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The Yukagir Bison: The exterior morphology of a complete frozen mummy of the extinct steppe bison, *Bison priscus* from the early Holocene of northern Yakutia, Russia



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ABSTRACT

The paper presents analyses of the exterior morphology of one of the extinct and dominating species of the Late Pleistocene megafauna of Eurasia, the steppe bison, *Bison priscus*. The frozen mummy of the Yukagir Bison found in northern Yakutia, Russia represents the most complete specimen of this species in the world. It belongs to a young, 4.1–4.5 year old male, which dates back about 10,500 cal BP. The analyses revealed that the overall size of this specimen was comparable to a 6-year old European and American bison. Its horn spread falls within the upper limits of *B. bison athabasca* and *B. bison* males, as well as within the average sizes of *B. priscus occidentalis* from East Siberia and North America. While most of the not fully-grown Yukagir Bison body size fell within the average parameters of both grown modern species, the body and hind foot lengths were closer to the lower limits of the European bison. The color and hair pattern appeared to be close to the Blue Babe mummy (*B. priscus*) and modern Wood bison (modern morphotype of *B. bison athabasca*) and European (*B. bonasus*) bison. The geological age of the Yukagir Bison, along with the data from other specimens indicate that this species, which survived the Pleistocene-Holocene boundary, became rare but was still widely distributed in the northern part of centraleastern Siberia until about 8000 years ago. The juxtaposed data from arctic latitude sediments and the *Bison priscus* stomach content pollen indicate that it was selective grazer in the environment dominated by unfavorable shrub and forest-tundra vegetation. The scarce Holocene steppe bison remains in Eastern Siberia reflects the dramatic decrease of suitable habitats and pastures during the early Holocene climatic optimum in the high Arctic, which was a major factor of irreversible population fragmentation and decline leading to the species' extinction.

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1. Introduction

Skeletal remains and frozen corpses of fossil mammals preserved in the permafrost have exceptional scientific value. A

considerable number of such remains have been found in the Arctic zone of Yakutia in the regions containing ice sediments of the Yedoma suite. To date, more than 15 frozen corpses, including mammoths, woolly rhinoceroses, horses, bison, and a wolverine, have been found and described scientifically (Vereshchagin and Tikhonov, 1999; Lazarev et al., 2001; Boeskorov et al., 2007; Lazarev, 2008; Boeskorov et al., 2011; Maschenko et al., 2012 and references therein). Studies of mummified corpses of the Quaternary mammals preserved in the permafrost give much more information than is available from bones, the most common paleontological material found everywhere. Over the past 20 years, the microbiological, genetic, and isotope studies of the recovered mummies have largely expanded our knowledge of the paleoecology and paleogeography of the Pleistocene and Holocene mammals (Guthrie, 1990; Vereshchagin and Tikhonov, 1999; Rogaev et al., 2006; Boeskorov et al., 2007; Gilbert et al., 2007; Rountrey et al., 2007, 2012; Zazula et al., 2009; Boeskorov et al., 2011; Meiri et al., 2014).

Fossils of the steppe bison (*Bison priscus* Bojanus, 1827) are among the most numerous finds, along with the mammoth remains, collected from the Quaternary deposits of the unglaciated regions in Eastern Siberia particularly, and Beringia in general. In Eastern Siberia (Western Beringia), the majority are recovered from the river valleys on the mainland and on islands in the Arctic Ocean, indicating that the species was very widespread in these regions, with the exception of the mountains (Rusanov, 1975; Lazarev and Tomskaya, 1987; Guthrie, 1990).

In general, most of the *Bison priscus* remains are represented by isolated skeletal elements and rarely by complete skulls with preserved horn sheaths. Skeletons of the steppe bison, let alone the complete frozen mummies, had never been discovered and reported in the Palearctic before this find (Boeskorov et al., 2014a,b).

