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# Late Pleistocene mummified mammals

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## Abstract

The article reviews key milestones of more than 200 years of study of late Pleistocene (MIS3–2) mammal mummies with an emphasis on woolly mammoth, which dominates the sample of finds. The review contains a comprehensive list of complete and partial mummies with preservation of soft tissues representing significant or important portions of the body, such as the head and/or internal organs. Arranged chronologically within taxon, the review highlights specimens that revealed unique or previously unknown features and traits that significantly contributed to our knowledge of the extinct species, including their morphology, phylogeny, paleobiology, behavior and the means of adaptation to the Pleistocene environment.

## Keywords

Bison; *Bison priscus*; *Bootherium*; *Coelodonta*; DNA; Equus; Mammals; *Mammuthus*; Morphology; Mummies; *Panthera spelaea*; Permafrost; Pleistocene

## Key points

- To illustrate the geographic distribution of mummified mammals (in the Holarctic) (Map).
- To provide a comprehensive list of Late Pleistocene specimens (given by taxa) preserved as mummified carcasses with references to their initial discovery (Table 1).
- To give a brief summary of research history and description of the mummies that contributed to our understanding of the morphology and paleobiology of extinct Pleistocene megafauna.
- To provide a comprehensive list of references, including many sources that remain largely unknown to the public and researchers.

## Introduction

Mammals, like other animals and humans, have been found in a preserved, mummified state due to unusual environmental conditions. The conditions that produce such finds include low temperature, low humidity, lack of oxygen, and geochemical properties of the deposits (e.g., ozokerite) which have acted to preserve the mummies from hundreds to tens of thousands of years. A majority of mummies are found in arctic and subarctic permafrost and icy deposits, which serve as an immense freezer for animals that were trapped and buried in mud holes, crevices, or floodplains (e.g. see references in [Table 1](#), [Lazarev, 1980](#)). Outside the Arctic and Subarctic, the remains of mummified animals are found in dry caves and desert settings, typically confined to remnants of soft tissues (tendons, skin, and muscles) attached to the bones (e.g. [Harington, 2013](#)).

In Eurasia, mummified mammals are found primarily in the “northern belt” of the continuous permafrost zone in Siberia. In the north, this belt encompasses the coastal lowlands and islands of the Arctic eastward from the Yamal Peninsula across the middle and lower basins of the Yana, Indigirka, and Kolyma Rivers. In the south, the belt significantly expands from the lower Yenisei River basin eastwards, incorporating the upper basins of the Yana, Indigirka, and Kolyma Rivers ([Fig. 1](#), [Map](#)). In North America, mummies are found mostly in the discontinuous permafrost zone in Alaska and the Yukon.

Most of these mummies lie within the range of radiocarbon dating ( $\leq 50,000$  years ago). Some of the oldest mummies, such as Igor the mammoth infant, “Blue Babe” and Anyuy bison, “Klondike” reindeer and wolf, and the Bilibino horse (see [Table 1](#)), probably date to the relatively cold Marine Oxygen Isotope Stage (MIS) 4 period, which ended before 50,000 years ago. Mummies from permafrost deposits of the early Late, Middle or Early Pleistocene are unknown.

## Mummies from the permafrost

Most mummified mammal remains from the permafrost zone were recovered during the last century and the majority of the carcasses belong to woolly mammoth. However, a significant number of the mammoth mummies were discovered earlier ([Tolmachoff, 1929](#)). According to the legends of Siberian tribes and ethnographic accounts related to prehistoric mummies in Siberia, the local tribes retain in their language a word for “mammoth” ([Fig. 2](#)) as an animal living underground, in caves, or in the “underground world.” In late 1790s, Witsen ([Anuchin, 1879, p. 38](#)) recorded oral accounts from Moscow citizens about a mammoth of black-brown color and emitting a smell, indicating that finds of frozen corpses were already being made at that time. Unfortunately, due to the traditional beliefs of local Siberian tribes that encounters with the “underground creatures” would cause illness and death, the early finds were never reported (e.g., [Tolmachoff, 1929](#); [Illarionov, 1940](#)). Small rewards and poor treatment of villagers during excavation of the Adam’s mammoth led to deliberate destruction of the corpses, and many of the mummies were lost to science ([Lister and Bahn, 2007](#)).

In the 17th – 19th centuries, the situation improved due to the search for new land and natural resources, as well as the growing interest of European scientists in prehistoric animal remains. In 1722, Peter the Great issued a decree for collection of natural curiosities, including the complete or partial remains of mammoths. The decree was followed by the first publication on the woolly mammoth by Russian physician, historian, [ethnographer](#), and statesman Vasily N. Tatishchev ([Tatishchev, 1725](#)) who recognized the species’ affiliation to modern elephants. Reissued papers, edited by Tatishchev (Tatishchow) and Johan Georg Gmelin, were published in 1729, 1730, 1732 and 1743 in Sweden, Russia and England, followed by publication of Tatishchev’s instructions on how to collect and record geological and paleontological objects with notes on their taphonomy ([Garutt, 2001](#)).

The woolly rhino carcass discovered in 1771 in eastern Siberia ([Brandt, 1849](#)) became the first recovered mummy, salvation of which involved scientists and Russian statesmen ([Fig. 3](#)). The preserved remains were studied by famous German zoologists, Peter Simon Pallas in late 1860s and German Johann Friedrich von Brandt in late 1840s, who devoted decades of their lives to the study and exploration of the natural history of Russia ([Potapova et al., 2018](#)). Overseas, in 1804, a similar interest in paleontology inspired President Thomas Jefferson to instruct Lewis and Clark to search for living mammoths, which he believed existed in the lands of the Louisiana Purchase (and for which he received the nickname “Mr. Mammoth”).

In mid-1930s, the President of the Academy of Sciences of the USSR had announced an award of up to 1000 rubles (equivalent to roughly \$20,000 today) for the discovery of mummified remains of Pleistocene megafauna ([Fig. 4](#)). The Soviet government began to pursue reports of frozen mummies seriously during the 20th century (after the upheavals of the 1917 Revolution and two world wars), following the resumption of arctic exploration and increased hunting for mammoth ivory (which produced most of the unique finds). During that time, Russian and American industrial gold mining operations in remote areas of the North brought forth recovery of significant numbers of Ice Age mummies. These activities led to the 1948 discovery of the partial body of “Effie,” the baby woolly mammoth, and the nearly complete carcass of the steppe bison “Blue Babe” in Alaska (1979), as well as the Selerikan horse (1968) and “Dima” baby woolly mammoth (1977) in Eastern Siberia. Major discoveries of the 21st century have been stimulated by growing interest of the worldwide public and scientific community in Quaternary extinctions, Ice Age animal paleoecology, and aDNA research ([Potapova et al., 2022](#)).

**Table 1** Chronology of the Pleistocene mummies' discoveries in the northern Holarctic with basic data of the salvaged mammalian specimens (Taxa are validated and listed following (McKenna and Bell, 1997) and ITIS, (2024); mammoth/rhino age groups follow Kahl and Santiapillai, 2004).

<i>Taxa</i>	<i>Specimen name (synonyms)<sup>a</sup>// discovery yr/specimen # (if available)</i>	<i>Individual Age (based on external morphology and/or teeth in place/wear// [completeness]<sup>b</sup></i>	<i>Calibrated Yrs BP (median)<sup>c</sup> or (C14) date</i>	<i>Gender</i>	<i>General Location</i>	<i>First Report/ [initial "Taxa" ID] (if different from 1st column)</i>
<b>Lagomorpha</b>						
<b>Ochotonidae</b>						
<i>Ochotona</i> (?) <i>collaris</i> (?) Collared pika)	"Chatanika Chatanika" Pika //(1933)	undetermined	undetermined	undetermined	Chatanika pit, Fairbanks, Alaska	Guthrie (1973)
<b>Leporidae</b>						
<i>Lepus americanus</i> (Snowshoe hare)	"Fairbanks" snowshoe hare// (1949)	undetermined	undetermined	undetermined	Fairbanks Creek, Alaska (USA)	Zimmerman and Tedford (1976) and Guthrie (1990a)
† <i>Lepus tanaiticus</i> (Don's hare)	"Yunyungen" Don hare-1 //(2016)	undetermined// [incomplete]	[ca.32,500]	undetermined	Yunyugen, Verkhoyansk Distr., mid- Yana River basin, NE Siberia (Yakutia), Russia	Sharko et al. (2023)
	"Abyi" Don hare// (2019)	undetermined //partial (head)	[ca.52,700]	undetermined	Ayan tract, Badyarikha River, Abyi Distr., (Yakutia) NE Siberia, Russia	
	"Nizhnekolymsk" Don hare// (2020)	undetermined// [partial]	[ca.43,300]	undetermined	Nizhnekolymsk Distr., Lower Kolyma River, NE Siberia, Russia	
	"Ogorokha" Don hare// (2021)	adult// [complete]	(C14) >45,000 (date from <i>Martes zibellina</i> skull from the same location)	undetermined	Ogorokha River, Abyi District, (Yakutia), NE Siberia, Russia	Boeskorov et al. (2023)
<b>Rodentia</b>						
<b>Sciuridae</b>						
<i>Urocitellus parryii</i> (Arctic ground squirrel)	Three "Elga's"/ "GULAG's" ground squirrels/(1946)	undetermined// [all complete]	ca.33,100 (paralectotype ZIN 34046)	undetermined	Dirin'yuryakh River, trib. El'ga River (Indigirka River basin), NE Siberia, Russia	Vinogradov (1948) [n.sp. <i>Citellus glacialis</i> , Vinogradov, 1948]
(?) <i>Urocitellus</i> sp. (Arctic ground squirrel)	"Eva" ground squirrel// (1939), F:AM 7177			undetermined	Eva Creek, Alaska, USA	Guthrie (1990a) [ <i>Spermophilus</i> sp.]
<i>Urocitellus parryii</i> (Arctic ground squirrel)	Moonrock Arctic ground squirrel// (1981)	undetermined// [partial]	(C14) 47,000	undetermined	Sixtymile River, loc.3, near Dawson, Yukon, Canada	Youngman (1987)
<b>Muroidea</b>						
<i>Microtus gregalis egorovi</i> (Narrow-headed vole)	Five Egorov's narrow-headed voles// (before 1968)	undetermined// [complete/ incomplete/ partial]	unknown; found together with Indigirka ("Sana") horse mummy [ca.41,200].	undetermined	Surovyi Creek basin, trib. of Diring-Yuryakh River (Indigirka River basin), NE Siberia, Russia	Golenishchev (2008) [ <i>Mynomis miurus egorovi</i> (Baranova & Fejgin)]
<i>Lemmus</i> cf. <i>sibiricus</i> (Siberian lemming)	"Tirekhtyakh" Lemming// (2016)	undetermined (possibly adult-OP)// [complete]	[ca.41,800]	undetermined	Tirekhtyakh River, trib. of Moma River (mid-Indigirka River basin), NE Siberia, Russia	Lopatin et al. (2019)
<b>Artiodactyla</b>						
<b>Cervidae</b>						
<i>Cervalces</i> sp. (Stagmoose)	"Eldorado Creek-1" stagmoose// [1942]	yearling// [incomplete]	undetermined	male	Little Eldorado Creek, Chatanika River basin, Alaska, USA	Guthrie (1990b)
	"Eldorado Creek-2" stagmoose// [1942]	young//[partial]	undetermined	female		

(Continued)

Table 1 (Continued)

