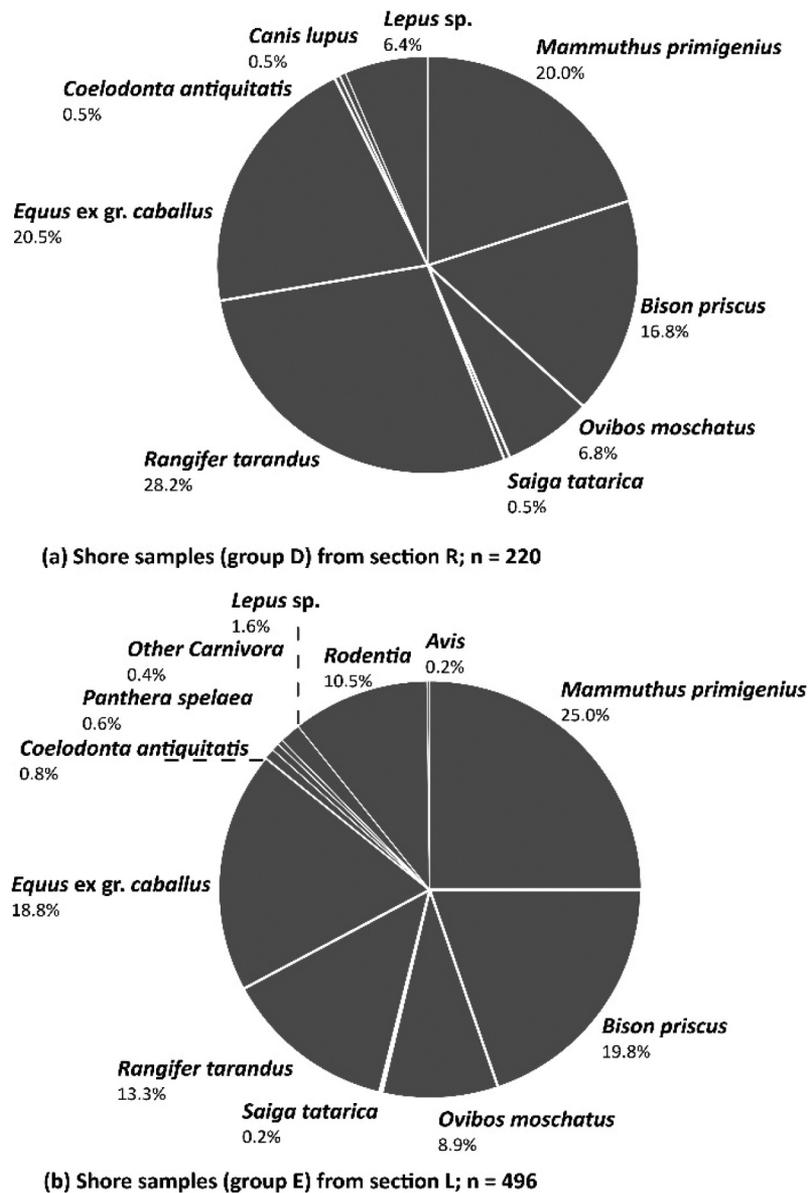
Figure 8. Composition of the large mammal bone collections from the shore, separated by (a) group D at section R (*n* = 220) and (b) group E at section L (*n* = 496). The percentages are calculated from the total number of identified samples.

sixty-four large mammal specimens were collected. One sample (BL-O1001-L) contained fifty-two teeth and various skeletal parts of small mammal remains, as well as five hare bone fragments and a raptor bone fragment. Among the large mammal finds at this site are two rare ones: a large fragment of a woolly mammoth skull, including two cheek teeth (Figure 10b), and pathological woolly mammoth tusks (Figure 10a). Among the specimens belonging to *M. primigenius*, fragments of cheek teeth and tusks prevail (fourteen specimens). Among thirteen samples belonging to *B. priscus* is a fragment of a horny sheath. *O. moschatus* includes six specimens, including a fragment of the skull. A damaged thoracic vertebra of *S. tatarica* was also found here (Table 2).

Collection from the Zimov'e River (group F)

Group F samples were collected along the banks and in the floodplain of the Zimov'e River: a total of forty specimens (Table 2), including thirty-eight samples of bone material, one sample of mammoth wool (Figure 10c), and a musk ox skin fragment (Figure 10d). The majority of the material is from *M. primigenius*, comprising nineteen specimens (47.5 percent). Many of them (twelve specimens) most likely belong to an individual whose leg, with soft tissues and a fragment of skin, was found, as we wrote earlier, in 1995 in the floodplain of the Zimov'e River (Saige et al. 1995). Twelve samples include the thoracic vertebrae with tendons, thoracic vertebrae, lumbar vertebrae, two

Figure 9. Finds of pathological remains: (a) metacarpal of *R. tarandus* (BL-O478-L) and (b) a tusk fragment of *M. primigenius* (BL-O646-L). The black scale corresponds to 1 cm.

a maxillary fragment with a milk premolar (dP4). Among the other samples are rare remains, including a complete male musk ox skull and a fragment of skin, both of which belong to *O. moschatus*.

Collection from the different locations of the Bol'shoy Lyakhovsky Island (group G)

The last group of specimens, group G, is a composite group. It includes 102 specimens (9.2 percent). The main part was collected by "hunters for mammoth tusks" from the entire southern part of Bol'shoy Lyakhovsky Island. Remains of *E.* ex gr. *caballus* predominate in this group (41 specimens, 40.2 percent), of which twenty-seven specimens are phalanges. In addition, there is a fragment of a skull, a fragment of the right branch of the upper jaw, individual teeth, an atlas, and, mostly, whole limb bones. Two complete scapulae of *M. primigenius* were found on the tundra surface in a ravine valley, approximately 5.6 km east of the camp. Significantly fewer specimens belong to *R. tarandus* (eighteen specimens, 17.6 percent), primarily consisting of small limb bones and four individual upper teeth. *M. primigenius* is represented by seventeen specimens (16.6 percent), including eleven tooth fragments and a tusk. *B. priscus* includes twelve specimens (11.8 percent), mostly small limb bones. Of the ten bones (9.8 percent) of *O. moschatus*, nine are distal limb

vertebral fragments, rib and rib fragment, humerus, small bones of the wrist (ulnare, pisiforme), phalanx posterior, and patella. Among other *M. primigenius* bones collected in the floodplain, a rare specimen is

Figure 10. (a) Find of damaged tusk *M. primigenius* and fragment of tusk on the east shore (section L) (credit: V. Tumskoy), (b) a large fragment of a woolly mammoth skull (section L, credit: V. Kunitsky), (c) wool of *M. primigenius* from the floodplain of the Zimov'e River (credit: T. Kuznetsova), and (d) fragment of the skin of *O. moschatus* from the floodplain of the Zimov'e River dated to 51,640 +3,210/-2,290 a BP (credit: T. Kuznetsova). The black scales in (c) and (d) correspond to 5 cm.

bones. Two specimens belong to *Lepus* sp., one to *C. lupus* (left mandibular branch with teeth), and one to *C. antiquitatis* (tooth).