Across the Holarctic, isolated body parts and remains of partial carcasses with mummified tissues of the adult steppe bison, *Bison priscus*, have been discovered and reported. These include two mummified distal legs of the Clearly Creek Bison found in Alaska in 1934 and 1936; a mummified distal leg of the Goldstream Creek Bison in Alaska found in 1936; the mummified distal forefoot with hoof of the 2.5–3 year old bison from the Struyka River, a tributary of the Indigirka River in Eastern Siberia found in 1946; the isolated remains of the mummified skin with hair, some hair from the tail, and partial horn sheath of the bison from the Muogdaana River, a tributary of the Vilui River in Eastern Siberia; and the mummified middle portion of a hind leg of the adult bison from the Yana River in Eastern Siberia found during 1885–1886 (Popov, 1948; Guthrie, 1990). More complete finds of steppe bison frozen corpses have been found in Eastern Siberia and represented by the almost 75% complete specimen of the 2.5 year old, female Mylakhchyn Bison from the Indigirka River basin, which exhibited damage to the frontal part of the body (29,500 BP; Flerov, 1977); the complete Batagai Bison calf from the Yana River basin (Lazarev et al., 2011); the rear portion of the carcass from the Rauchya River (Kirillova et al., 2013), in Western Beringia; and the almost complete bison from the Anuy River (Nikolskiy and Shidlovsky, 2014).