<i>Taxa</i>	<i>Specimen name (synonyms)// discovery yr/specimen # (if available)</i>	<i>Individual Age (based on external morphology and/or teeth in place/wear// [completeness])</i>	<i>Calibrated Yrs BP (median) or (C14) date</i>	<i>Gender</i>	<i>General Location</i>	<i>First Report/ [initial "Taxa" ID] (if different from 1st column)</i>
<b>Bovidae</b>						
† <i>Bootherium bombifrons</i> (Helmeted muskox)	"Fairbanks" helmeted muskox// (1940)	immature/adolescent (2.3 yrs)// [incomplete]	[tissues ca. 28,100; dung ca. >40,000]	female	Fairbanks Creek, Alaska, USA	McDonald (1984b)
† <i>Bison priscus</i> (Steppe bison)	Dome Creek bison/ (1952)	adult, 7 yrs.//[partial]	(C14) 28,000	male	Dome Creek, Alaska, USA	Guthrie (1990a)
	Indigirka (Mylakhchin) bison// (1971)	Spike horn (2.5 yrs)// [partial]	[ca.34,100]	female	Mylakhchin tract, Indigirka River, NE Siberia, Russia	Flerov (1977b)
	Blue Babe// (1979)	adult// [complete]	>50,000	male	Pearl Creek, trib. of Fish Creek, Alaska, USA	Guthrie (1990a)
	Tsiighchic bison// (2007)	adult// [partial]	ca.13,700	not determined (possibly male-OP)	Lower Mackenzie River, Northwest Territories, Canada	Zazula et al. (2009)
	Anyuy bison/(2009)	adult// [complete]	(C14) >48,000	male	Lower Alazeya River basin (Yakutia), NE Siberia, Russia	Nikolskyi and Shidlovskiy (2013)
<b>Perissodactyla</b>						
<b>Equidae</b>						
† <i>Equus lenensis</i> (Lena horse)	Indigirka ("Sana") horse with embryo// (1953)	filly (3–4 yrs)// [partial] with embryo (unknown age)/ [partial]	[ca.41,200]	female/ embryo sex undetermined	Sana River, Upper Indigirka River basin, NE Siberia, Russia	Garutt and Yuryev (1966)
	Selerikan Horse († <i>Equus lenensis</i> )// (1968)	adult (ca. 7–8 yrs)// [incomplete]	[ca.42,700]	male	Selerikan Goldmine, Balkhan Creek, trib. of Bolshoi Selerikan River (Upper Indigirka River), NE Siberia, Russia	Vereshchagin and Lazarev (1977)
	Dukarsk Horse// (1981)	filly (4.5)// [partial]	(C14) 29,500	undetermined	Dukarskoe Lake, Lower Indigirka River, NE Siberia, Russia	Lazarev (2002)
	Bilibino Horse// (2004/2005)	yearling (1.5 yrs)// [partial]	>58,500	female	Vicinity Bilibino village, NE Siberia, Russia	Sher et al., (2007)
	Batagai Foal// (2018)	suckling (1–2 weeks)// [complete]	[ca.43,400]	male	Batagai thermokarst depression, Verkhoyansk District, NE Siberia, Russia	Cheprasov et al. (2021)
† <i>Equus lambei</i> (Yukon wild horse) find flyer!	"Yukon" horse// (1993)	undetermined// [partial]	[ca.30,546]	undetermined	Last Chance Creek, Alaska, USA	Harington et al. (1995)
<b>Rhinocerotidae</b>						
† <i>Coelodonta antiquitatis</i> (Woolly rhino)	Vilui Rhino// (1771) <sup>e</sup>	adult//[partial]	unknown	unknown	Vilui River, NE Siberia, Russia	Brandt, (1849)
	Yana (Khalabui) Rhino <sup>e</sup> // (1877)	adult//[partial]	unknown	unknown	Khalabui River, Yana River basin, NE Siberia, Russia	
	Starunia woolly rhino-1// (1907)	young//[partial]	unknown	female		Niezabitowki-Lubicz (1911)
	Starunia woolly rhino-2// (1929)	adult//[complete]	[ca.37,150]	female	Starunia ozokerite mine, Western Ukraine	Nowak et al. (1930)
	Malaya Filippova (Kolyma) Rhino// (2007)	adult (ca. 20 yrs)// [incomplete]	[ca.42,703]	female	Malaya Filippova River, Lower Kolyma River basin, NE Siberia, Russia	Boeskorov et al. (2009)
	Sasha rhino// (2014)	infant (3–4 mo) <sup>d</sup> // [partial]	>45,300	undetermined	Semiyulyakh River basin, Indigirka, Abyi District (Yakutia), NE Siberia, Russia	Protopopov et al. (2015)
	Abyi rhino// (2020)	calf (3–4 yrs)// [incomplete]	undetermined	undetermined	Tirekhtyakh River, Indigirka River basin, Abyi District (Yakutia), NE Siberia, Russia	Plotnikov (2021)

**Carnivora****Felidae**† *Panthera spelaea*  
(Cave lion)

Uyan cave lion// (2015)	cub (ca. 1 week// [complete])	>30, 000	unknown	Yuandina River (Indigirka River basin), Abyi District (Yakutia), northeastern Siberia, Russia	Protopopov et al. (2016)
Dina cave lion// (2015)	cub (ca. 1 week// [complete])	>30,000	unknown		
Boris cave lion// (2017)	cub (1–2 mo// [complete])	[ca.45,900]	male	Semyuelyakh River, Abyi District (Yakutia), NE Siberia, Russia	Chernova et al. (2020)
Sparta cave lion// (2018)	cub (1–2 mo// [complete])	[ca.31,900]	female		

**Canidae***Canis lupus*  
(Gray wolf)

Tumat wolf-1// (2011)	pup (? 3 mo// [complete])	(C14)ca.12,500	(?) female	Syala'akh River, Ust-Yana District (Yakutia), NE Siberia, Russia	Bergström et al. (2022)
Tumat wolf-2// (2015)	pup (? 2 mo// [complete])	ca.14,122	female		Smith et al. (2019)
“Klondike wolf”// (2016)	pup (2 mo// [complete])	>50,000	undetermined	Paradise Hill, Hester Creek, Klondike & Indian River Gold Fields, Yukon, Canada	Under study. <a href="https://yukon.ca/en/news/mummified-ice-age-specimens-unveiled-dawson">https://yukon.ca/en/news/mummified-ice-age-specimens-unveiled-dawson</a>
Dogor wolf// (2018)	pup (ca.2 mo// [complete])	ca. 18,200	male	Indigirka River basin, Belaya Gora, Abyi District, (Yakutia), NE Siberia, Russia	Bergström et al. (2022)
Tirekhtyakh wolf//(2018)	2–3 yrs.//[partial]	ca 32,000	female	Tirekhtyakh River, Indigirka River basin (Yakutia), NE Siberia, Russia	

**Mustelidae***Mustela nigripes*  
(Black-footed ferret)

“Molly’s” black-footed ferret//(1984)	young adult // [incomplete]	[ca. 43,158]	male	Sixtymile River, loc.3, near Dawson, Yukon, Canada	Youngman (1987)
“Hunker Creek” black-footed ferret// (1987)	adult//[partial]	[ca.34,900]	undetermined	Hunker Creek, loc.12, Yukon, Canada	Youngmen (1994)

**Proboscidea****Elephantidae**† *Mammuthus primigenius*  
(Woolly mammoth)

Adams mammoth// (1799)	adult (65–70 yrs) // [incomplete] <sup>e</sup>	[ca. 40,200]	male	Bykovsky Peninsula, Lena Delta River	Adams (1807)
Berezovka mammoth// (1900/[1899])	adult (ca.50 yrs)// [complete/ incomplete] <sup>e</sup>	[ca.47,500]	male	Berezovka River, Lower Kolyma River basin, NE Siberia, Russia	Hertz (1902)
Sanga-Yuryakh mammoth// (1908)	adult [incomplete] <sup>e</sup>	(C14) ~ 37,000	female	Sanga-Yuryakh River, Omulyakh Bay of east-Siberian Sea (Yakutia), NE Siberia, Russia,	Vollosovich (1909)
Effie mammoth// (1948)	infant (4–5 mo)// [partial]	[ca.27,500]	unknown	Alaska (USA)	Guthrie (1990a)
Shandrin mammoth// (1971)	old adult (ca.60 yrs)// [partial]	[ca.44,600]	male	Shandrin River, Lower Indigirka River basin (Yakutia), NE Siberia, Russia	Yudichev and Averikhin (1975)
Dima (Kirgilyakh) mammoth// (1977)	infant (4–5 mo)// [complete]	[ca.49,800]	male	Dima Spring, trib. of Kirgilyakh Creek, Ayan-Yuryakh River basin (Kolyma River basin (Magadan District), NE Siberia, Russia	Shilo et al. (1977)
Yuribey mammoth//(1979)	young adult (ca.10–12 yrs)// [incomplete]	[ca.11,500]	female	Middle Yuribey River (bank terrace), Gydan Peninsula, northern West Siberia, Russia	Sokolov (1982)

(Continued)

**Table 1** (Continued)

<i>Taxa</i>	<i>Specimen name (synonyms)// discovery yr//specimen # (if available)</i>	<i>Individual Age (based on external morphology and/or teeth in place/wear// [completeness])</i>	<i>Calibrated Yrs BP (median) or (C14) date</i>	<i>Gender</i>	<i>General Location</i>	<i>First Report/ [initial "Taxa" ID] (if different from 1st column)</i>
	Masha (2nd Yamal mammoth// (1988)	infant (1 mo)// [complete]	ca.45,300	female	Yuribeche-Yakha River, Yamal Peninsula, western N. Siberia, Russia	Tikhonov and Khrabryi (1989)
	Gosha (Mylakhchin/ Abyi) mammoth// (1990)	Calf (ca.1 mo)// [incomplete]	ca.33,400	unknown	Mylakhchin tract, Indigirka River basin (Abyi District, Yakutia), NE Siberia, Russia	Lazarev (1999)
	Mongochen (Yaptunay) mammoth// (2002)	adult (35–40 yrs)// [partial]	[ca.22,200]	male	Mongoche-Yakha River, Gydan Peninsula, western N. Siberia, Russia	Kosintsev (2007)
	Yukagir mammoth// (2002)	adult (ca.49 yrs)// [partial]	[ca.22,700]	male	Maksunuokha River, Ust-Yana District (Yakutia), NE Siberia, Russia	Moi et al. (2004)
	Sasha (Oimyakon/Olchan) mammoth// (2004)	infant (7.5 mo) <sup>d</sup> // [incomplete]	ca.44,800 (Enk et al., 2016)	unknown	Olchan Mine, Yana-Oimyakon Highlands (upper Indigirka River), (Yakutia), NE Siberia, Russia	Lazarev and Boeskorov (2004)
	Lyuba (1st Yamal) mammoth// (2007)	infant (ca.1 mo) <sup>d</sup> // [complete]	ca.45,300 (Enk et al., 2016)	female	Yuribei River, Yamal Peninsula, western N. Siberia, Russia	Kosintsev et al. (2010)
	Igor (Khroma) mammoth // (2008)	infant (ca.2mo)// [partial]	(C14) >50,000	(?) male	Lower Khroma River, Allaikha District, NE Siberia, Russia	Maschenko et al. (2012b)
	Yuka// (2010)	young juvenile (3–5 yrs)// [partial]	ca.39,500	(?) female	Oyogos Yar (south coast of Dmitry Laptev Strait, Yakutia), NE Siberia, Russia	Maschenko et al. (2012a)
	Maly Lyakhov mammoth// (2012)	Adult/old (ca.47 yrs)// [partial]	ca.32,700	male	Maly Lyakhov Is., (Yakutia) NE Siberia, Russia	Grigoriev et al. (2017)
	Tadibe mammoth// (2020)	adolescent ((?) 10–12 yrs)// [partial]	(C14) 42,150	male	Pechevalava-to Lake shore, Seyakha District, Yamal Peninsula, Russia	Sadykov and Kosintsev (2021)
	Nun-cho-ga mammoth// (2022)	infant // [complete]	(?) MIS3 (Under study)	under study	Klondike Goldmine, Eureka Creek, Yukon, Canada	Under study. ( <a href="https://gizmodo.com/calf-woolly-mammoth-mummy-yukon-1849137599">https://gizmodo.com/calf-woolly-mammoth-mummy-yukon-1849137599</a> )

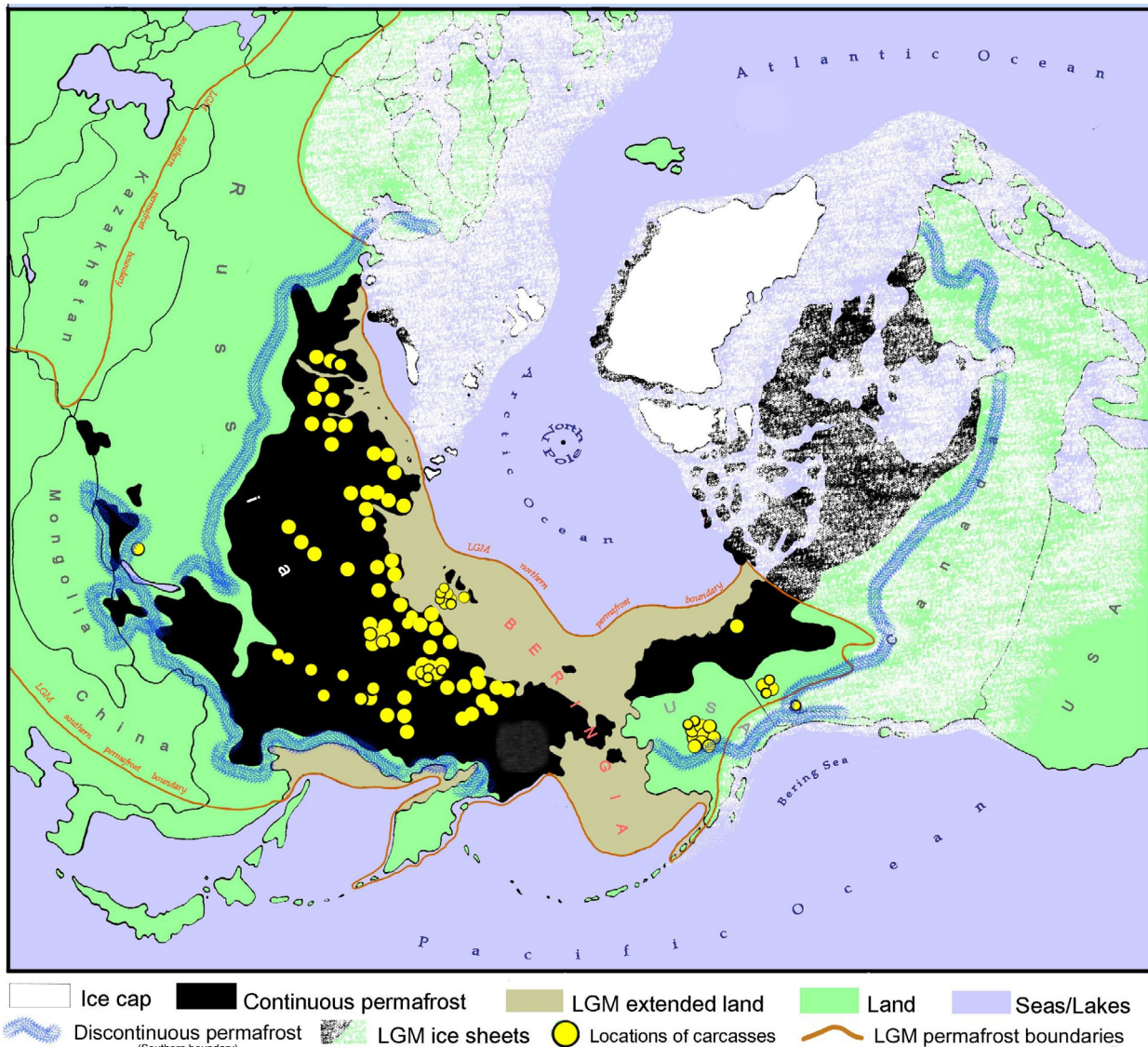
<sup>a</sup>Specimen's name in quotations marks is informal (not initially assigned) and given here based on location for convenience of citing in this paper.