Findings of rodent remains in section L

In addition to the remains of large herbivorous mammals, jaw fragments, individual teeth, and fragments of the postcranial skeleton of rodents were found at this site, located approximately 10 km east of the camp: *D. ex gr. simplicior-henseli* (twenty specimens), *L. ex gr. sibiricus* (twenty-eight specimens), *M. middendorffii* (three specimens), and *Cl.* cf. *rufocanus* (three specimens). A.S. Tesakov carried out the determinations (Kuznetsova and Tesakov 2003). The most diagnostic upper first molar tooth ($M^{1/}$; four specimens) is represented by the primitive morphotypes *simplicior* (two specimens) and *henseli* (two specimens). Among the lower first molars ($M_{/1}$; eleven specimens), the morphotypes *simplicior-henseli* (four specimens), *henseli* (six specimens), and *henseli-torquatus* (one specimen) were identified. The remains of the Siberian lemming (*Lemmus*), which dominate the association, are morphologically indistinguishable from those of Late Pleistocene and modern forms. The presence of Middendorff's vole and forest vole remains is noteworthy. Remains of the forest red-gray vole were found for the first time on Bol'shoy Lyakhovsky Island. Possibly, the remains of two voles (Middendorff's and red-gray forest voles) indicate closer connections between the island and the mainland in the past. Both forms are absent in the modern fauna of the island. In the modern fauna, *M. middendorffii* is sporadically found in the tundra zone (less frequently in forest–tundra) along the Arctic coast, from the Yamal to the Kolyma rivers. Of modern forest voles, red voles *Cl. rutilus* and red-gray voles (*Cl. rufocanus*) inhabit the north of Eastern Siberia. The only identified remnant of the upper first molar ($M^{1/}$) is close in size and morphology to that of the red-gray vole.

Collection of the Museum of the Lena-Delta Reserve

In 2005, as part of the Russian–German System Laptev Sea collaboration, we identified and studied the paleontological collection stored in the Lena-Delta Reserve in Tiksi (Kuznetsova 2007b). Of the 292 specimens in this collection, 48 were found on Bol'shoy Lyakhovsky Island. Of those, 44 were bones, teeth, and fragments, and 4 were specimens of *M. primigenius* wool. The material was collected mainly at the westernmost part of the island, Cape Shalaurova, and from the area of the mouth of the Zimov'e River.

Nine specimens were collected from Cape Shalaurova, including two fragments of ribs from *M. primigenius*,

a damaged femur, and an ulna of *E. ex gr. caballus*; the first phalanx and atlas fragment of *R. tarandus*; and a small wrist bone of *B. priscus*. One wool sample of *M. primigenius* was collected in the eastern part of the island near the Eterikan River.

Thirty-six specimens were collected from the Zimov'e River mouth, including one sample of mammoth wool. Thirty bone specimens of *M. primigenius* prevail. Of the woolly mammoth remains, ribs and their fragments are the most abundant in the collection. Ten of the eighteen ribs are most likely to have belonged to one individual. The other two damaged ribs belonged to another individual. In addition to the woolly mammoth, the collection from the Zimov'e River mouth contains four specimens belonging to *B. priscus*, two of which are fragments of skulls with horny rods and a damaged skull of a female *O. moschatus* with a left horny rod.

Radiocarbon ages of bone material

Prior to our work on Bol'shoy Lyakhovsky Island, only two radiocarbon dates were obtained on the island from a single woolly mammoth bone: 32,030 ± 1,170 a BP and 32,100 ± 900 a BP (Table S1; Lozhkin 1977; Sulerzhitsky 1995). Additional specimens (bones, bone fragments, teeth and their fragments, wool, and skin fragments with wool) of large mammals of the mammoth fauna were dated and summarized in the course of the present study (ninety-six) and literature search (ten; Table S1; Kuznetsova, Sulerzhitsky, and Siegert 2001; Sher et al. 2005; Andreev et al. 2009; Wetterich et al. 2011).

A total of forty-three radiocarbon ages, of which fourteen were infinite, belong to samples from outcrops (groups A, B, and C). Samples from shores (groups D, E) sum up to forty-two dates, of which half are infinite (Figures 4 and 5). Two finite samples belong to group F (floodplain). For samples from other areas of the island, nine radiocarbon dates were determined, of which five were infinite (Table S1).

Five specimens from Group A were collected from Sartan Yedoma Ice Complex deposits (Yana Formation, MIS 2; Figure 4b), which had not been recognized during the first field season on the island in 1999. However, the ten dates on bones found in the debris or on the shore under the outcrop allowed an expectation of the presence of MIS 2 deposits. Deposits of MIS 2 age were later identified and studied in more detail (Wetterich et al. 2011; Wetterich, Meyer et al. 2021). Dated reindeer metatarsal fragments show ages of 21,692 ± 117 a BP, 21,713 ± 117 a BP, and 21,972 ± 116 a BP, and horse metacarpal III yields an age of 29,390 ± 200 a BP (Wetterich et al. 2011). The bison thorax vertebrae and ribs collected in situ with an age of 34,360 ± 400 a BP

and a bison rib fragment, dated to 53,300 ± 1,900 a BP (Shapiro et al. 2004), probably belong to samples redeposited from more ancient times in the MIS 2 deposits (Table S1, Figure 4a).

In addition to the specimens collected in situ, thirteen dates were obtained from group B bones; five are infinite. Because this group includes bones from 'bone fields' collected at the foot of the steep frozen thaw slump walls, the obtained dates indicate the age of the sediments above. The ages of samples from bone fields III and V (Figure 4) in the first thaw slump are not younger than 34,800 ± 1,000 a BP, and more than half of the dates are infinite (Table S1). The large number of radiocarbon dates with infinite ages indicates that the lower part of the thaw slumps in the Oyogos Suite is older than 50,000 years. Of the bones collected from bone field IV, located in the central part of the first thaw slump, there is one younger date of 12,500 ± 50 a BP, indicating the presence of much younger deposits than those of the main part in the upper part of this thaw slump (Figure 4). This dating is based on a tusk fragment of *M. primigenius*, one of two young woolly mammoth dates from Bol'shoy Lyakhovsky Island. The ages of bones collected in bone field O VI below the third thaw slump are not younger than 37,800 ± 900 a BP (Table S1), similar to bone fields O III and O V. From the eastern profile (section L), there is only one date from a humerus of *M. primigenius*, from the third thaw slump, at 38,700 ± 500 a BP, which falls within the age range of dates from the bone fields of the western profile.

Of the twenty-one radiocarbon dates from group C, seven are infinite at the western profile (section R), and from the eastern profile (section L), eight are infinite. From the bones collected in the debris below the first thaw slump of section L, five specimens have radiocarbon dates that are close together, ranging from 38,000 ± 1,100 a BP to 35,100 ± 1,200 a BP. The discovery of a fragment of *M. primigenius* pelvis with an age of 25,900 ± 600 a BP in the debris below the first thaw slump confirms our assumption about the presence of MIS 2 deposits in the upper part of the first thaw slump. In the debris below the outcrop of the western profile, a fragment of a pelvis with copulae of *Equus* ex gr. *caballus* was also found. The radiocarbon age of this specimen is 2,200 ± 50 a BP, the youngest known date for horses not only from Bol'shoy Lyakhovsky Island but also from the entire Arctic region of Yakutia (Kuznetsova, Sulerzhitsky, and Siegert 2001; Table S1, Figure 4).

From the shore under the western outcrops (group D), only ten samples were dated, four of which are infinite. Finite dates of *C. antiquitatis* and *S. borealis*

(Table S1) are rare from this region. From the coast, east of the Zimov'e River mouth (group E), radiocarbon dates were obtained for thirty-two samples, of which seventeen dates are infinite (Table S1, Figure 4).