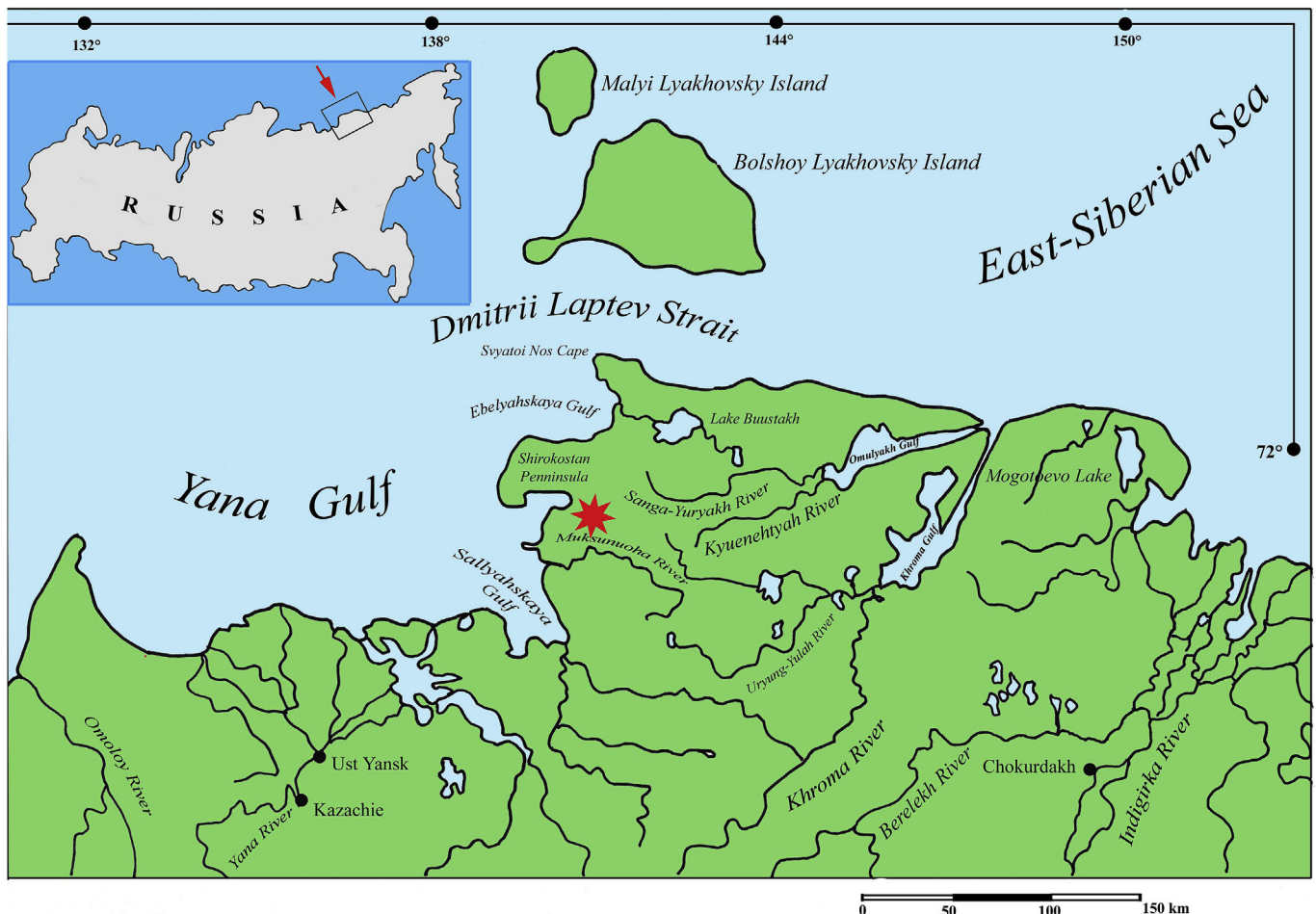


Fig. 1. The location of the Yukagir Bison site in northern Yakutia.



Fig. 2. The Yukagir Bison *in situ*, on the thawing Chukchalakh Lake bank, northern Yakutia, Russia.

Mummified remains from Eastern Beringia (North America) include the partial carcass of the 7 year old female, Fairbanks Creek Bison, retaining the neck, head and horns with sheaths found in Alaska in 1952 (11,950 BP; Flerov, 1977; Guthrie, 1990); the partial carcass of the mummified Dome Creek young adult male bison (28,000 BP), the partial carcass with piece of hide, intestines and some mummified tissues covering postcranials found in Tsiigehtchic, Northwest Territories, Canada (11,830 BP; Zazula et al., 2009), and the most famous and well known to the public, almost complete mummified carcass of the 8–9 year old male bison nicknamed “Blue Babe”, from Pearl Creek, Alaska (36,000 BP; Guthrie, 1990).

A frozen mummy of a steppe bison named “Yukagir Bison” was discovered in the summer of 2011 from the thawing northern slope

of the Chukchalakh Lake in the Yana-Indigirka Lowland of northern Yakutia, Eastern Siberia, Russia (Figs. 1 and 2). The site location is 72°17'30"N, 140°54'05"E, based on Anonymous (1956). The find represents the second, after the Blue Babe discovery of an adult specimen of the species in the world that had over 50% of the skeleton and soft tissues remains preserved. The bison mummy received its name after the Yukagir Community members who recovered this specimen and played key roles in recent discoveries of many bones and frozen carcasses in the northern part of Yakutia. Among these, in 1994, they discovered a whole “mammoth cemetery” on the Maksunuokha River bank, encountering bones from five woolly mammoths, and the remains of one mammoth mummified carcass (Boeskorov et al., 2006; Lazarev, 2008). In 2002,



Fig. 3. The Yukagir Bison mummy condition as of February 2012 (Photo by G. Boeskorov, 2012).