<sup>b</sup>Complete (over 90%), incomplete (over 50% to below 90%), partial (over 30% to below 50%, or entire head, or skeleton with significant amount or important internal organs).

<sup>c</sup>[In brackets] – rounded to closest hundred years of the calibrated and calculated mean value (2 $\sigma$  range), and using IntCal20 calibration curve (Reümer et al., 2020) and based on the available oldest C14 dates.

<sup>d</sup>Age identified based on the dentin histology.

<sup>e</sup>Initially discovered as complete body, but only parts of the soft tissues were salvaged and preserved.



**Fig. 1** Locations of the Pleistocene mammal mummies discovered in the Holarctic. From Table 1, data from Tolmachoff, 1929, Potapova et al., 2018, 2022 and references therein. Drawn by Olga Potapova.

### Mummies from dry caves

Dry caves in North and South America provided suitable conditions for preservation of hair, hides, claws and dung of extinct species, which was recognized in the 19th century. To date, however, none of the recovered remains represented whole specimens. Dry tissue remains were reported from several extinct species, including Jefferson's, Shasta and Patagonian ground sloths, and Harrington's mountain goat (Harrington, 2013).

### Diversity and geological age

Most Pleistocene mammal mummies have been discovered in the former Beringia (northeastern Siberia, Alaska and Yukon) and belong to woolly mammoth (Tolmachoff, 1929) (Fig. 1, Map). The frozen mummies found in the northern Palearctic belong to 16 species from 12 Families of six Orders. Nine species or subspecies (woolly mammoth, woolly rhinoceros, Lena and Yukon wild horses, helmeted muskox, stag-moose, steppe bison, cave lion and the Don's hare) are extinct, while seven taxa (gray wolf, black-footed ferret, collared pika, snowshoe hare, Arctic ground squirrel, Siberian lemming, and narrow-headed vole) represent extant species (Table 1). However, some of the mummies of the extant species belong to DNA clades that did not survive the Pleistocene-Holocene boundary (e.g., Don's hare). Most of the mummies from the northern latitudes have been radiocarbon-dated to the MIS3 stage that precedes the Last Glacial Maximum (LGM) (i.e., >26,500 years ago), while the rest of the very few finds belong to the MIS2 and periods that lay beyond radiocarbon dating limits.





**Fig. 2** Lands inhabited by the indigenous ethnic groups of Europe, Siberia, and China, indicated by mammoth icons that have a word for mammoth in their native language. Modified from Potapova O, Maschenko EN, and Agenbroad LD (2022) *Mammoth Mummies: The Story of Infant Mammoths Frozen in Time*, p. 4. South Dakota: The Mammoth Site of Hot Springs, SD., Inc., Hot Springs.



**Fig. 3** The mummified head of the Vilui Rhino, *Coelodonta antiquitatis* found in 1771 in Eastern Siberia and exhibited at the Zoological Museum in St. Petersburg, Russia. Photo by Olga Potapova.

## Studies of mummies of the extinct species

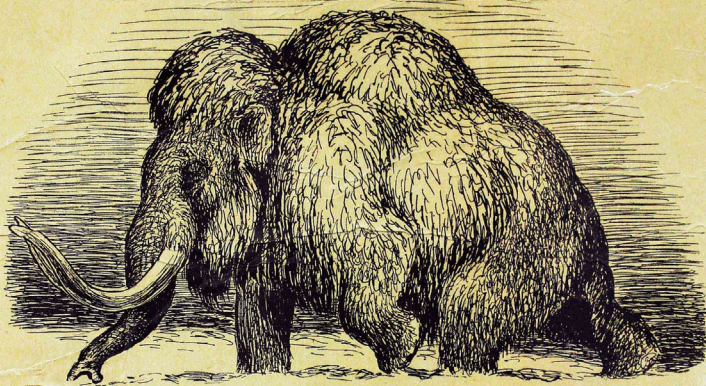
### Woolly mammoth

#### Species identification

Although Paleolithic hunters, who lived, hunted and depicted these animals in the caves of Europe, had extensive knowledge of the Pleistocene megafauna (e.g. Guthrie, 2005), the passage of more than 10,000 years since their extinction has erased their memory of their appearance in the oral history of northern peoples.

Among all the species of the frozen mummies discovered during the last several centuries, the woolly mammoth carcasses have most excited the imagination of the general public due to the enormous size of this animal, covered by thick and long hair. Woolly

## О НАХОДКАХ ИСКОПАЕМЫХ ЖИВОТНЫХ



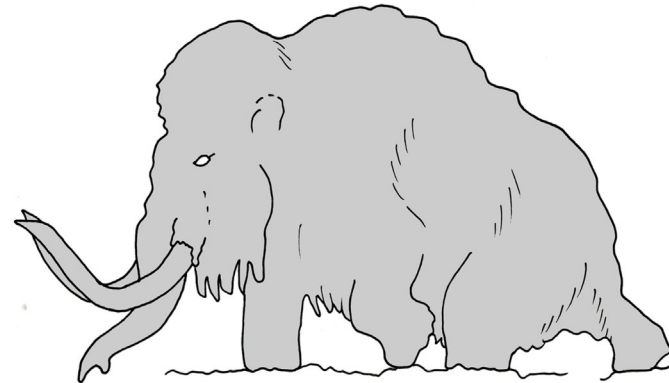
По берегам северных рек, ручьев и морей вымываются водой из слоев земли остатки давно вымерших животных, когда-то живших в Сибири и на севере Европейской части СССР: отдельные кости, *череп*а или даже *целые скелеты* и *трупы* мамонтов, носорогов, диких быков, лошадей, оленей и других. Все эти находки трупов с мясом кожей и шерстью, а также целые скелеты и череп*а* представляют большой научный интерес. Они нужны Академии Наук СССР для изучения и для выставки в музеях.

Поэтому Академия Наук СССР просит всех граждан, нашедших такие остатки вымерших животных или слышавших о них, во-первых, принять меры к их охране от уничтожения дикими животными или от дальнейшего размыва водою, во-вторых, возможно скорее сообщить по радио или почтой в Москву, в Академию Наук, об этих находках.

За это Академия Наук СССР будет выдавать *денежное вознаграждение*, в зависимости от научной ценности находки, размером *до тысячи рублей*.

Президент Академии Наук СССР академик В. Л. Комаров

## ON FINDS OF ANIMAL FOSSILS



There are extinct animals that lived in Siberia and northern European part of the USSR, the remains of which have been washed out of deposits along northern rivers, creeks and seas: isolated bones, skulls and even entire skeletons and corpses of mammoth, rhinoceros, wild ox, horse, elk and others. All these finds of corpses with flesh, skin and hair, as well as the whole skeletons and skulls, have significant scientific value and are needed for study by the Academy of Sciences of the USSR and for use as museum exhibits.

The Academy of Sciences of the USSR requests all citizens who found or are aware of such remains: first, take necessary measures to safeguard and protect them from destruction by wild animals or further erosion by streams; second, as soon as possible report these finds to the Academy of Sciences by radio or mail.

For such actions, the Academy of Sciences of the USSR will give out monetary rewards depending of the value of the find, up to a thousand rubles.

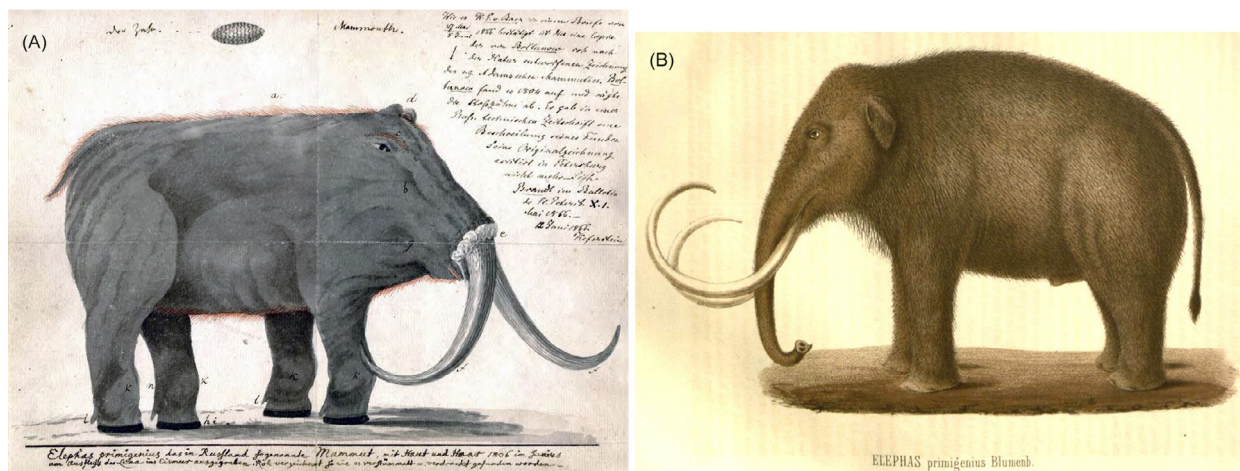
President of the Academy of Sciences of the USSR, Academician V.L. Komarov

Fig. 4 An official poster announcing monetary awards to those who find and report the locations of mummies and other fossils, issued by the USSR Academy of Sciences in 1938. Photo by Olga Potapova.

mammoth ivory (“mammuttekoos” in Dutch) belonging to some kind of elephant was known to Europeans as early as the second half of 17th century from the Amsterdam governor Nikolaes Witsen (Garutt, 2001), but the overall appearance of this extinct species remained unknown. It was not until early 18th century when the Western World learned more about the woolly mammoth from Dutch entrepreneur and merchant Evert Ysbrants Ides, who lived in Russia for about 20 years until his death in 1708. Travelling through southern Siberia to China as a member of Russian delegation, he collected tales and legends about the mammoth, which he published in Dutch in 1704. Similar descriptions of the woolly mammoth’s appearance, habits and habitats were collected in 19th and 20th centuries from Siberian tribes by other researchers (Potapova et al., 2022) indicating that the tribes had regularly observed large mummies thawing from the permafrost. In the East, the earliest descriptions of the woolly mammoth’s exterior and natural history were known as early as the 5th century BCE. However, it was not until early 19th century, when German-born, Russian anthropologist of Asia, Heinrich J. von Klaproth (1809) brought to light a Chinese “Great Natural History” (“Ben-tsoo-gan-mu”) book dated back to 16th century. There, he found a description of the woolly mammoth appearance and habits, which was called “fin-shu” or “un-shu” (hiding mouse), referring to the ancient Chinese ceremonial written by Liyi in the 5th century BCE. Similar descriptions and habits of the woolly mammoth under the name “tien-shu” (mouse), were collected by Klaproth (1809) from the Buryatian and Mongolian lamas. These stories matched the mammoth descriptions in the Manchurian manuscript dating to 1771 that Klaproth found in the archives of the Library of Imperial Academy of Sciences in St. Petersburg.

The papers published between 5th century BCE and 20th century CE, revealed remarkably similar tales and legends of the Siberian tribes that remained unchanged for almost 25 centuries! In these tales, the woolly mammoth was depicted as a huge mouse or mole that lived underground, in caves or dark places, and would die when exposed to day- or lunar- lights (Klaproth, 1809). Some Siberian tribes believed that the mammoth was the underground reindeer shedding giant antlers (tusks) or a transformed and enlarged centenarian vertebrate living in the water – water bull, moose or pike (Potapova et al., 2022). Never having seen an elephant, Siberian tribe members attempted to describe the thawed out mammoth carcasses in terms of the animals they already knew, endowing them with mythical abilities for living in the “underground world.” These descriptions of the woolly mammoth rule out the possibility that the tribal legends had been passed down from generation to generation, since Paleolithic times.