Of the seven subgroups into which the samples collected on the east shore from the mouth of the Zimov'e River (section L) were divided, material from five subgroups was dated (Table S1). The rarest and most interesting are tibia belonging to *P. spelaea*, collected on the shore near the camp, and are dated to infinite (>62,100 a BP). Two cervical vertebrae, a fragment of a cervical vertebra, and a damaged epistropheus of *O. moschatus*, found under the first alas, may all belong to the same individual, but three of them have infinite dates (Table S1) due to an insufficient amount of collagen in the samples, because these dates were made by the conventional radiocarbon age determination method. One finite date, 38,200 ± 900 a BP, probably can characterize all four samples. The youngest date for woolly mammoths in our collection from Bol'shoy Lyakhovsky Island (12,030 ± 60 a BP) was obtained from a proximal fragment of the ulna, collected on the shore under the first alas of section L at a distance (L-17 + 70). Three bones of *C. antiquitatis* collected on the east shore have finite dates from 19,940 ± 320 a BP to 45,000 ± 650 a BP. The final date of 23,300 ± 110 a BP was obtained from a fragment of a woolly mammoth skull, collected on the shore 10 km east of the mouth of the Zimov'e River (Table S1).

Only one date, 32,500 ± 500 a BP, from a woolly mammoth thoracic vertebra with remnants of tendons, one from the twelve samples, probably belongs to the one individual, is from bones collected in the floodplain of the Zimov'e River (group F). Probably this date also belongs to a carcass fragment of *M. primigenius* with soft tissues (leg and fragment of skin) found in this area in 1995 (Saige et al. 1995). A skin fragment of *O. moschatus* with an age of 51,640 + 3,210/−2,290 a BP was also found on the floodplain (Figure 10d).

Of the seven samples collected elsewhere on Bol'shoy Lyakhovsky Island, the tooth of *C. antiquitatis*, which has been dated twice, is of particular interest. One of the later dates for the woolly rhinoceros is 13,330 ± 50 a BP. Tibia of dwarf *M. primigenius* dated to >45,000 a BP, and the metapodia of *P. spelaea* dated to >62,100 a BP (Table S1). Two dates were made on wool finds in the area of the Bol'shoy Eterikan River: 50,200 ± 900 a BP, >63,500 a BP, and one on wool found on Cape Shalaurova >58,000 a BP (Gilbert et al. 2008).

Preservation of mammal fossils

Preservation of bones from the outcrop (groups A, B, C)

Group A comprises 39 in situ specimens, including one that contains wool. Whole bones prevail (21 samples). Bone fragments (17 samples), one of which is indeterminate, among whole bones predominate vertebrae of different spine sections (13). Group B consists of 55 specimens with prevailing fragments (34). If we consider species, the greatest number of fragments (12) and whole bones (9) belong to *E.* ex gr. *caballus*. The taxonomic affiliation of one rib fragment has not been determined. Group C, identified in the debris from the sections, comprises 144 specimens: 82 fragments and 62 whole samples. Among the fragments, the greatest number is large limb bones (35), and all other fragments are much less frequent. There are three indeterminate bone fragments. Horse and woolly mammoth remains are almost equal. *E.* ex gr. *caballus* comprises 43 specimens, and *M. primigenius* comprises 40 specimens. In group C, there are 5 specimens (one whole bone and four fragments) belonging to *Lepus* sp., a taxon not encountered in groups A and B (Table S2).

The largest number of samples from groups A, B, and C consists of large limb bones (71 pieces), comprising 50 fragments and 21 complete bones (Figure 11). This is an unexpected result, because it is more logical to assume that more vertebrae would have been found on the transect, because the number in one individual of a large mammal is much greater than six large limb bones. The number of vertebrae (41) is lower. Finds of limb bones, such as whole bones and especially their fragments, prevail over all other bones from the transect. Out of 237 samples, 130 are bones and fragments of limb bones (including large and small limb bones, metapodials, and phalanges). There are three times fewer vertebrae.

The large number of limb bones and their fragments indicates probably both the great strength of these bones and the peculiarities of the burial of skeletal remains. The samples belong to *E.* ex gr. *caballus*: thirty-four were whole bones and hooves and thirty-two were fragments (Figure 12a, Table S2). There are significantly fewer complete bones (seventeen samples) of *M. primigenius* than fragments (forty). They are also fewer in number compared to the number of complete horse bones, although mammoth bones are significantly stronger than horse bones. This is most likely due to the number of animals that inhabited the area under study. *B. priscus* presented thirty-two whole bones and eighteen fragments; *R. tarandus*, thirteen whole bones and twenty-eight fragments; *O. moschatus*, six whole bones and four bone fragments; *Lepus* sp., one whole and four bone fragments (Figure 12a), and *P. spelaea*, one whole and one fragment (Table S2).

Preservation of bones from the shores (groups D, E)

Specimens of group D collected on the shore of section R total 227, comprising 100 complete bones (44 percent) and 127 fragments (56 percent; Figure 13a). At the species level, there are more remains of reindeer and horses than of woolly mammoths (Figure 12b). The largest number of specimens belongs to *R. tarandus* (62). There are 31 whole bones and 31 fragments, each equally. Thirty whole bones and 15 fragments belong to *Equus* ex gr. *caballus*. Only 8 whole bones and 36 fragments belong to *M. primigenius*. There are significantly fewer of both whole and fragmentary remains of all other animals (Figure 13b). Among the completely preserved specimens, phalanges (26) predominated; the largest number of fragments belonged to large limb bones (43), along with two indeterminate bone fragments (Table S2).

The group of mammal remains collected on the eastern shore, section L (group E), comprises 448 specimens, without rodents and bird bones, of which 184 are whole bones, teeth, and horns and 264 are fragments. Among the whole ones, small limb bones (55) and vertebrae (44) predominate. The largest number of fragments are fragments of large limb bones (54) and teeth (49); 9 bone fragments from group E were not identified (Table S2). The greatest number of specimens belongs to *M. primigenius* (124), of which 25 specimens are whole bones and 99 are fragments. Of the whole bones, the largest number is teeth (9 samples; Table S2). Among the fragments, tooth fragments (45) and tusks (23) predominate. The large number of tooth fragments is due to the lamellar structure of the woolly mammoth tooth. Tusks are well preserved in the fossil state and produce a large number of fragments when split.