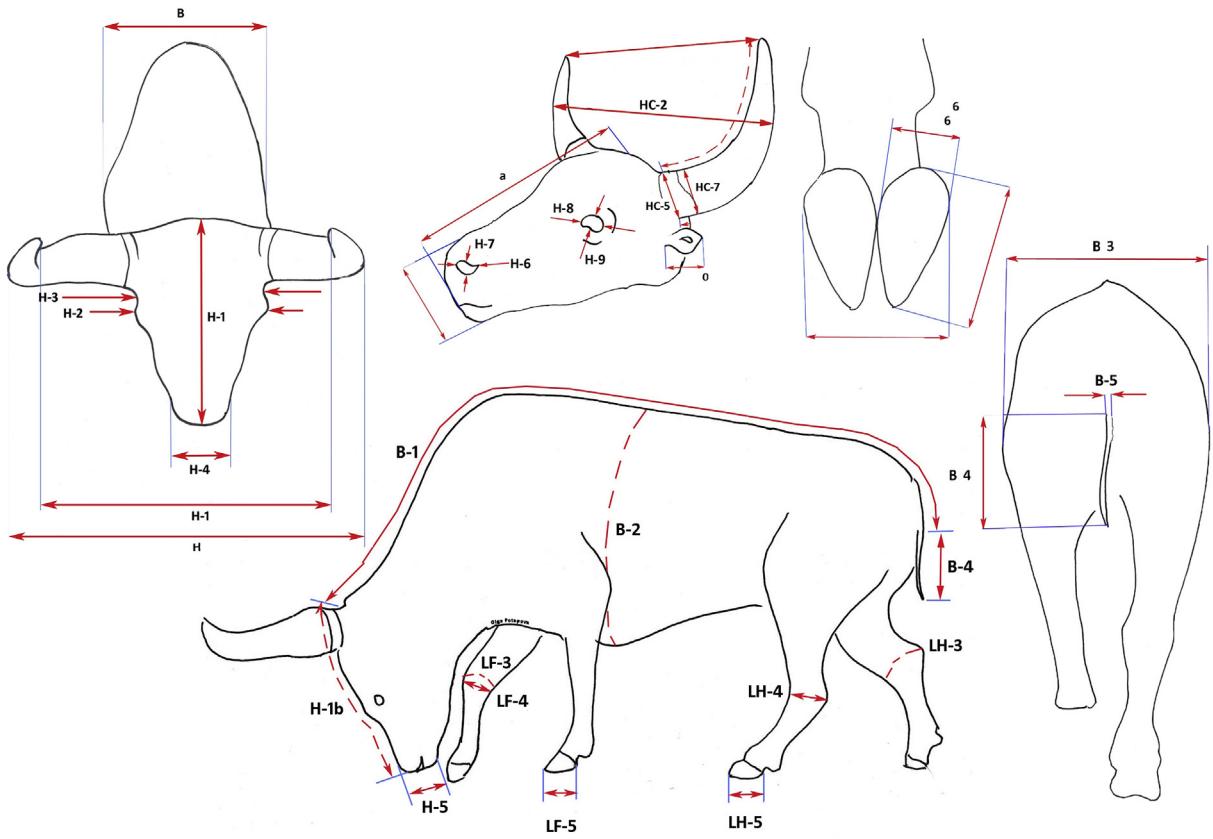


Fig. 4. The major measurements of the Yukagir Bison mummy (after Gromov et al., 1963; Van Zyll de Jong, with modifications).