Early historic drawings of the woolly mammoth based on observations of the mummies are attributed to 19th century. One of the earliest (~1804–1806) was drawn by the Yakutian merchant Roman Boltunov. He observed the Adam’s (Lena’s) Mammoth in situ on the Bykov Peninsula (Lena River delta, Yakutia, northeastern Siberia,) and sketched a trunkless, boar-looking animal. At the time when he visited the in-situ carcass, most of the body was below the ground surface and much of the exposed flesh, including the trunk, had been scavenged by modern carnivores. Boltunov’s drawing was examined by German physician, naturalist, physiologist, and anthropologist Johann Friedrich Blumenbach, who recognized its deficiencies (Fig. 5A), but apparently included it among his materials used to define a new species, *Elephas primigenius* in 1799, for the extinct taxon. The earliest scientific 2D depiction of this species (Fig. 5B) was done by Brandt (1866, Plate), although it is lacking long hair and the inward-curved morphology of the tusks, which already had been established (Sevastyanov, 1809). This image of the “short-haired elephant” was less accurate than the woolly mammoths drawn by Late Paleolithic hunters in the caves of France (Fig. 6A) and Spain (e.g., Guthrie, 2005; Potapova et al., 2022, p. 31, 67, 79, 114).



**Fig. 5** Early drawings of the woolly mammoth. (A) – by the Yakutian merchant Roman Boltunov between 1804 and 1806 of the Adam’s mammoth showing few elephant features. J. F. Blumenbach’s handwriting in German on the image states: “*Elephas primigenius*, otherwise called mamut in Russia, dug out with skin and hair in June 1806 at the Lena River mouth. Roughly painted as it was found in a mutilated and desiccated state.” From Anuchin (1879), p. 44–45. (B) – Scientific illustration by Brandt (1866), Plate, the shape of which is similar to the Asian elephant with a long tail. Brandt correctly depicted small ears, but gave the mammoth a very modest coat of short body hair. (A) From Anuchin DN (1879) On the restoration of a mammoth for an anthropological exhibition. *Bulletin Imperial Society of Amateurs in Natural History, Anthropology and Ethnography* 35(5), Part 2(1), 35–52 (in Russian), p. 44–45. (B) – Scientific illustration by von Brandt JF (1866) Sur Lebensgeschichte des Mammuth. *Bulletin de l’Académie Impériale des sciences de St.-Petersbourg* X, 111–118.



**Fig. 6** The Berezovka mammoth. (A) – the in situ excavations in October 1901 led by senior zoologist Alfred Otto Hertz, on the right, and senior preparator Eugen Wilhelm Pfizenmayer, left, both from the Zoological Museum, Imperial Academy of Sciences, St. Petersburg, Russia (from Hertz, 1902, Table III). (B) – the mounted hide. Photos credit Archives of Russian Academy of Sciences, St. Petersburg, Russia.

### External gross-morphology

**Pelage.** The presence of a thick coat of hair covering the whole woolly mammoth body became known only after discovery of the Adam's (Lena) mammoth carcass in 1799 (Table 1) in the Lena River Delta (Eastern Siberia). However, 7 years later, when the rescue expedition arrived at the site, most of the soft tissues, together with the hair, were gone, although the detached hair was described by Sevastianov (1809, p. 130): "Our Mammoth has hair of two kinds, which alone distinguishes it from all known breeds of elephants; the first one is made up of thick fur, which, like a short downy hair, covers his entire skin. . . The second type of hair, similar to the coarse hair of Indian elephants, . . . extends up to an "arshin" [ $\sim 71$  cm, OP] or more in length, while on other [modern-OP]elephants it is short."

Two types of hair (underwool and guard) with coloration varying from black (bristles and guard) to ash/blond and the longest strands on the shoulders also were recorded by Hertz (1902, p. 163–164) on the Berezovka Mammoth (Fig. 6). Zalusky (1909) observed a third type of hair (bristle) on the same specimen. Later, tiered hair types (underwool, intermediate/guard and overhair) that were colored differently, were recognized on several other specimens, including the Yuribey mammoth, hair of which was found around the in situ skeleton (Vereshchagin and Mikhelson, 1981, p.85–104; Tridico et al., 2014a; Chernova et al., 2015).

Zalusky reconstructed the pattern of hair for the adult woolly mammoth, providing the following description (Zalusky, 1909, p. 40): "The body was covered with thick wool, especially well developed along the sides of the lower parts of the body, where it formed a hairy fringe composed of long hair. . . The tail covered by a large bundle of long, black and bristly hairs at the end was short." The "fringe" was also found on the Yuribey mammoth in 1979, retaining some soft tissues with longest hair on the tail (74 cm), forearm (68 cm) and thighs (60 cm) (Vereshchagin and Mikhelson, 1981, p.85–104). Similarly, the 3–5 year old Yuka mammoth had the longest hair on the shoulders and hips ( $\sim 40$  cm long; Maschenko et al., 2021). The "fringe" of hair resembling a skirt is known from many Late Paleolithic drawings and is especially emphasized on the mammoth engravings from the Principal Gallery of the Font-de Gaume cave, France where the tails are covered by long hair (Guthrie, 2005). Vereshchagin and Tikhonov (1999) suggested the presence of a hairy "bonnet" on the head of adults reminiscent of that of the North American bison.

Generally, scholars agree on the recognition of a color gradient from the lightest shades for underfur, to slightly darker shades for the guard/intermediate, and darkest shades for the overhairs. However, some describe the guard hairs as lighter than the underfur, based on studies of young- to senior adults (Yuribey, Adam's and Berezovka mammoths). The shades of color also varied among specimens: the underfur was described as yellowish to reddish-brown, light ginger and ginger-red, such as seen on the Yuka mammoth (Fig. 7) (Table 1; Zalusky, 1909; Vereshchagin and Mikhelson, 1981, p.85–104; Vereshchagin and Tikhonov, 1999). The hide/intermediate hairs were reported to be straw-colored, light ginger to chestnut shades and the guide hairs color were light to dark/black (Yuribey mammoth; Vereshchagin and Mikhelson, 1981, p.85–104). Additional studies proposed an overall mottled/variegated appearance of the coat and seasonal molting, with the lighter fur color in winter (Tridico et al., 2014a; Chernova et al., 2015).

The true colors and their pattern within the hair shaft and root of the woolly mammoth coat are still debated. Tridico et al. (2014a,b) ruled out the presence of the reddish/orange colors as a function of postmortem pigments' photo oxidation of the melanin granules in the hair, chemical alteration of the keratin, and the effects of fungi and bacteria during extended burial in the permafrost. Molecular studies added new uncertainties: Römpler et al. (2006) demonstrated that the nuclear melanocortin type 1 receptor (Mclr) gene had fully or partially active variants (three polymorphic positions), suggesting that mammoth's coat could have been brown, red and yellow, and expressed in dark and light shades. Others (Workman et al., 2011) disputed this, showing the presence of the allele for light-colored fur in the Siberian samples at a very low frequency.



**Fig. 7** The hide with preserved hairs of the Yukka mammoth before the hide was mounted. (A) – Yukka in field, (B) - right hindfoot. Note the bright reddish-brown and dark orange coloration of the upper parts of the long hair strands. Photo courtesy of A - Vasily Gorokhov, B - Innokenty Pavlov.

Contrary to that of the adults, the hair of the infants was relatively homogenous with insignificant variation of size (length) and color. The carcass of the 4–5-month-old Dima became the first specimen to yield information on the 4–5 month-old infant’s fur, which was preserved on few parts of the body. The hair was classified into two types: the underfur up to 8 cm long, and guard hairs up to 22 cm long (Vereshchagin, 1999), suggesting that the infants did not shed their “baby fur,” but continuously grew it into the winter pelage (Vereshchagin and Mikhelson, 1981, p.52–80; Vereshchagin and Tikhonov, 1999). Later discovered one-month-old Masha retained few patches of hair on the body, allowing a distinction among three types of hair: underfur, intermediate and guard, with the last reaching up to 9 cm in length on the thighs (Vereshchagin, 1999). Dima’s and Masha’s hair demonstrate that the “baby hair” grew slowly during the first summer of the infant’s life. Overall, the hair of mammoth infants and adolescents was lighter than that of the adults (see references in Table 1; Vereshchagin and Tikhonov, 1999), which can be partly explained by degradation of the hair pigment. However, the consistent occurrence of the lighter hair also may indicate that it was characteristic for immature individuals and might have had the same adaptive significance as in modern large mammals (e.g., bison, deer infants).

#### Body shape and other exterior features

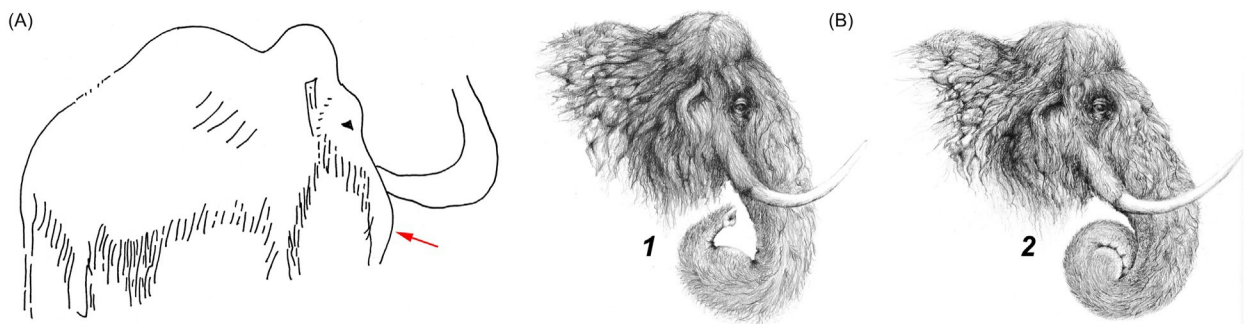
After a long hiatus following the discovery of the Berezovka mammoth and its study, analyses of the external gross anatomy of Pleistocene mummies resumed in the 1970s. These analyses were undertaken in conjunction with osteological studies of complete skeletons, some of which retained soft tissues: Taimyr, Yuribey, Bolshoi Lyakhov, Kastatiyakh, Zhenya, and Pavlov mammoths, to mention a few (Dubrovo, 1982; Tikhonov, 1996; Kirillova et al., 2012; Maschenko et al., 2017; Potapova et al., 2020). Kubiak (1982), Vereshchagin and Baryshnikov (1982) and Vereshchagin and Tikhonov (1999) reviewed and summarized the data from available mummies, complete and partial skeletons, and two infant mummies, Dima and Masha (Vereshchagin and Mikhelson, 1981, p.52–80; Kuzmina, 1999), to give a general description of woolly mammoth external morphology. New discoveries and detailed studies of the complete bodies of infant and adult mammoths (Table 1) allowed further comparisons of the extinct species with their living relatives, uncovering the morphological peculiarities of various age groups that were distinct from or absent in modern taxa. In addition to information received from studies of woolly mammoth skeletons, such as the overall size and proportions of the body (large skull with topknot, longer body with slanted back, relatively short legs and short tail (Kubiak, 1982; Boeskorov, 2021), and bone diseases (e.g., Mol et al., 2006), the mummies found and analyzed in 1990–2020 yielded new information on the external morphology that skeletons or bones could not provide. Discoveries and research of the one-to-7.5-month-old infants yielded priceless information on their body shape and size, and the presence of a neck hump for storing brown fat (Fisher et al., 2012), which might have been present (and “recharged”) in juveniles up to 8–10 years of age (Maschenko et al., 2017).

The studies of the woolly mammoth mummies in the 21st century confirmed the presence of high shoulder hump for fat storage; small ears of varying size in different age groups; lip morphology of the adult, sizes and shapes of the two long finger-like tips of the trunk; and new data on hair types, their color and microstructure in infants (Maschenko et al., 2012a,b, 2013; Mashchenko et al., 2013); Maschenko et al., 2021; Fisher et al., 2012; Tridico et al., 2014a; Chernova et al., 2015).

After thorough examination of the Yukagir Mammoth head (Mol et al., 2006), discovery of the temporal duct confirmed presence of the temporal gland in the extinct species, indicating similar mating behavior and physiological processes as that of modern elephants (Fig. 8). The temporal duct had an opening in the 7.5-month-old Sasha infant (Rountrey et al., 2011), but it was not present in younger infants, such as one-month-old Lyuba and Masha and four-five-month-old Dima (see references in Table 1). The clearly visible markings of the temporal excretions behind the eyes are depicted on the drawings of adult mammoths in Late Paleolithic caves in France, such as Combarelles, Font-de-Gaume, la Madeleine and Rouffignac (Fig. 6A), some as old as 35,000 years (Potapova et al., 2022, p.67–68).



**Fig. 8** The mummified head of the Yukagir mammoth being examined in the lab by Dick Mol, left and the organizer and sponsor of the excavation of the mammoth Bernard Buigues in the fall 2003. The arrow indicates the opening of the temporal duct. Photo courtesy Dick Mol and Francis Latreille, Cerpolex-Mammuthus.