Preservation of samples from the Zimov'e River (group F)

From forty samples belonging to this group, thirty-eight are bone specimens, twenty-four of which are whole, and fourteen are fragments. Additionally, one skin fragment and one hair sample were found (Table S2). The largest number of samples belongs to *M. primigenius* (nineteen), of which twelve are whole bones, six are fragments, and one is a hair sample. As we mentioned earlier, the majority of the bones likely belong to an individual. A fragment of skin, in addition to the entire skull, also represents *O. moschatus*.
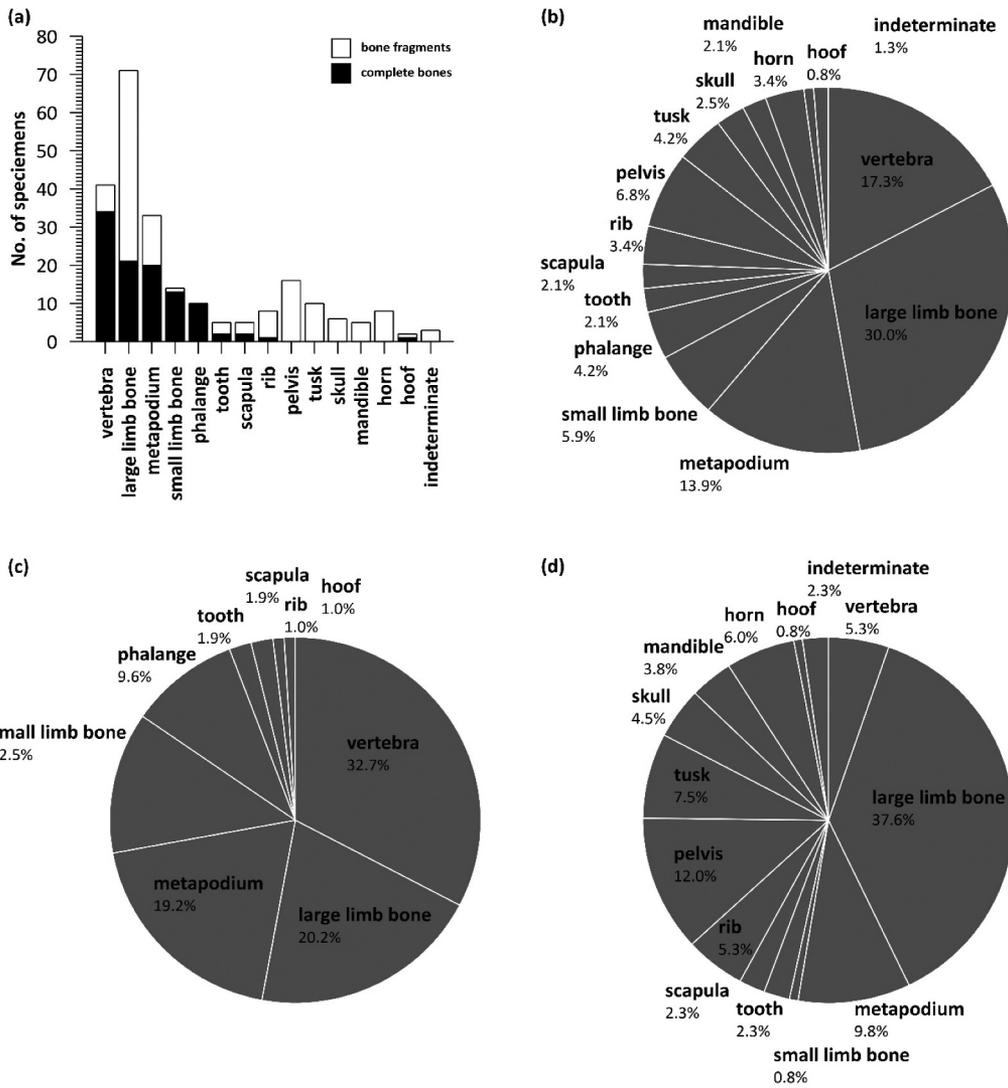
Figure 11. Mammal fossils of groups A, B, and C according to the preservation of their skeleton parts showing (a) the distribution of all bones including complete bones and bone fragments ($n = 237$), (b) the percentage of all bones including complete bones and bone fragments ($n = 237$), (c) the percentage of only complete bones ($n = 104$), and (d) the percentage of only bone fragments ($n = 133$).
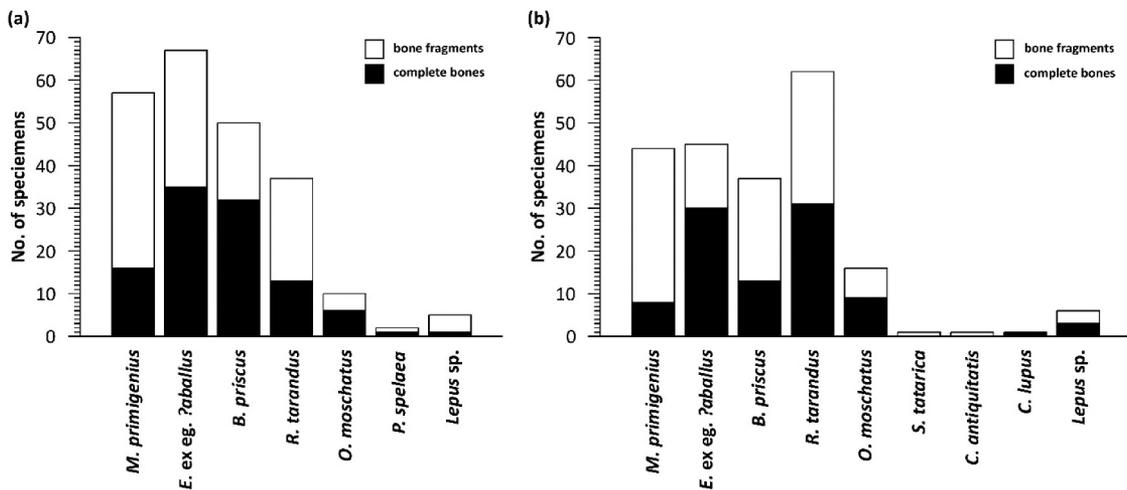

Figure 12. Mammal fossils, according to the preservation (complete bones and bone fragments), show (a) the distribution by species of groups A, B, and C and (b) the distribution by species of group D.
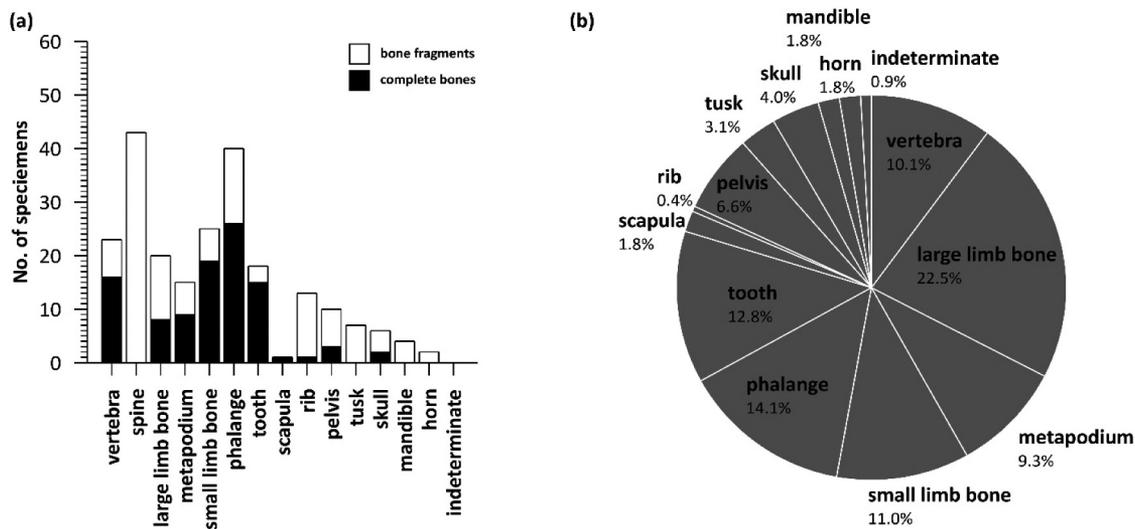
Figure 13. Mammal fossils of group D, according to the preservation of their skeleton parts, show (a) the distribution of all bones, including complete bones and bone fragments (*n* = 227), and (b) the percentage of all bones, including complete bones and bone fragments (*n* = 227).