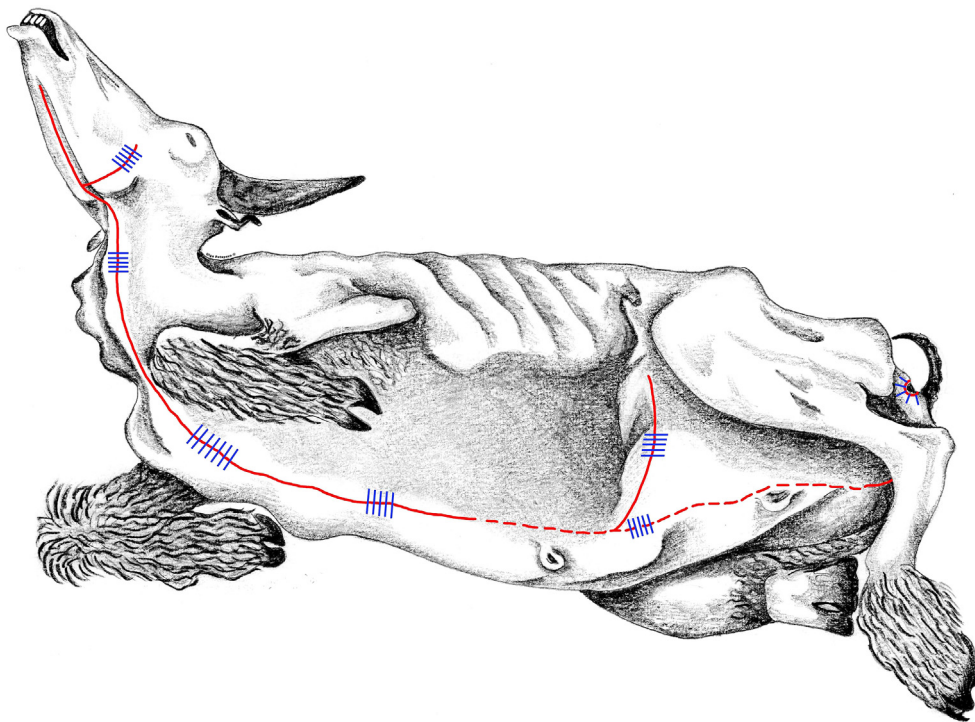


Fig. 5. The Yukagir Bison mummy, left side view, with the locations of the skin measurements in February 2014: Red line – the ventral and lateral cuts through the skin; Blue transverse lines – the approximate locations of the skin measurements (see Table 4). The cut on the parietals not shown (drawing by Olga Potapova). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

the sons of the Community leader Mr. Gorokhov, found the Yukagir Mammoth remains consisting of a frozen head with tusks, a left foreleg, hide pieces and postcranials, which were studied by an international, multidisciplinary research team (Boeskorov et al., 2007). Among other fascinating discoveries by the Yukagir Community members were the frozen woolly mammoth named “Yuka” (2009) and the extinct wild horse named “Yukagir Horse” (2010), both found on the Oyagossky Yar on the coast of Dmitry Laptev Strait, about 100 km north from the Yukagir Bison site (Boeskorov et al., 2013, 2014; Maschenko et al., 2014).

The sites of these finds are located in the tundra zone of the Yana-Indigirka Lowland. It is largely represented by the Upper Pleistocene Yedoma suite, composed of icy silts alternating with massive polygonal ice veins. The area is heavily waterlogged and covered by numerous lakes. The northern part of the lowland is dominated by arctic, hilly tundra (Boeskorov et al., 2006, 2007). The soil types of the locations are typical for the tundra zone and are represented by permafrost tundra humus-gley and peat-gley soils (Elovskaya et al., 1979).

The studies of the buried humus soils from the Upper Pleistocene of the Yukagir Mammoth site, which is located nearby to the south, revealed their steppe origin (Shchelchkova, 2009). The Yukagir Bison site is within 25 km of the Yukagir Mammoth site, where obvious differences of the landscape relief with the Yukagir Mammoth site are absent. The sediments composing this hilly plain cut by the Maksunuokha River and flecked by numerous tundra lakes is represented by the Yedoma deposits of Late Pleistocene age. In the Late Pleistocene, this ancient plain was covered by the vast tundra-steppe with rich herbaceous vegetation supporting abundant and diverse mammal fauna (Lazarev, 2008).

2. Material and methods

2.1. Material

Shortly after its recovery in the summer of 2011, the Yukagir Bison mummy was brought to a dugout ice storage in the Yukagir village, where it was kept under frozen conditions. Later that year, the mummy, owned by the Yukagir Community and led by the late

Mr. Vassily Gorokhov, was loaned to the Yakutian Academy of Sciences, Yakutsk (catalogue # OYu 3; Department of Mammoth Fauna Studies) for this study. In January 2012, the mummy (Figs. 3 and, 7A–K) was delivered to Yakutsk and tested for infectious diseases (foot and mouth disease, anthrax, brucellosis, rinderpest etc.), which yielded negative results. The results of this paper are based on the studies of exterior morphology of the mummy conducted in February 2012 and February 2014.

2.2. Measurements and terminology

The mummy carcass was described and measured following the methods proposed by Gromov et al. (1963) and Van Zyll de Jong (1986) with some modifications (Fig. 4). The skin was measured by digital calipers with accuracy of 0.1 mm in locations shown on Fig. 5. The hoof sizes were calculated based on the sole prints traced on 1 mm graph paper. The anatomical terms followed Burdas and Habel (2003), and König and Liebich (2009).