**Fig. 9** Mammoth drawings. (A) - from Late Paleolithic Rouffignac cave, with red arrow showing visible extension of the trunk on the distal end. (B) – the functioning wings of the trunk, 1 – the trunk is in semi-curved, 2 – completely curled position. From Potapova O, Maschenko EN, and Agenbroad LD (2022) *Mammoth Mummies: The Story of Infant Mammoths Frozen in Time*. p. 115. South Dakota: The Mammoth Site of Hot Springs, SD., Inc., Hot Springs.

Discovery of the Yuka mammoth revealed the unique morphology of the woolly mammoth trunk, which exhibits a feature completely absent in modern elephants: the presence of the lateral muscular extensions at the distal end of the trunk (Fig. 9B1; Plotnikov et al., 2015). Guthrie (1982, Fig. 3A; (Guthrie, 1990a, p. 26)) noticed these extensions on the distal fragment of the “Kolyma” trunk, naming these extensions as the “wings” and correctly reconstructing the cross-section in the “wing” area. It appeared that “wings” were also present on the trunks of older infants, such as Effie and Dima (Potapova et al., 2022), as well as adults, such as the Maly Lyakovsky mammoth (author’s personal observations of the photos; Grigoriev et al., 2017, Fig. 3A and C). In very young infants, such as one-month-old Lyuba, the “wings” were not yet developed, but the edges exhibited the scalloped skin along the entire length of the trunk (Potapova et al., 2022, Figs p. 78), which needs further investigation.

Guthrie, (1990a) and Plotnikov et al. (2015) suggested that the wings functioned to assist grasping vegetation, and bringing snow to the mouth to stay hydrated during winter. Although the latter is possible, the former is problematic because the thin muscle layer of the “wings” appears to lack sufficient strength to function as a grasping tool. A more important function of the “wings” would be protection of the hairless trunk tip (inlet) from the cold (Fig. 9B2; Maschenko et al., 2021). The hairless condition of the trunk tip was noted and depicted on many mammoth drawings in Late Paleolithic caves in Europe (e.g., “Grandfather #107” with other unnamed mammoths in Rouffignac cave, France; see Guthrie, 2005; Potapova et al., 2022, p.31b, c, 109, 114 c) (Fig. 9A). The mammoth coprophagy discovered by van Geel et al. (2011a,b) may indicate other function of the trunk. As a monogastric-hindgut fermenter, mammoth was capable of subsisting on low quality forage, passing large amount of it through the guts (if the sufficient forage volume was available). The digesting efficiency of the mammoth probably was low, similar to that of modern elephants, which digest only 20–50% of their consumed forage (Greene et al., 2019). Mammoth dung retained substantial moisture and did not pelletize, forming dry boluses during the winter, also observed on the feces of various living ruminants. Dung was a source not only of essential gastric bacteria, but also of supplemental nutrients from partially digested plants during winter when fodder was limited, especially in the Arctic and Subarctic. We suggest that consumption of dung among mammoths was more significant than it is among modern elephants. Heavier consumption of dung may have led to a more effective use of the trunk’s “wings,” which probably were initially developed to protect the tip from extreme cold. The trunk may have provided a more effective means of holding and transferring directly to the mouth all the dung retrieved from the rectum of another mammoth by expanding its “wings” into a bowl-like shape. Although Plotnikov et al., (2015) suggested that the “wings” might have been used to collect snow (for hydration), this function probably was not needed by the semi-hibernating mammoth’s (see “Skin and fat” section below).

### Internal gross-morphology

Necropsies of mammoth mummies from the Pleistocene have been performed on a few specimens, including the Berezovka, Dima, Lyuba, Yuka and Maly Laykhovsky mammoths. To varying degrees of detail, these studies have included gross morphology, macroscopic and microscopic examinations, and biochemical analyses of the internal organs and their tissues.

### Organs

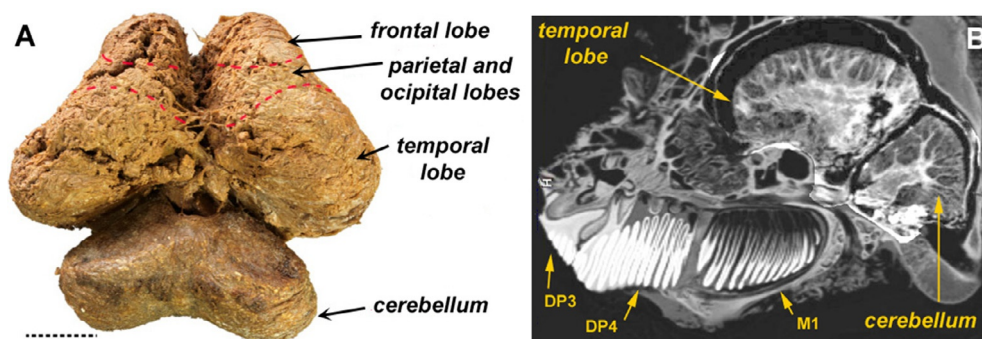
The Berezovka Mammoth was the first specimen subject to macroscopic and microscopic analyses of gross morphology, although the partly skinned specimen delivered to the lab in pieces precluded a traditional full-body necropsy. Zalensky (1903, 1909), Byalynitsky-Birulya (1903), and Maliev (1903) provided a thorough description of the osteology and limb muscles, and examined in detail the stomach, blood vessels and penis.

The first full lab necropsy of a mammoth mummy was performed on the Dima infant in the late 1970s. Part of its skeleton, including complete fore and hind legs, were extracted from the left side of the body for further anatomical studies involving X-rays and determination of the age of the animal (Vereshchagin and Mikhelson, 1981, p.52–80; Potapova et al., 2022). The remaining soft internal organs were removed for examination and preservation, before the rest of the carcass was embalmed in paraffin for long-term preservation and permanent exposition at the Zoological Museum, St. Petersburg, Russia (Vereshchagin and Mikhelson, 1981, p.279–288). The necropsy, followed by extraction of the organs, revealed a shrunken and disintegrated brain covered by *dura mata* (the outmost and thickest membrane of the brain and spinal cord), the heart and fragments of the blood circulatory system, as well as the intact trachea, lungs, kidneys, bladder, uterus, left testes and penis, and incomplete digestive system. The latter included the dentition, tongue, esophagus, stomach (with silty mass containing some plant debris), liver, mesentery (the membrane supporting intestines), large intestine and colon (Vereshchagin and Mikhelson, 1981, p.52–80, 128–154, 242–246; Sokolov, 1982, p.106–112, 120–148). Suzuki et al. (1992) reconstructed the morphology of the heart in 3D and determined that it was larger than that of the Asian elephant and in a healthy condition at the time of death.

Yuka is the only mammoth that yielded an intact brain. It was complete, but slightly shrunken (Fig. 10). The brain was stabilized, extracted, CT-scanned, and analyzed using MRI. Many internal features were detected, such as the conduction system of the forebrain and cerebellum, cerebral architectonics (the structural arrangement of the brain), a well-defined pituitary gland, *corpus callosum* (white matter structure connecting left and right hemispheres of the brain), and thalamic and anterior brainstem morphology. The similarity to the morphology of the African elephant suggests that the woolly mammoth had comparable communication skills, social behavior and intelligence (Kharlamova et al., 2015).

Partial necropsy was also performed on the Lyuba infant and Maly Lyakhov mammoths, to determine the age, female's reproductive cycles and diet, study the histology of different tissues and cells, and conduct CT scanning of the body parts. It entailed extraction of samples (complete teeth, tusk dentin, etc.) and contents from stomach and intestines (Fisher et al., 2012, 2014; Rountrey et al., 2011; Grigoriev et al., 2017).

The internal organ sets were either incomplete or partially preserved in other mummified specimens and were detected by direct examination or using CT scans. These organs were morphologically and macroscopically studied and described for the Berezovka mammoth (blood vessels, stomach and penis; Zalensky, 1909; Byalynitsky-Birulya, 1909), Yuribey mammoth (aorta, small intestines with mesentery, colon with lymph nodes, liver, pancreas, and kidneys; Sokolov, 1982, p.120–128; Vereshchagin and Tikhonov, 1999), Shandrin mammoth (diaphragm, stomach, intestines, pancreas, liver, kidney and spleen (Yudichev and Averikhin, 1982), Igor infant mammoth (diaphragm, lungs and liver; Maschenko et al., 2013) and Maly Lyakhov mammoth (stomach, intestines, pericardium and diaphragm; Grigoriev et al. 2017).



**Fig. 10** The brain extracted from Yuka, which exhibits a shape typical for modern elephants and oversized temporal lobes and cerebellum. (A) – dorsal side of the hemispheres. The left side has a deep transverse cracks possibly caused by brain shrinkage. (B) – Axial CT slice of the head showing the internal structures of the cheek teeth and slightly shrunk brain. (A) Photo by A. Kharlamova. (B) Photo by Olga Potapova.

## Tissues

### Hair

The first microscopic studies of hair partially preserved on the Trofimov mammoth's remains from the Gydan Peninsula (northern West Siberia) allowed Gleboff, (1846) to observe the cortical and medullar components. These same hair components were also recorded for the Berezovka mammoth (Zalensky, 1909). However, macroscopic studies of the hair cores yielded contradictory conclusions: while Sokolov (1982, p.99–103) and Tridico et al. (2014a) interpreted the cores as medulla; Chernova et al. (2015) believed that they represented other cellular structures.

### Skin and fat

The first information about woolly mammoth skin (up to ~2 cm) and subcutaneous fat thickness (up to 9 cm) was collected from the Berezovka mummy by Hertz (1902) and Pfizenmayer (1939) who reported that the muscles of the upper arm, thigh and pelvis were streaked with thick layers of fat. The biochemistry of the fat sampled from the Berezovka mammoth as well as from the "Lyakhov" mammoth's feet collected by 1855–1856 Bunge expeditions, was studied by Shestakov (1914). He determined qualitative and quantitative compositions of the fatty acids among which the oleic (>63%) and palmitic (>34%) acids predominated, while stearic fatty acid was not detected. The absence of the latter was probably caused by its complete degradation in the tissues, and the presence of this acid's in mammoth fat was confirmed 100 years later (Guil-Guerrero et al., 2014) based on analyses of the Lyuba and Yuka mammoth.

Subsequently, the presence of subcutaneous fat was reported in many other adult mammoth specimens that retained soft tissues. Among these were the Bolshoi Lyakhov mammoth (Vollosovich, 1915), Sanga-Yuryakh mammoth (about 9-cm-thick subcutaneous fat; Pfizenmayer, 1939), Zhenya mammoth skeleton (fat in the nuchal, upper torso and rump areas; Maschenko et al., 2017) and Maly Lyakhov mammoth (Grigoriev et al., 2017). However, fat distribution, structure and chemical profiles of these specimens have never been studied in detail.

Among the mammoth calf mummies, Dima completely lacked subcutaneous (white) fat (Sokolov, 1982, p. 99–103), which was considered one of the factors of his demise. Other examined infants, such as Lyuba and Sasha, contained a substantial quantity of fat, with up-to-4-cm thick subcutaneous fat layer and a 7-cm-thick lens of fat forming a noticeable hump in the nuchal (neck) area (Maschenko et al., 2013; Fisher et al., 2012). Lyuba's nuchal fat was composed of brown fat (Fisher et al., 2012), which in extant cold-adapted mammals helps maintaining core body temperature and is critical for survival during the first months of life (Nedergaard and Cannon, 2018).

Adult and calf mammoths depended on both of these types of fat that is also found in modern endothermic (warm-blooded) animals. While white fat tissue ensures lipid storage, insulation and is source of nutrients, energy and water, the thermogenic brown fat rich in mitochondria, functions as a source of heat and is essential for classical nonshivering (and energy saving) thermogenesis (Young, 1976; Cannon and Nedergaard, 2004). For mammals born in cold environment, the cold stress activates metabolic heat production in neonates that greatly helps prevent hypothermia (Nedergaard and Cannon, 2018; Bienboire-Frosini et al., 2023).

Based on studies of brown adipose tissues in extant mammals (Cannon and Nedergaard, 2004), woolly mammoth calves as precocial (well-developed at birth) cold-adapted mammals probably were born with some prenatally accumulated brown adipose tissue. Studies of the mammoth neonates and calves showed that this tissue was primarily concentrated in the cervical hump (e.g. Lyuba; Fisher et al., 2012; Table 1).

Detection of noticeable amounts of saturated even-chain fatty acids, such as myristic and palmitic acid (Yuka), and eicosatrienoic acid (Lyuba), along with other linoleic acids, were found in amounts similar to those usually found in hibernating animals, such as badgers, bears and beavers. Based on this finding, it has been proposed that the woolly mammoth had semi-hibernating behavior similar to the modern Yakutian breed of horse, advantageous for surviving winters with minimal food supplies (Guil-Guerrero et al., 2014). This semi-hibernation, or torpid condition during winter is found in the modern Yakutian horse, which accumulates large amounts of subcutaneous and abdominal fat and has evolved various physiological strategies, including regulation of body metabolism, and reduction of temperature and heart rate to conserve energy (see "Horse" section).