Discussion

The faunal record of Bol'shoy Lyakhovsky Island

The large mammal bones collected near the mouth of the Zimov'e River on the southern coast of Bol'shoy Lyakhovsky Island are typical of the mammoth fauna of North Siberia in their species composition. However, the percentage of species differs from that of other mammoth fauna collections in the Laptev Sea Region (Schirrmeister, Siegert et al. 2002; Kuznetsova et al. 2022). In our entire collection (Figure 6), the percentage of horse remains (23.5 percent) is comparable to that of the woolly mammoth (23.9 percent). Looking at the finds from the transects (Figure 7a), however, horse remains (28.8 percent) predominate over those of mammoth (24.5 percent). In the collection of Oyogos Yar (Figure 1), the geologic structure closest to the described Zimov'e River locality, the remains of mammoths (39.9 percent) significantly predominate over those of all other animals, including horses (19.2 percent). For samples collected from transects at Oyogos Yar, the prevalence of mammoth is even higher, reaching 47 percent, whereas horse samples were only 9.6 percent (Kuznetsova et al. 2022). In the collection from Mamontova Khayata (Bykovsky Peninsula, Figure 1), mammoth remains also dominate, though not as significantly as at Oyogos Yar. In the entire collection, the remains of mammoths (36.9 percent) and horses (23.7 percent) are predominant; in the transect collection, mammoths (36.3 percent) and horses (15.2 percent) are also the most abundant (Kuznetsova et al. 2019). In the collection from Bol'shoy Lyakhovsky Island described by D.I. Chersky (Chersky 1891), the number of horse

remains significantly exceeds that of mammoths. Most likely, the southern coast of Bol'shoy Lyakhovsky Island was drier during the Late Pleistocene, when the Yedoma Ice Complex deposits formed, and snow cover was thinner than in more southern areas, creating favorable conditions for horses. Our data, obtained during a multidisciplinary study of outcrops in the Laptev Sea region (Schirrmeister, Siegert et al. 2002; Andreev et al. 2009), indicate a dry, sharply continental climate (Schirrmeister et al. [2025a] and quotations therein). Mosaic soil and vegetation patterns were present on both Bol'shoy Lyakhovsky Island and Oyogos Yar during the formation of the Yedoma Ice Complex. However, the number of hard, dry, well-drained soil patches on Bol'shoy Lyakhovsky Island was greater than that on Oyogos Yar. The findings of *S. tatarica* support this conclusion (Danilkin 2005), which remained on Bol'shoy Lyakhovsky Island, and, indirectly, by the absence of remains of representatives of *Alces alces*. The northern limit of moose distribution coincides with the forest–tundra, although they can range further north along river valleys overgrown with shrubs. Modern saigas inhabit desert–steppe regions. They are unable to move quickly and forage for food in dense snow depths greater than 30 cm; the critical level is 35 to 40 cm of loose snow. Seasonal migrations from south to north are characteristic of these animals (Danilkin 2005).

A sample of metacarpal bone of reindeer with the distal part missing, and the proximal joint is incorporated into the diaphysis, indicating that the animal reached adulthood. This finding indicates that during

the life of this animal, there was no food deficit and tough competition from congeners. "Large amounts of Podospora and Sordaria spores (dung-inhabiting fungi) suggest the presence of numerous grazing mammals, such as mammoths, bison, and horses" (Andreev et al. 2009, 79).

Discovery of several dwarf mammoth remains indicates the presence, albeit in small numbers, of this form of mammoth on Bol'shoy Lyakhovsky Island (Kuznetsova et al. 2022). It is believed that some part of the *M. primigenius* population may have been smaller (Boeskorov et al. 2017). This is due to nutritional stress and unfavorable geochemical conditions. It is possible that normal-sized individuals and small mammoths inhabited different landscapes and utilized different food sources (Nikolskiy, Sulerzhitsky, and Pitulko 2011).

The bone dating record of Bol'shoy Lyakhovsky Island

The increase in the number of dates up to 106, including 66 finite ages (Table S1), compared with those analyzed in Andreev et al. (2009), supports our conclusions regarding the distribution of dates. The maximum number of dates falls in the interval from 43.5 to 20 ka BP (Figure 14), which is close to the age distribution of the Kondratyev Yedoma (43–22.5 ka BP) on the Oyogos Yar mainland coast (Kuznetsova et al. 2022). On Bykovsky Peninsula, the maximum number of dates spans 36 to 23 ka BP (Kuznetsova et al. 2019), attributed to the distinct geological structure of the Mamontovy Khayata outcrop. This distribution of dates on both shores of the Dmitry Laptev Strait suggests favorable conditions for the existence of large mammals during the Kargin interstadial (MIS 3) considered as the "warm" and "cool" periods of the tundrasteppe (48–23.5 ka BP; Sher et al. 2005) and at the very beginning of the Sartan stadial (MIS 2) period. Obviously, this was a time when conditions were favorable for preserving bones. Because the territory is located farther north than the Bykovsky Peninsula, it is likely that the number of large animals inhabiting it did not vary significantly. As can be seen from the data on vegetation and insects on Bol'shoy Lyakhovsky Island, located north of the Bykovsky Peninsula, it had more stable conditions, with less summer temperature fluctuation and no significant changes in humidity. It was maintained by a constantly sharp continental climate caused by the low sea level and the enormous extent of the shelf land (Schirrmeister, Siegert et al. 2002; Andreev et al. 2009).

As soon as the continentality of the climate begins to decrease and climate warming starts at the end of MIS 2, a sharp reduction in large animals inhabiting the study area occurs. The youngest age of mammoth remains from these three locations is from the southern shore of Bol'shoy Lyakhovsky Island, with a bone age of 12,030 ± 60 a BP (Table S1); a slightly older mammoth bone age was found in Bykovsky Peninsula, with an age of 13,100 ± 500 a BP (Kuznetsova et al. 2019) and a much older one from Oyogos Yar, with an age of 17,100 ± 300 a BP (Kuznetsova et al. 2022).

The youngest Holocene bone date was also obtained from an outcrop near the mouth of the Zimov'e River locality on Bol'shoy Lyakhovsky Island: a fragment of a horse pelvis dated to 2,200 ± 50 yr BP (Table S1). Several fragments of a horse mummy (Yukagir horse) with an age of 4,630 ± 35 yr BP (Boeskorov et al. 2014) were found in the outcrops of the Oyogos Yar mainland coast. These findings support the earlier assumption that horses lived in the eastern Siberian Arctic during the Holocene (Lazarev 1980; Kuznetsova, Sulerzhitsky, and Siegert 2001; Schirrmeister, Siegert et al. 2002). During the Holocene, musk oxen also inhabited the eastern Siberian Arctic, on the coast of the Laptev Sea (Kuznetsova et al. 2019).