2.3. Isotope analysis

The radiocarbon analysis of the bison horn core bone and hair (see the Table below) was performed in the Center for Isotope Research, University of Groningen, The Netherlands. Standard procedures for the chemical pretreatment of samples followed Mook and Streurman (1983). The routine treatment of samples consists of the “AAA” (Acid-Alkali-Acid) method which was applied to the hair sample. For bone, collagen was extracted following a procedure originally developed by Longin (1971). The bone mineral was dissolved by repeated treatment with an acid solution (1–2% HCl). This took several days, and 10–20% of the bone collagen was dissolved during the process. The crude collagen containing the contaminating carbonaceous substances was washed thoroughly with demineralized water before being treated with slightly acid demineralized water. During this treatment, ‘pure’ collagen dissolved into gelatine, insoluble material was removed by centrifuging, and the gelatine was collected by evaporation.

The prepared and purified sample fraction of hair and bone collagen was combusted into gas (CO_2 and N_2) using an Elemental Analyzer, coupled to an Isotope Ratio Mass Spectrometer (IsoCube/IsoPrime). The IRMS provides the stable isotope ratios $^{13}\text{C}/^{12}\text{C}$, $^{15}\text{N}/^{14}\text{N}$ as well as the C and N yields.

For ^{14}C analysis, part of the CO_2 was routed to a cryogenic trap to collect the samples for further processing. The CO_2 was transferred into graphite powder by the reaction $\text{CO}_2 + 2\text{H}_2 \rightarrow 2\text{H}_2\text{O} + \text{C}$ at a temperature of 600 °C and using Fe powder as catalyst (Aerts et al., 2001).

Next, the graphite was pressed into target holders for the ion source of the AMS. The AMS then measured the $^{14}\text{C}/^{12}\text{C}$ and $^{13}\text{C}/^{12}\text{C}$ ratios of the graphite (van der Plicht et al., 2000). From these numbers, the conventional ^{14}C age was determined and calibrated into calendar ages using the calibration curve IntCal13 (Reimer et al., 2013). The calibrated ages are reported in calBP, which are calendar ages relative to 1950 AD.

3. Results

3.1. Geological age

The processed sample materials of the horn tip and hair were of excellent quality. The hair sample was chemically pretreated by the AAA method, and the bone sample collagen was extracted. The C and N parameters and stable isotope ratios $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ were well within the expected range.

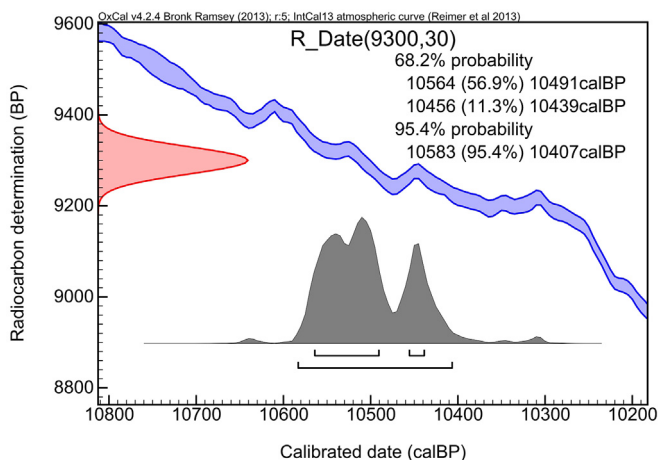


Fig. 6. Calibration diagram of the Yukagir Bison specimens; Red – the radiocarbon date (9300 ± 30 BP made by the OxCal program; <https://c14.arch.ox.ac.uk/>); Blue – the calibration curve IntCal13 (with error limits); Gray – the calibrated age distribution. The numbers show the calendar age distribution with 1σ and 2σ . In the text we use the 1σ , the two regions taken together and rounded to 5. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