Isotopic analyses indicate that mammoths accumulated thick subcutaneous fat to prepare for winter, and their efficient use, although geographically variable (e.g. Szpak et al., 2010), is reflected in significantly higher of  $\delta^{15}\text{N}$  and slightly lower  $\delta^{13}\text{C}$  isotopes in their tissues compared to other megaherbivores (Bocherens, 2003; Bocherens and Drucker, 2013; Drucker et al., 2018). Besides genetic adaptation to cold, aDNA analyses revealed storage and metabolism of adipose tissue and change in circadian systems (Lynch et al., 2015). We suggest that a semi-hibernating physiological condition was common among woolly mammoths, and probably was expressed to a much greater extent than that of the modern Yakutian horse, especially in the high Arctic. Exposed to low temperatures, food shortages and lack of water, mammoths were capable of lowering their metabolism and transforming their bodies into a torpid state for prolonged interval, until the return of more favorable conditions.

According to Repin et al. (2004) studies, the woolly mammoth had well-developed sweat and sebaceous glands, although these glands were not detected in the Berezovka and infant Dima's skin. None of the other mammoth mummies was examined for this feature.

### Muscles

Macroscopic analyses of the tissues of mummified mammals began in the 19th century with the work of leading Russian scientists. Studying the Trofimov (Mochulsky) mammoth in 1846, Gleboff (1846) identified muscle, connective and fat tissues, as well as



tendons and brain tissue. Excavating the Berezovka mammoth in 1901, Hertz (1902) and Pfizenmayer (1939) noted the fresh look of the thawed body. Hertz wrote (1902, p. 163) wrote: “The fibrous and fat-layered meat from under the shoulder is dark red in color and looks as fresh as a fresh, heavily frozen bovine or horse meat. ... The mammoth meat thrown to the dogs was eaten by them quite willingly.”

At the beginning of 20th century, Zalensky (1909) and Maliev (1903), and Byalynitsky-Birulya (1903) performed microscopic analyses of the internal organs of the Berezovka mammoth, including the connective tissues and muscles of the tongue. These scholars noted good preservation of the collagen fibers and the striated fiber pattern of the muscle tissues, which exhibited complete deterioration of all cellular structures. The striated pattern of the extraorbital skeletal muscles and the muscles underlying the skin was reported for the Effie, Dima, and Yuribey mammoths (Zimmerman and Tedford, 1976; Sokolov, 1982, p. 120–148). Examining the distal limb muscles of the Berezovka mammoth muscles, Maliev (1903) discovered four highly developed lateral fibular muscles (m. peroneus longus, m.p. brevis, m. fibularis tertius and m. fibularis anticus) and unusually well-developed ligaments of the metapodial, upper forearm and lower leg, in comparison with modern elephants.

After an extended hiatus, studies of the muscle tissues were performed on Dima, which comprised only the tongue (Sokolov, 1982, p. 106–112). The histology of the tissues of the Lyuba carcass were examined by Papageorgopoulou et al. (2015), revealing well-preserved muscle tissues and detecting the blood vessels and nerves in the intestine walls.

### Blood

The presence of “blood” in mammoth remains was reported in the early 18th century by Russian ethnographers Grigory Novitsky in 1715 (Novitsky, 1884) and Vasilii N. Tatishchev in 1725, after collecting anecdotal accounts from the local western Siberian tribes. Novitsky (1884, p. 16), who was later tragically killed by Ostyaks whom he studied, wrote in 1715: “Sometimes these horns (i.e. tusks – OP) are said to be dug up with pus mixed with blood and filled at the roots, which is the sign of some animal, and [had] not just the horns, but also [had] other bones: the ribs, head and legs are dug up: I was a witness of these bones ...”. Tatishchev (1730, p. 12) wrote about the mammoth carcasses: “Some people allegedly happened to see a body intact and not damaged in any way... they broke out the horns from the mountains with blood, and then they think it must be from a living or recently deceased [animals], or [from] a whole body”. Klaproth (1809, p. 164) cited the old Manchurian manuscript from the Imperial Academy of Sciences Library in St. Petersburg, Russia, which mentions the mammoth’s blood: “The Tien-Shu beast looks like a mouse, but is as tall as an elephant, afraid of light and lives underground in dark caves. . . The blood in it is cold, and the meat is great.”

Woolly mammoth’s “blood,” represented by a liquid containing blood elements in various conditions, was discovered in several frozen mummies. The first scientific investigation of blood included thorough cytological and biochemical analyses performed on the Berezovka mammoth. Zalensky (1909) and Byalynitsky-Birulya (1909) noted the “formed crystals of the hemin in the “blood” and compared it to that of modern elephants.

Coagulated blood was reported from the infant Dima’s heart and abdominal vein. The large subcutaneous hematoma was discovered around the perforated hole in the right forefoot, which was interpreted as a wound from a spear that could have caused a demise of the infant (Vereshchagin and Mikhelson, 1981, p. 274–278). Dima’s muscle and portal vein contained preserved leucocytes, thrombocytes, and even red cells lacking the nuclei (Vereshchagin and Mikhelson, 1981, p.191–217). Columns of erythrocytes joined together were also found in the small blood capillary of muscles. The lymphatic nodes contained two types of cells, one retaining the membrane and nucleus in different stages of degradation (likely lymphocytes) and another with the degraded membrane and nucleus with chromatin granules (Sokolov, 1982, p.191-217).

Macroscopic examination of the internal organs of the Shandrin mammoth revealed blood cells in the large blood vessels of the liver and clotted blood (hematoma) within the spleen. Significant hemorrhages were found in the thin intestines and the colon (Yudichev and Averikhin, 1982).

An extensive hematoma with coagulated and hemolyzed blood was found between the ribs in the Maly Lyakhov mammoth (Grigoriev et al., 2017, Fig. S4–6, 8) and dark “liquid blood” was collected from its body in the field and lab. Within the massively hemolyzed blood with high iron concentration and destroyed cellular elements, there were isolated preserved cells of varying size and contents (nuclei) interpreted as neutrophils, leucocytes, lymphocytes and monocytes, respectively (Table 1).

### Bones

The first comparative osteological analyses of the woolly mammoth were performed on several elements, including the skull, tusks and molars by Sevastyanov (1809), after discovery of the Adam’s (Lena) mammoth in 1799. The most thorough osteological description of the mammoth skeleton of the mummies was carried out by Zalensky (1903), followed by Dubrovo (Dubrovo, 1982) on the Yuribey mammoth. Studies of the skeletons of other mummies, such as Dima, Lyuba, Yuka, Yukagir and Maly Lyakhov were performed on selected elements, aided by X-rays and CT scans (Table 1) (Vereshchagin and Mikhelson, 1981, p.52–80; Rountrey et al., 2011; Fisher et al., 2012, 2014; Potapova et al., 2022), revealing the age and condition, injuries, and post-depositional alteration of the chemical composition of the bones.

### Teeth

Mammoth dentition has been the primary basis for individual age identification, with reference to the dentition of modern elephants. New methods that entailed studies of dentin and enamel histology have yielded more precise estimates of the age of individual mammoths, including Lyuba, Sasha, Yukagir, and Maly Lyakhov. Studies of the dentin increments and their patterns in

the tusks of the Yukagir and Maly Lyakhov mammoths revealed latitudinal migration patterns, the male age of maturity, eviction from the matriarchal family and onset of the musth, and female pregnancy cycles (Fisher et al., 2010, 2012; Rountrey et al., 2012; Grigoriev et al., 2017).

### DNA

Attempts to recover undamaged cells containing functional organelles and intact DNA from the nuclei, among which the sex cells were especially sought after (for cloning) have failed (e.g. Potapova et al., 2018; Yamagata et al., 2019). During the last two decades, over 750 woolly mammoth specimens from the Holarctic have been tested and analyzed for nucleic and mitochondrial genomes (mtDNA). From 2007, the complete mitogenomes were sequenced for the Dima, Adam's, Mongochon, Yukagir, Sasha (Oimyakon), Lyuba and Maly Lyakhov mammoths, and all but the last were included in paleogenomic datasets for phylogenetic analyses for the Palearctic and Nearctic regions (Gilbert et al., 2007; Palkopoulou et al., 2013, 2015; Chang et al., 2017; van der Valk et al., 2021 and references therein). With one exception (Sasha; Clade II), belonging to the haplotypes D/E (Clade I), the above listed mummies trace their origin to North America. Their ancestors crossed the exposed Bering-Chukchi Platform (Bering Land Bridge) and occupied Siberia during MIS4 or earlier replacing the carriers of the haplotypes A and B (Enk et al., 2016). The mammoths that inhabited northeastern Siberia during the terminal Pleistocene apparently died out, allowing mammoths, including the DNA-tested mummies, from northern West and Central Siberia to repopulate Wrangel Island in the early Holocene (Dehasque et al., 2021).

Samples from the Adam's, Dima and Yukagir mammoths were among those analyzed for mitochondrial protein-coding genes, which indicated the metabolic mitogenome basis for adaptations to extreme cold environments (Ngatia et al., 2019).

Woolly mammoth mummies yielded the samples for DNA analyses that provided information on population demography (Bayesian age models) and population dynamics, adaptation to cold (skin and adipose developments, hair growth, cold tolerance and temperature sensitivity, adjusted circadian systems and hemoglobin O<sub>2</sub>-offload-enhancement), genetic diversity, mitogenomic and nuclear phylogeny and phylogeography, and patterns of regional extinction in various parts of the world (Campbell et al., 2010; Palkopoulou et al., 2015; Lynch et al., 2015; Dehasque et al., 2021; Table 1).

### Parasites

Mammoth parasites were first discovered in the Berezovka mummy. The "problematic corpuscles" in the stomach described by Zalsky (1909) were similar to the Dima baby microscopic remains identified as a larval stage of tapeworm cysticerci (Vereshchagin and Mikhelson, 1981, p. 128–154). The Dima calf was heavily infested with parasites: most of his blood vessels were packed with helminth eggs, larvae, among which a fragment of a helminth body was preserved, identified as a round worm (Serduk and Maschenko, 2018). The helminth's cysts and eggs of substantial size covered the exterior walls of Dima's vena cava and carotid arteries. The eggs of the parasite permeated the walls of blood vessels and adjacent organs and may have caused necropsy of some tissues leading to the infant's death (Vereshchagin and Mikhelson, 1981, p. 128–154). The Shandrin mammoth preserved a stomach filled with undigested food, in which Grunin (1973) discovered a larva of the gastric gadfly and described a new species *Cobaldia rusanovi*, a close taxon to the gadflies that often parasitize the Indian elephant. Later studies of other mammoth specimens also revealed the presence of parasites. The egg-like remnants of nematodes and cestodes were found in the liver and probable stomach tissues of the Zhenya mammoth, and roundworms were reported in the dung associated with the Tadibe (Seyakha) mammoth skeleton from the Yamal Peninsula (Glamazdin et al., 2014). These discoveries suggest that the gadfly myiasis and helminthiasis were probably common in the woolly mammoth.

### Diet

The Berezovka mammoth was the first woolly mammoth mummy to provide information on diet. With a stomach filled with vegetation, he even retained traces of plants on the tongue and compressed grass between clenched teeth, all of which were studied by Voronin, Dobropistsev and Sukachev V.N. (Sukachev, 1914; Hertz, 1902). Other specimens, such as the Yuribey, Shandrin and Mongochon mammoths also preserved stomachs or parts of digestive tracts filled with plant material (Sokolov, 1982, p.37–43; 99–103; Table 1). Along with data suggesting the nature of the mammoth's deaths, the plant material, particularly macroremains (including fungi fruit-bodies) extracted from the adult individuals listed above yielded information on diet and season of death. (Sukachev, 1914; Kosintsev et al., 2012; Ukraintseva, 2013).

Similar studies were performed on two unique specimens of Proboscideans from the Great Lakes region of North America - the Burning Tree and Heisler mastodons. Buried in lake sediments, these specimens preserved intestines with micro- and macrofossil content yielding direct information on diet and season of death for each individual (Birks et al., 2019).

Studies of mammoth dung also have provided a wealth of information on diet. The analyses of the intestinal tracts of the Yukagir and Lyuba baby mammoths showed that adults and neonates as young as one-month practiced coprophagy, which was confirmed by other studies (van Geel et al., 2008, 2011a,b).

Discoveries of mammoth mummies or skeletons with their (as an isolated bolus(es) or retained by colon) dung, such as the Dima, Yukagir and the recently discovered Tadibe mammoth skeleton from the Yamal Peninsula (2020) are rare (Table 1). While studies of such specimens provide information on diets, feeding habits and season of death of these individuals, the isolated finds of dung boluses yielded data on the general feeding preferences of the species. Studies were performed on the dung from the permafrost deposits in northeast Siberia (e.g. the Megin Site, Yakutia; Potapova et al., 2016) and Alaska (the Cape Blossom mammoth; van Geel et al., 2011b, Polling et al., 2021) and dry caves in North America (e.g. Bechan cave on the Colorado Plateau;

Davis et al., 1984). More advanced methods, such as DNA metabarcoding applied to the dung analyses revealed a greater variety of plant species in the mammoth diet than that indicated by traditional methods (macrofossils or pollen) (Polling et al., 2021).

More than two centuries of study of the woolly mammoth has shown that they subsisted on high floristic diversity of grasses and herbs, occasionally supplemented by woody shrubs. Comprising assemblages of species without modern analog in the Pleistocene (and the first half of the Holocene on some arctic islands inhabited by mammoths), these plants survived the megafauna extinction in the Palearctic, but today represent less diverse assemblages in the former habitat of the mammoth (Ukrainitseva, 2013; Willerslev et al., 2014).