The preservation of fossil bones of Bol'shoy Lyakhovsky Island

When describing the groups of bones by preservation status, group A had a higher percentage of whole bones than the other groups. This is understandable, because the bones of all other groups were not sampled in situ and were thus broken by the thawing of the frozen sediments, the collapse of the exposure, and subsequent transport. In group A, there are skeletal fragments with soft tissues, most often bones connected by tendons, which indicates the burial of an animal carcass or a fragment of a carcass directly at the site of sedimentation. Bones with soft tissues were found in deposits of Sartan thaw slumps but not in deposits of other thaw slumps (Figure 4). This can likely be attributed to the varying sedimentation conditions bones encountered during their entry into the sediment. This once again confirms the assumption of Tumskoy and Kuznetsova (2022) that the deposits of the I, II, and III thaw slumps have a proluvial–deluvial–solifluction genesis and the deposits of the Sartan thaw slump have a proluvial–alluvial genesis.

A comparison of the number and preservation of specimens found on the transects (groups A, B, C) and specimens collected from the western part of the shore (group D) revealed the following. The number of whole bones found on the transect (43.9 percent) is equal to the number of whole bones found on the shore below the transect (44.0 percent). Bones do not break in mass when they hit
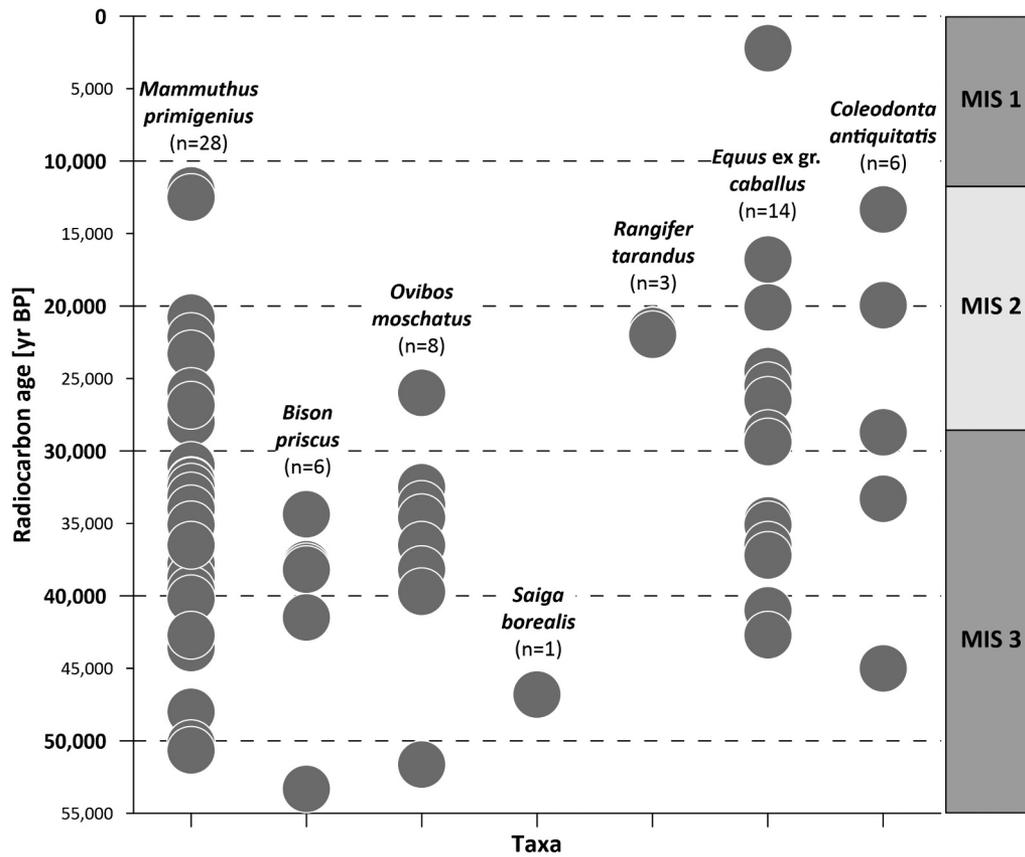
Figure 14. Distribution of finite radiocarbon ages of mammal bones (*n* = 66) from Bol'shoy Lyakhovsky Island, differentiated by taxa (Table S1). Dates are given as uncalibrated ages.

the shore, and the number of bone fragments collected onshore (56.0 percent) is equal to the number of bone fragments collected on transects (56.1 percent). The ratio of whole bones and their fragments on transects and shores is very close. This refutes the long-held belief that bones actively break during thawing and transport to the shore.

A comparison of the distribution of bone preservation groups in sections and on the shore was made (Figures 11–13), but no patterns have yet been identified. Prior to analyzing the preservation of the material, it was assumed that small limb bones would be the most abundant on both the transect and the shore; however, this was not the case. In the groups of bones collected from the transect, small limb bones account for only 5.9 percent and from the west shore 11 percent. The distribution of bone preservation groups from the western (group D) and eastern (group E) shores differs somewhat, but no pattern in their differences is discernible (Table S2). When comparing the number of bones collected from the sections and the shore below them described here with those from Oyogos Yar (Kuznetsova et al. 2022), the following picture emerges. On Bol'shoy Lyakhovsky Island, 196 samples were collected from the

western outcrops. In contrast, only 83 samples were collected from the outcrops of the Oyogos Yar, which is 2.4 times less. In addition, 227 samples were collected from the shore under the western outcrops on Bol'shoy Lyakhovsky Island. Under the outcrops on Oyogos Yar, there were 766, which is 3.4 times more. The difference between the number of fossil bones collected on the outcrops and the shore at Oyogos Yar is 9.2 times. On Bol'shoy Lyakhovsky Island, this difference is only 1.2 times. The significant differences in numbers within closely spaced sections can be attributed to variations in the relief of the outcrop, resulting from the geological structure. The Kondratyeva Yedoma of the Oyogos Yar lacks such a wide and high thermal terrace beneath the outcrops of the Oyogos Suite (MIS 4–3), which accumulates a large number of bones that have thawed from the section (groups B and C). Over a significant part of the outcrop, the lower boundary of the Oyogos Suite goes below sea level, and the bones from the outcrop, along with mudflows, immediately reach the shore (Kuznetsova et al. 2022). At the Mamontovy Khayata outcrop on Bykovsky Peninsula, 209 samples were collected in the outcrop, and 696 were collected below it

(Kuznetsova et al. 2019); the difference is 3.3 times. The topography of the Mamontovy Khayata outcrop allows for the collection of material from the talus beneath the outcrop; however, no developed thermal terrace is present either (Sher et al. 2005). As it turns out, the wide beach and shoal on Mamontovy Khayata do not significantly affect the number of samples collected from the shore.

Paleoenvironmental implications, regional and historical comparison

To compare the collections presented here, we calculated correlation coefficients from the bone frequencies in the collections (Table 3). We find a low correlation between the Bol'shoy Lyakhovsky collections and the Yana collection, suggesting that these locations differ in their faunal composition. This may suggest that they represent different paleoenvironments, offering distinct conditions for the fauna.

The three collections from Bol'shoy Lyakhovsky exhibit distinct differences in their similarities. This is not surprising, because they were collected during expeditions with goals and capabilities that were quite different. A significant part of the collection of the New Siberian Polar Expedition under the leadership of A.A. Bunge, studied by D.I. Chersky, as noted by the researchers themselves, were bones "in a washed-out state, along the mouths of rivers, and mainly near the so-called Small Zimov'e River, in the western part of the southern shore of the island. ... In spite of the most diligent search, Bunge succeeded in obtaining ... from the primary locality only one mammoth tusk and a reindeer tooth" (Chersky 1891, 75).

The collection studied by E.A. Vangenheim (1963) was sampled during a comprehensive study of the geological structure of Bol'shoy Lyakhovsky Island by the geologist V.D. Lebedev and is smaller in terms of both the number and diversity of bones.