### Woolly rhino

Discoveries of complete carcasses or complete skeletons of the woolly rhino are extremely rare (Table 1). The earliest finds of complete frozen mummies were the Vilui and Yana rhinos, only the heads and legs of which were salvaged (Fig. 3) and described by Brandt (1849) in his Latin monograph with colored illustrations. The latest find of a rhino mummy (partial carcass) occurred in 2020 (Abyi rhino). The most complete specimens are represented by two adults from Starunia and one adult from Filippova, which have been described in detail (Boeskorov et al., 2011; Nowak et al., 1930).

### External morphology

Finds of the mummies of adult females provided data on body size (up to 360 cm long and 150 cm high at withers; Boeskorov et al., 2011) and specific body parts, estimates of the weight of both genders (1 and 1.5 tons for females and males, respectively) and allowed comparison to modern rhinos. Morphological characters suggested that the woolly rhino was most similar to the Sumatran rhino (Boeskorov, 2012).

### Pelage and skin

With the exception of the Sasha infant rhino, a limited amount of body hair, mostly on the head and legs, was observed on the mummies. The limited data make it impossible to determine the color of the coat and hair length topography, although examination of the follicle sizes and distributions on the Starunia-2 rhino hide shows that the hair shafts in this area were bristle-like thick and the species may have had mane (Nowak et al., 1930). However, none of the known images from Paleolithic rock art support the presence of the latter.

The absence of adult mummies retaining hide with hair precludes confirmation of the presence of two varieties of coat known from depictions of adult rhinos in Paleolithic rock art. The drawings, which date back as early as 30,000 years ago, depict one variant as relatively uniform (Gönnersdorf, Germany; Guthrie, 2005, p. 59, left, D), while the other exhibits a dark band of different widths vertically encircling the belly in the middle, or a narrow band just behind the shoulders (Chauvet cave, France; Guthrie, 2005, p. 61, left E; p. 109, left 1-9; p. 171 N; p. 245 upper right; p. 272 lower left E). The two variants could reflect differences in gender and age (e.g., males with the belt, young and females with a uniform coat).

Studying the hair preserved on adult mummies, Tridico et al. (2014a) concluded that woolly rhinos had a shorter and less dense coat than that of the woolly mammoth. Schrenck (1880) studied the Yana rhino head, observing reddish-brown hair, but Tridico et al. (2014b) concluded that the reddish/orange color was probably the result of postmortem discoloration. The examination of other specimens revealed a predominance of ash/yellowish and brown hair, interspersed with dark/black guide hairs, such as on the Filippova rhino (light brown with isolated inclusions of the dark hairs; Chernova et al., 2015).

The discovery of the 3–4-month-old Sasha yielded information on general and individual hair coloration and structure (Fig. 11; Protopopov et al., 2015). In comparison to adults, the infant's coat was significantly lighter (light ash and blond) and covered the body relatively uniformly. The hairs were short (14–15 cm long) and differentiated into only two types (underfur and guard) (Chernova et al., 2016).

Measurements of the skin showed that the woolly rhino had thicker skin than that of the woolly mammoth, up to about 3 cm in thickness (Boeskorov, 2012).

Four of the adult mummies, including Yana/Khalabui, Starunia (2) and Filippova, possess lancet-shaped ears (Boeskorov, 2012) and, based on the images, had a short and narrow tubular bases, which has yet to be measured or examined. These features differ from that of the modern relatives with rounded apex and a wide tubular base.

Paleolithic rock art either lack clearly depicted ears (e.g., Gonnorsdörf site, Germany; la Colombiere and Rouffignac caves, France), or the ears are depicted having the crescent- or lancet-shapes (e.g. Font de Gaume, Les Combarelles, Lascaux, Rouffignac "panel" and Chauvet caves, France; Guthrie, 2005, p. 171; 245, upper right; 272, lower left, E). The former images probably represent rhinos with winter pelage completely covering small ears, while the latter show a lighter summer coat that did not cover the ears, which probably could either stand upright or had hanging tips. According to the Allen's rule (size of limbs and other external organs of animals are smaller in cold climates to minimize their surface to retain heat), the woolly rhino's narrow ears with downsized surface suggest adaptation to cold. The reduced size of the pilla may also indicate that the woolly rhino's hearing ability was lower than that of the modern species.

### Internal morphology

None of the complete mummy specimens have been necropsied. Preliminary studies of the Sasha rhino infant have been performed on the head (CT scan) in order to examine the cranium bones and determine its individual age (Protopopov et al., 2015).



**Fig. 11** The Sasha woolly rhino mummy before examination and sampling by Russian-American team in August 2015 in Yakutsk. Photo courtesy Academy of Sciences of Sakha/Yakutia.

#### Tissues

##### *Hair*

The woolly rhino hair's cuticle and cortex does not differ from the modern species (Chernova et al., 2015). However, the micro-morphology of the overhairs remains the subject of debate: the hair core structure has been interpreted as nuclear remnants, pigmentation (Lister and Bahn, 2007), or largely dismissed with the exception of some thick hairs for increasing stiffness (Chernova et al., 2015), while others consider it a true multiple medulla that is best developed in the coarse hair for enhancing insulation (Tridico et al., 2014a).

##### *Muscles*

In 1849, the Russian physiologist, paleontologist and anthropologist Johann Friedrich Brandt performed detailed histological and cytological analyses on the well-preserved Vilyuy rhino's muscles, connective tissues and cartilage. In the early 20th century, Russian zoologists Vladimir M. Zalsky (1909), Nikolai N. Maliev (1903), and F.A. Byalynitskiy-Birulya (1909) examined the Vilyuy rhino tissues, noting the complete deterioration of cellular structures, but reporting that the striated fiber pattern of the muscle tissues and the collagen fibers was preserved.

##### *Dentin*

Studies of the woolly rhino's dentin and enamel were undertaken with the deciduous teeth from the Shasha rhino by Dirks et al. (2016), revealing the age of the infant of about 4–5 months.

##### *DNA*

Among the known mummies, only the Sasha infant has been subject to whole-genome analysis, which indicated that the effective population size of woolly rhinoceros remained stable, following an increase about 30,000 years ago, until the time of its extinction (Lord et al., 2020).

#### Steppe bison

Despite frequent discoveries of bison bones in the Palearctic, complete Pleistocene mummies of the steppe bison are rare. The most complete mummies are the 8-to-9-year-old Blue Babe from Alaska and the adult Anyuy bison (Fig. 12) from Eastern Siberia, both of which are displayed in museums (University of Alaska Museum of the North, Fairbanks and Ice Age Museum, Moscow). None of their bones or internal organs were measured and morphologically described (Guthrie, 1990a; Nikolskyi and Shidlovskiy, 2013), while the remains of other mummies were too fragmentary to reveal the characteristics of entire individuals (Flerov, 1977b; Zazula et al., 2009).

The color of preserved hairs on the studied mummies shows that the winter pelage of the Eastern Beringian bison was in general slightly darker than that of the bison of Western Beringia. Guthrie, (1990a) described Blue Babe winter pelage as a dark bay horse with black areas in his face and very dark/black lower limbs (lacking chaps), while the rest of the hair had a rusty-brown color.



**Fig. 12** The Anyuy bison mummy in the Ice Age Museum, Moscow, Russia. Photo courtesy Pavel Nikolsky.

Flerov (1977a) published a brief description of the winter pelage of the Western Beringia bison and measured their hooves based on examination of remains belonging to three individuals. These were the partial carcass of the 2.5-year-old Indigirka bison that lived about 34,000 calendar years ago and three incomplete limbs (“Struika/Elga”, “Muogdaana/Vilui” and “Yana”) found in the Yana-Indigirka Lowlands; none of these were radiocarbon dated. The Indigirka female exhibited “bay-type” coloration with the exception of lighter hairs in the hump area. She had 75 cm long almost black beard and 50 cm long suspended hair under the neck. The hair from the top of the head was also long, reaching 50 cm. The head was dark brown with lighter muzzle and temples. The hair of the nape, dorsal neck, and withers (hump) was ochre- and ginger-brown, becoming ginger-red and darker cherry-brown on the lower neck and shoulders, and dark-ginger and dark brown on the back. The rump had grayish-brown hair, turning chocolate-brown on the flanks, thighs and upper rear limbs. The canons were ochre-ginger, similar to the color of the hair on the nape, however the ginger- and ochre- colored hairs might be due to postmortem discoloration (Tridico et al., 2014b) and more research needs to be done on this specimen. The underfur of the whole body was predominantly light brown and ochre-brown. The bison had almost black hair of the tail that reached 65 cm in length. The legs of the other specimens had almost black hairs with brown underfur.

To the portrait of the steppe bison male from Western Beringia may be added the 4-to-4.5-year-old Early Holocene Yukagir bison mummy, with hair lighter on the face and belly and lacking a shoulder mantle typical for American bison. He had brown shoulders and withers. The hair on the pasterns was dark brown (Boeskorov et al., 2016) indicating that the distal limbs probably had dark color.

## Helmeted muskox

### Exterior morphology

This endemic North American species was similar to the modern muskox, differing from the latter only with respect to its longer head and higher and laterally spread horn cores, fused at the base. Its greater mobility was provided by a taller, more slender, and shorter body. Based on studies of the horn cores, the helmeted muskox also was similar to modern muskox in social behavior and predator defense (Guthrie, 1992; Harington, 2002a). Studies of mitochondrial DNA support a single helmeted muskox genus *Bootherium* and its sister-status to the tundra muskox, *Ovibos moschatus*, which diverged from the former over 3 million years ago in Central Asia (Bover et al., 2018).

With a very wide geographic range in the Middle-Late Pleistocene, muskox has never been numerous among the megafauna and finds of its mummified remains are extremely rare. Discovery of an almost complete carcass (the “Fairbanks” immature female) from the permafrost of Alaska was therefore a gift from Nature. A short report (McDonald, 1984a) stated that the female had dark hair on her legs and a longer tail than that in the modern muskox. The analyzed dung associated with this mummy consisted entirely of willow. Unfortunately, no further research has been conducted with this unique specimen.

The color of the hair on the adult male remains unknown but Guthrie (1992) suggested that males may have had more striking (possibly darker) pelage than that of the modern muskox. Hair discovered on the partial skeleton of a helmeted muskox male from Little Eldorado Creek in Alaska exhibited a dark color (Harington, 2002a). The hair on that specimen also was thinner and shorter

than that of the modern muskox. Studies of the “Fairbanks” female and skulls of this species indicate that the helmeted muskox had a longer tail and less protruding eye sockets. All these features show that the helmeted muskox was not adapted to extreme cold (Harington, 2002a, 2013; Guthrie, 1992). Lacking thick coat (necessary to withstand extreme cold or hot climates), it avoided both the higher northern and lower southern latitudes, preferring the temperate zones of the continent. These herd animals with superior mobility required space for feeding and probably occupied meadow/steppe/bush biotopes within the deciduous parklands. Indeed, analyses of the dung macrofossils (“Fairbanks” female) and plant contents extracted from the molar infundibula showed that the species was most likely a mixed feeder, consuming equally or alternatively upland graminoids and dwarf shrubs (Guthrie, 1992).

However, the helmeted muskox’s remains are mapped as far as the northernmost latitudes (Alaska, Yukon), and as far south as New Mexico and Texas, indicating that it shifted northward (following the northward spreading parklands) during warm climatic episodes and southward during colder phases. Accordingly, the age of specimens from Alaska dated to the LGM (Harington, 2003) needs to be verified; the disagreement in horn core identifications (*Bootherium* vs. *Bison/Ovibos*) from Alaska remains unresolved and their dating (based on conventional radiocarbon dates) needs to be revisited with new dates.

### Lena horse

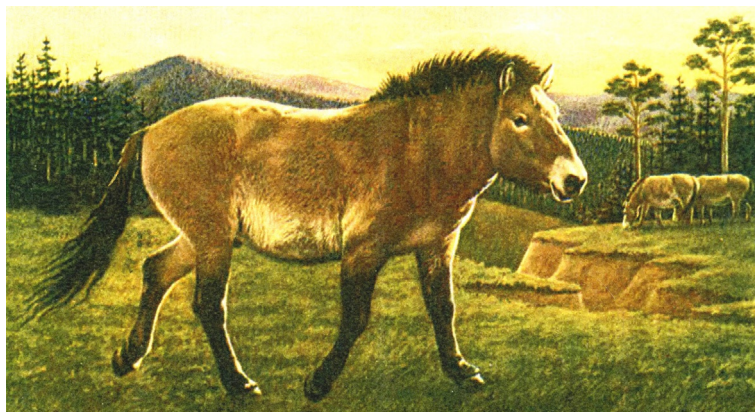
In the Late Pleistocene, the geographical range of this horse covered northeastern Siberia, including western Beringia, but the finds of horse mummies are rare. A total of six mummies have been recovered in Siberia to date, averaging one find for every 10 years between 1953 and 2018. All the remains have been assigned to the Lena/Chersky Horse, *Equus lenensis* Russanov, 1968 (Fig. 13), but only the Selerikan horse mummy has been described in detail (Vereshchagin and Lazarev, 1977; Guthrie, 2005). The overall appearance of this species has been reconstructed based on the Selerikan (partial torso with limbs), Sana (fragments) and Bilibino (head with neck and proximal torso) and the Batagai foal.