During the work of the Russian–German expedition, a separate task was assigned to conduct the most detailed paleozoological characterization of the Pleistocene–Holocene deposits in the study area. This involved collecting all paleontological material from the outcrops where the research was conducted, as well as from the shore below them, which is especially important. It is the different approach to collecting material that causes the differences in the collections.

The small percentage of mammoth remains (1.7 percent) in the New Siberian Polar Expedition collection (Chersky 1891) is attributed to the difficulty of transportation and the weight of mammoth bones, which resulted in the collection consisting mainly of small bones and teeth. The percentage of mammoth remains in the V.D. Lebedev collection, predominantly represented by teeth (18 percent), is not insignificant (Vangenheim 1963). As noted by all researchers, the large percentage of reindeer remains is explained by the presence in the collection not only of fossils but also of recent bones (Figure 2). Otherwise, all three collections are similar in their main parameters: a large number of horse remains (22–23 percent; Figures 2 and 6) slightly higher number of bison remains in the described collection (18 percent) than in the two historical collections (12–13 percent; Figure 2). Significantly less than for the species considered are the remains of musk ox, ranging from 7.6 percent (Vangenheim [1963] and our collection) to 4.5 percent (Chersky 1891; Figures 2 and 6). The collection of the New Siberian Polar Expedition (Chersky 1891) differs in the high amount of hare remains (18 percent) compared with the more than twice as many hare remains in the V.D. Lebedev collection (7.1 percent; Vangenheim 1963) and significantly fewer in our collection (2.7 percent). The collection we describe also differs from the collection from the Bykovsky Peninsula (6.2 percent) by the insignificant amount of hare remains (Kuznetsova et al. 2019).

Woolly rhinoceros remains are sporadic in all collections (Figures 2 and 6). Individual saiga ossicles have been identified in the collections of the New Siberian Polar Expedition (Chersky 1891) and in our collection (present study). All collections have a small number of Carnivora remains. Rodentia are more abundant in the described collection due to the targeted search for rodent remains. E.A. Vangenheim from Bol'shoy Lyakhovsky Island identified several specimens as *Alces*

Table 3. Pearson correlation coefficients of different collections from Bol'shoy Lyakhovsky Island (Chersky 1891; Vangenheim 1963; this study) and the Yana River Lowland (Pitulko et al. 2014).

	Chersky (1891)	Vangenheim (1963)	This study	Pitulko et al. (2014)
Chersky (1891)		0.82	0.56	0.65
Vangenheim (1963)	0.82		0.91	0.50
This study	0.56	0.91		0.48
Pitulko (2014)	0.65	0.50	0.48	

sp., *Cervus elaphus*, and *Bos* sp. (Table 1). However, in general, all three collections are similar in their systematic composition and species percentages, except for the mammoth.

Most notably, Vangenheim (1963) is highly correlated with the collection presented in this study (Kuznetsova 2007a) and with Chersky (1891); however, the correlation between Kuznetsova (2007a) and Chersky (1891) is low. This is mainly driven by the distinct differences in the occurrence of mammoth, reindeer, and Pleistocene hare bones (Figure 15), which set Chersky (1891) apart from the other two collections, an effect that is more pronounced than with Kuznetsova (2007a) but less so than with Vangenheim (1963). This could partly be due to differences in how bones are classified as Pleistocene or recent in the Chersky collection for hare and reindeer. Assuming that the environmental conditions that determine bone exposure at the Bol'shoy Lyakhosky site have remained relatively constant between the acquisition of the different collections, the differences may be due to variations in collection strategies. These results suggest that, for interpreting collection data in a paleoenvironmental context, it is necessary to be aware of the conditions under which the collections were assembled to assess their comparability. We recommend consulting the detailed reports of each collection, rather than relying solely on numerical data, to fully appreciate the implications of these differences on species distribution and environmental reconstructions.

It is very interesting to compare the Bol'shoy Lyakhovsky collection of outcrop and shore species composition and percentages with the collection of fossil animal remains from archeological excavations at the Yana site (Pitulko et al. 2014). Here, the total number of finds is 2,440, of which 870 specimens were not identified. The list of 1,570 identified specimens includes sixteen species, one of which is a fish. The methodology for collecting archeological paleozoological collections differs significantly from collecting bone material from outcrops, as evident in the specimen ratios. In the collection from the Yana archeological site, the remains of three species predominate: bison (38.6 percent), reindeer (23.3 percent), and hare (20.6 percent). There are significantly fewer remains of horses (7.0 percent), mammoths (5.2 percent), and wolves (4.0 percent), and finds of all other animals are sporadic. The preservation and composition of the mammal collection differ fundamentally from those collected from the outcrop and most likely reflect not so much the species ratio in the fauna inhabiting the area as the food ration of ancient humans.

Collections from the Bykovsky Peninsula, Oyogos Yar, and the southern shore of Bol'shoy Lyakhovsky Island have already been compared in general
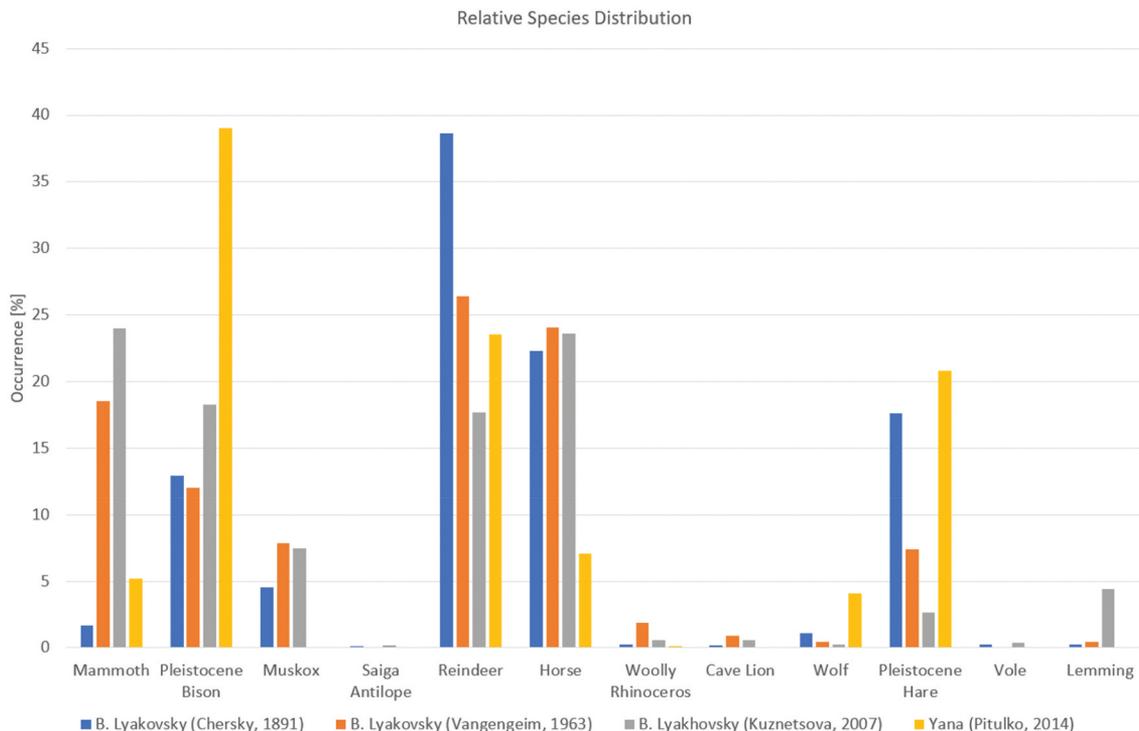

Figure 15. Relative species distribution of the compared collections.

Table 4. Ratio of the remains of the main mammal species of the mammoth fauna in different areas of the Laptev Sea region.

Taxon	Zimov'e river mouth region, Bol'shoy Lyakhovsky Island (percent)	Kondratev Yedoma, Oyogos Yar (percent)	Mamontovy Khayata, Bykovsky Peninsula (percent)
Mammuthus primigenius (Blumenbach, 1799)	22.5	40.9	37.4
Equus ex gr. *caballus* L., 1758	22.7	18.0	23.1
Rangifer tarandus L., 1758	22.5	18.6	13.1
Bison priscus (Bojanus, 1827)	18.9	17.7	9.2
Ovibos moschatus (Zimmermann, 1780)	5.0	4.3	2.0
Lepus sp.	4.5	0.4	8.3

(Kuznetsova et al. 2022). However, comparing fossil remains from outcrops and the shore beneath them reveals additional peculiarities in the ratios of mammoth fauna species that inhabited the described territories at the end of the Pleistocene. Based on the species composition of mammals in the collections of all three locations, it can be assumed that the number of mammoths in the percentage ratio was greater in the area of Oyogos Yar than on the Bykovsky Peninsula and almost two times greater than on the territory of the present-day southern shore of Bol'shoy Lyakhovsky Island (Table 4). In general, the number of mammoths and horses among the tundra–steppe inhabitants on the territory of the modern southern shore of Bol'shoy Lyakhovsky Island was equal. Most likely, the conditions there were not very favorable for mammoths. In the territory of Bykovsky Peninsula and Oyogos Yar, horses were much less common than mammoths.

The territory of the southern shore of Bol'shoy Lyakhovsky Island is characterized by the presence of a large number of bison remains in the collection. The number of bison bones was similar on the Oyogos Yar, whereas on the Bykovsky Peninsula it was almost two times less. A similar distribution was identified for remains of musk ox and reindeer (Table 4). The change in the number of reindeer in the collections should be interpreted carefully, because this is a modern species that, until recently, inhabited the study areas. We believe that the number of animal remains and their ratio in our case cannot indicate the total number of animals but rather the ratio of animals that lived in a given area.

The percentage of ungulates in the mammoth fauna on the southern shore of Bol'shoy Lyakhovsky Island was considerably greater than that on Bykovsky Peninsula and Oyogos Yar. There were nearly twice as many ungulates (excluding reindeer) in the fauna of Bol'shoy Lyakhovsky Island than mammoths. On the Oyogos Yar and the Bykovsky Peninsula, this ratio is more in favor of mammoths; the number of ungulates living in these territories was slightly higher or approximately equal to that of mammoths.

Sharp differences can be observed in the number of hares inhabiting the described territories. According to the number of *Lepus* sp. remains, it is the fourth animal in the collection from Mamontovy Khayata, indicating that the animal was very widespread in the territory of the modern Bykovsky Peninsula. On the southern shore of Bol'shoy Lyakhovsky Island, the number of finds was somewhat smaller but still substantial, whereas on Oyogos Yar the hare remains are sporadic.

Conclusions

Species attributed to the mammoth fauna have been determining components of the Late Pleistocene Beringian ecosystem. Extensive field sampling, systematic documentation of the finding conditions, and numerous radiocarbon dates on bone (and, in part, soft tissue) material enhance the information value of fossil bone collections and their comparability. The present collection from Bol'shoy Lyakhovsky Island (New Siberian Islands), which has been sampled both in situ and ex situ, represents one of the most comprehensive collections of fossil remains of the mammoth fauna in western Beringia. The species composition reflects the prevalence of remains of the herbivore *M. primigenius* and *E.* ex gr. *caballus* over those of *B. priscus* and *R. tarandus*, whereas *O. moschatus* and *Lepus* sp. are much less frequent, and *C. antiquitatis* and *S. tatarica* are very rare. Rodent remains are rare, and those of the carnivores *P. spelaea* and *C. lupus* are even rarer. Given the similarity in species composition with other collections, however, interpreting these as paleoassemblages requires consideration of sampling locations and strategies to assess the comparability of different collections. Much emphasis should be given to the preservation state of the material as fragments or complete bones, their size, and anatomic position in the skeleton.

The proposed new approach to analyzing the preservation of paleontological material revealed certain taphonomic features of bone burial. The opinion that bones undergo significant destruction during thawing

and further transportation down the outcrop has been refuted. It is revealed that the ratio of whole bones and their fragments on the sections and on the shore is very close. This confirms the proluvial–deluvial–solifluction genesis of the Oyogos Suite deposits (MIS 4–3) and indicates that bones were often broken even before they entered the sediments. The most well-preserved groups of bones in the conditions of ice complex formation—large limb bones, vertebrae, and metapodia—were revealed. The number of large limb bones and their fragments is more than two times higher than the number of vertebrae and metapodia. Radiocarbon dating of bone remains from large mammals in the present collection indicates that the lower boundary of the Yedoma Ice Complex is older than 50,000 years. The distribution of radiocarbon dates suggests that there were 23,000 years of favorable conditions for large herbivorous mammals. Finds of saiga remains indicate typical tundra–steppe conditions in the area around 46,500 BP: unswamped, hard soil surface in summer and shallow snow cover in winter. However, for mammoths, living conditions on Bol'shoy Lyakhovsky Island were not as optimal as in the more southern parts of the region. There were as many horses as mammoths, and the number of ungulates in the mammoth fauna of Bol'shoy Lyakhovsky Island outnumbered those of mammoths. Indirectly, the difficult conditions of mammoth existence on this territory are also indicated by the fact that whole corpses and fragments of mammoth corpses have been found on the island more frequently than in other areas of permafrost development.

The authors' primary goal was to provide a comprehensive description of the collection of mammal remains from Bol'shoy Lyakhovsky Island, making it available to the global community of mammal paleontologists. Unlike many modern scientific publications, which often contain only the authors' conclusions without providing the underlying data, this article primarily presents a description of the factual material as a basis for further, comprehensive scientific research.

The southern shore of Bol'shoy Lyakhovsky Island is a unique place for studying Late Pleistocene mammals, their distribution over the territory, and habitat conditions. A multidisciplinary approach to studying such unique "windows" into the Late Pleistocene history of the Arctic region makes it possible to elucidate the composition and relation of animal communities that inhabited the territory, habitat and the paleoclimatic conditions of that time, as well as paleoecology and sedimentation conditions.

Disclosure statement

No potential conflict of interest was reported by the authors.

ORCID

Sebastian Wetterich 🔟 http://orcid.org/0000-0001-9234-1192
Lutz Schirrmeister 🔟 http://orcid.org/0000-0001-9455-0596

Data availability statement

Data from the present study are freely accessible at the Data Publisher for Earth & Environmental Science, PANGAEA (Kuznetsova et al. 2007a; Kuznetsova 2009). Further information on single radiocarbon-dated bones can be found in Andreev et al. (2009), Wetterich et al. (2011), and Wetterich, Meyer et al. (2021).

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