### Features of adults

The most complete mummy is represented by the 7–8-year-old Selerikan horse, comprising an incomplete torso with partially preserved internal organs, two fore limbs, one hind limb, tail and hide. The skeleton was almost complete (no skull), and the internal organs included heart, lungs, liver, spleen, right kidney, stomach and colon fragments, large- and medium- sized blood vessels (without blood cells), and male genitals (left testicle and penis). Patches of hair were preserved on the lower frontal torso and rump, tail and limbs, allowing Vereshchagin and Lazarev, 1977 to reconstruct the winter pelage and to note similarities with Przewalski’s horse (*Equus przewalskii* (Poljakov)). The Selerikan sported a light bay/dun color coat that may have lightened during winter. It possessed a jet black upright standing and short mane (based on a very short fragment) and a dark brown dorsal stripe extending from the mane to the tail’s dock. The frontal cannons were dark brown and the back cannons were blackish brown (Vereshchagin and Lazarev, 1977; Sokolov, 1977).

The Selerikan was a short (135 cm in withers) but long-bodied, stocky horse with a weight of 300–350 kg and of comparable size and proportions to Przewalski’s horse and the semi-wild free-grazing Yakutian horse. Based on the bones, a similar body size was estimated for the 4–5-year-old, pregnant Indigirka/“Sana” horse, although the isolated hair remains from her spring coat indicated a brown color (Vereshchagin and Lazarev, 1977; Sokolov, 1982, p.120–148). The Bilibino female also had a very dark mane and dark hair on the distal limbs (Sher et al., 2007).

The Lena horse was small and stout with long and thick hairs and probably evolved physiological adaptations similar to those of the modern Yakutian breed. Unlike other horse breeds, the physiology of the small-sized, year-round free-ranging Yakutian horse is unique in its adaptation to extreme cold, withstanding temperatures of  $-70^{\circ}\text{C}$  ( $-94^{\circ}\text{F}$ ), reflecting phenotypic and genotypic changes that occurred within a few centuries (Librado et al., 2015). The Yakutian horse is up to 138 cm high at the withers with



**Fig. 13** The Lena horse reconstruction, based on Late Pleistocene remains found in Eastern Siberia between 1953 and 1977. The proportions of the body, the character of the mane and tail are shown correctly, while the overall hair coat of the body is depicted as darker than that described for the Selerikan horse (see text). Drawing by V.N. Laykhov.

roughly 10 cm-long, two-tier hairs. At the beginning of winter, it accumulates fat up to 23% of its total body weight with a subcutaneous layer up to 5 cm thick (Gabyshev, 1957). Its breathing rate is reduced from 20 breaths per minute in summer to 10–12 breaths/min during the winter. With the drop in temperature, the metabolic rate slows down narrowing the blood vessel lumens and lowering heat loss by almost 50 % (Alekseev and Stepanov, 2006; Akhremenko and Akhremenko, 2022).

The Lena horse (macro-remains from Selerikan), fed on predominantly sedges, herbs, some twigs (dwarf willow, birch) and mosses. The wear patterns on the hooves of the Selerikan horse indicate that it used its wide hooves for scraping or digging up snow to expose grass, as observed in behavior of modern Yakutian horses (Vereshchagin and Lazarev, 1977). To this date none of the horses listed in Table 1 have been studied using molecular approaches.

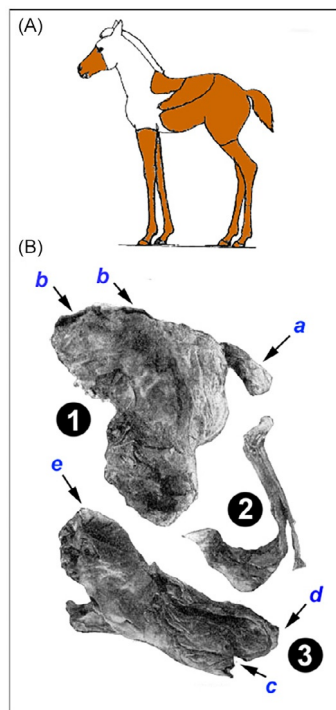
### Features of foals

The remains of foals are represented by two specimens: the “Sana” horse embryo and the one-to-two-weeks-old Batagai foal. Unfortunately, “Sana’s” embryo was dismembered (Fig. 14) by the explosion designed to remove the pregnant “Sana” mare mummy from a gold mine tunnel, but most of the body parts were salvaged and examined. X-rays of the bones revealed that the embryonic horse had relatively short and stout limbs and was about 10 months old. The embryo exhibited short yellowish and light ginger hair with a dark dorsal line and dark, almost black snout and feet (Garutt and Yuryev, 1966). The bay color was suggested for the Batagai foal that also had a black mane and feet. Both foal’s coats in the color pattern were considered to be similar to that of the adult Przewaslki’s horse (Cheprasov et al., 2021).

The Batagai foal’s complete body was necropsied with all internal organs removed and placed in a freezer for further studies and analyses.

### Yukon horse

The Yukon horse was the most common horse in East Beringia in the Late Pleistocene (including the MIS2 cold stage), although its remains have been rarely found. The horse’s appearance is reconstructed primarily on the basis of the partial carcass found at Last Chance Creek in the Yukon (Guthrie, 1990a). The small size of this horse was comparable to that of Przewalski’s and the Lena horse, but it was characterized by relatively slender legs and a broader skull. Unlike the horses from Asia, the Yukon horse possessed a long blondish mane and tail hair, whitish body coat and dark brown hair on the lower legs, which probably represented the winter pelt (Harington and Eggleston-Stott, 1996; Harington, 2002b). Guthrie and Stocker (1990) analyzed the hoofs of the Yukon horse mummified remains from MIS2 sediments on the North Slope of Alaska, concluding that during winter, it fed on grasses excavated from shallow snow cover and enjoyed a relatively sedentary style of life.



**Fig. 14** The Indigirka horse embryo remains. (A) – topography of the salvaged remains, (B) – photos of some of the remains. 1 – rear side, a – tail, b – dark dorsal stripe on the back, 2 – left foreleg; 3 – head, c – opened mouth, d – nostrils, e – ear. Modified from Garutt VE and Yuryev KB (1966) Mummified remains of a wild horse from the permafrost of the Indigirka River basin. *Bulletin of Committee on Quaternary Studies* 31: 86–92 (in Russian), Figs. 2 and 3.

## Cave lion

Finds of the cave lion mummies are extremely rare. Only four mummified cave lions have been discovered to date, all within the last 4 years (2015–2018). These discoveries were due in part to an intensified search for mammoth tusks in Yakutia in general and in the Abyi district (Indigirka River basin) in particular, resulting in numerous finds of mummies of various species (Protopopov et al., 2016; Potapova et al., 2022). Discoveries of skeletons and isolated hair remains of adult cave lion have provided information on body proportions, while the coat coloration remains unknown, being currently based on images from Late Paleolithic caves in Europe (e.g. Guthrie, 2005).

All the cave lion mummies belong to very young cubs and all but one (Dina) comprise complete carcasses.

Two one-to-two-week-old cubs, Uyan (Fig. 15) and Dina probably were siblings; found within 1–2 m from each other, their bodies had been deformed by the collapse of the den. The Uyan and Dina cubs were short-legged and light-colored. The Uyan cub had light yellowish brown hair on the torso and head, while the legs were slightly darker. He weighed 2.8 kg and was about 25–30% heavier than a newborn African lion.

Two other cubs, Sparta (female) and Boris (male) also were found close to each other (within about 15 m), but had lived about 14,000 years apart. Boris's body was damaged and deformed, suggesting that he probably died from a den collapse, while the cause of death of Sparta remains unknown. Both Boris and Sparta exhibited similar dental eruption stages and identified to be between one-to-two week and one-to-two month old. In comparison to African lion cubs of the same age, Boris and Sparta had smaller heads, interpreted as an indication of faster postnatal development of the extinct species to permit consumption of meat at a younger age (Boeskorov et al., 2021).

All the cubs possessed relatively long (up to 3 cm), thick and light hair, which varied slightly in color. Uyan and Dina had similar very light, yellowish brown hair, while Boris had very light yellowish gray hair; Sparta was darker, with light brown and yellowish brown hair and a brown tail tip. Boris and Sparta had dark hair on the tips on their ears. Neither cub had dorsal stripe or brown dots which are characteristic for the modern African lion (Boeskorov et al., 2021) and neither cubs had red and orange shades of hair indicative of postmortem discoloration according to Tridico et al. (2014b). The coat colors of the cubs probably were natural, their differences due to the varying age of the cubs or to temporal (i.e., ecological) variation: darker hair during warmer intervals and lighter pelage during colder episodes (Greenland Interstadial (GI)11 for Boris and Greenland Stadial (GS)4 for Sparta). The variation in pelage color also could be due to genetic differentiation. On the basis of mtDNA analyses, Sparta is assigned to mtDNA Haplotype B (Stanton et al., 2020); the haplotypes of Uyan, Dina and Boris have not yet been determined, but they may represent Haplotype C affecting their (lighter) color pelage. Further analyses of these mummies and other specimens will shed light on this unresolved issue and other aspects of the morphology of this extinct species.

## Preservation in the permafrost

The salvaged mummies have been found in various states of preservation (Fig. 16). In rare cases, the carcasses were completely mummified (e.g. Dukarsk horse, Igor mammoth infant), or were partially desiccated retaining very dry exterior tissues and relatively



**Fig. 15** The Uyan cave lion cub mummy. Photo by Olga Potapova, Aug. 2015.





**Fig. 16** Conditions of preserved tissues of mammoth mummies. (A) – Dima infant with desiccated soft tissues, (B) – Abyi mammoth with fresh-looking tissues. Photo by A - Olga Potapova, B - Albert Protopopov.

soft internal tissues and organs (e.g., Dima, Yukagir and Yuka mammoths, Bilibino horse). Other mummies exhibited semi-dry condition of the tissues (e.g. Lyuba neonate) and surprisingly soft, elastic and fresh-looking exterior and interior tissues (e.g. Abyi mammoth). Such tissue conditions permitted detailed anatomical description of the leg muscles, tendons and blood vessels (Berezovka mammoth; Maliev, 1903) and thorough investigation of the skin and its folds around the mouth, as well as reconstruction of anatomical function of the flexible trunk and other parts of the body (Maly Lyakhov mammoth; Grigoriev et al., 2017).

The state and completeness of the mummies in the permafrost was influenced by multiple biotic and abiotic factors that created a unique set of conditions for each mummy. These factors included the length of sub-aerial exposure (i.e., rapid versus slow burial) and air temperature (season of death) before and during burial, the presence of anoxic conditions (e.g., carcass submerged in a mud hole of exposed to the air) and accessibility to scavengers. In addition to these factors, the elasticity of the tissue depended on the amount of water/moisture around the body during burial and the longevity of favorable burial conditions. In some cases, microbial alteration of the tissues created acidic environment that helped preserving the initially buried in mud mummies, as well as protecting the mummies washed out from sediments and exposed to the air from decomposition and scavengers (e.g. Lyuba baby mammoth; Fisher et al., 2012). Bacterial modifications (including their conservation and degradation properties) of the tissues of other mummies from the permafrost probably varied significantly (e.g. Fisher et al., 2014), and in some cases even allowed to be consumed by dogs (e.g. Berezovka mammoth; Pflizenmayer, 1939) or humans (Guthrie, 1990a), but have not yet been studied properly on the majority of mummies. Other important variables included the chemical composition of the water/sediments, some of which represented an excellent medium for preservation. Such example represents the Starunia's rhino mummies that were discovered at the latitude far below the permafrost zone and Arctic Circle, but were preserved for millennia in ozokerite, a mineral of waxy substance permeated by brine (Nowak et al., 1930).

It should be noted that the preservation of mummies extends only to the level of gross anatomy, with retention of the overall shape and structure of the body, and the internal and external organs, along with some tissues and even cells that contain some organelles (see references in Table 1). The molecular preservation of tissues and cells of the mummies from the permafrost does not allow us to hope for the possibility of cloning any of the species (Shapiro, 2015).

### Conclusion/summary/outlook

The complete and incomplete specimens of mummified mammals represent 16 extinct and extant species of 12 Families, all of which were found in the northern Holarctic. All but a few of the mummies date to the MIS3-2 climate-stratigraphic unit of the Late Pleistocene. The mummies became objects of scientific study during the early 20th century; however, the past two decades have witnessed breakthroughs far surpassing the accumulated knowledge of the last few centuries. The application of new methods, along with traditional necropsies, have yielded new information on morphology (anatomy, the shape and size of body parts, woolly coat structure and coloration, etc.) and paleobiology (growth and development, life span, birth cycles, etc.), which are unobtainable from isolated fossil bones and skeletons. The mummies have also been subject to isotopic and paleogenomic studies regarding diet, migration, physiology, adaptation to cold, population dynamics and phylogeny.

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