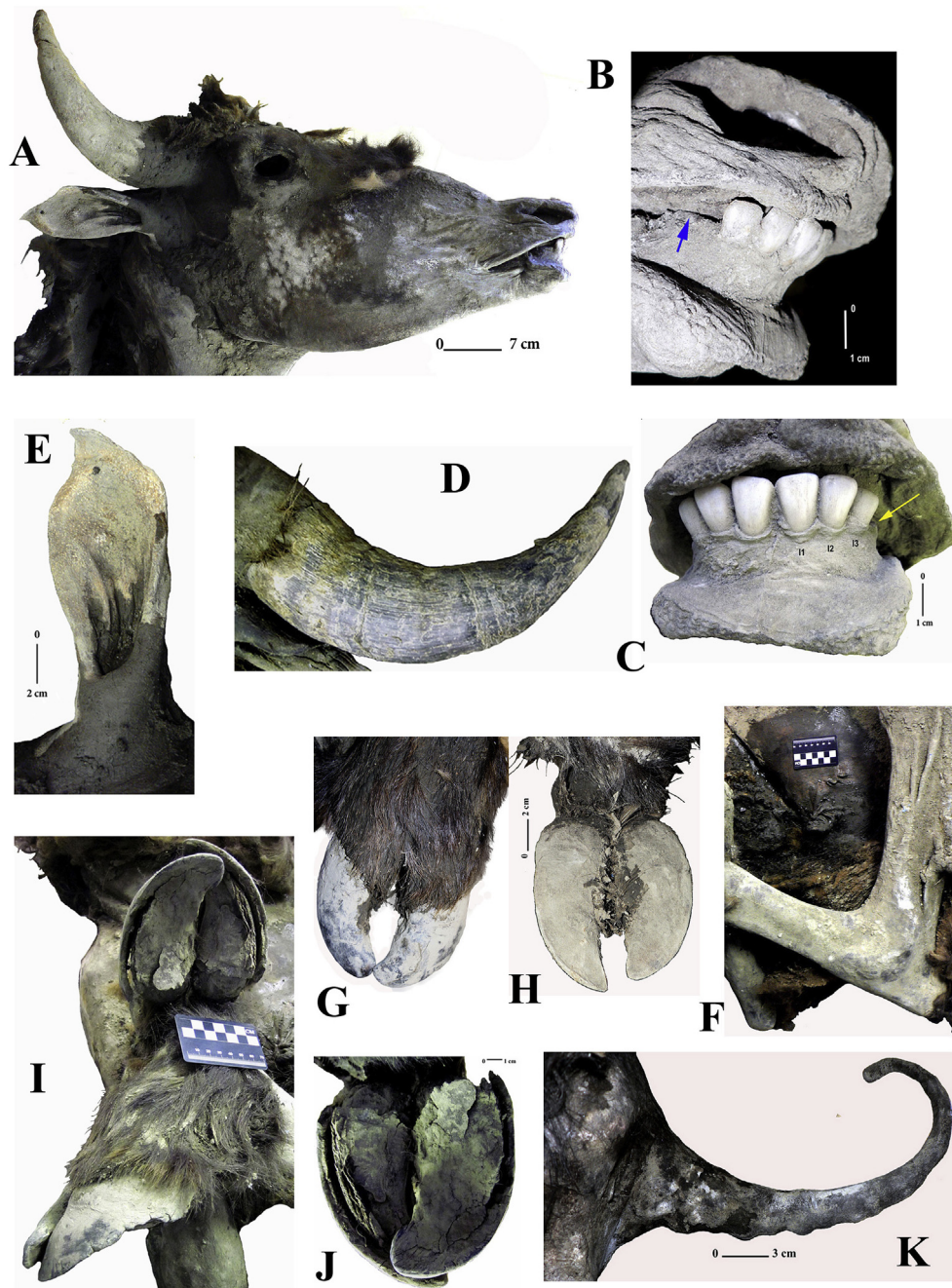


Fig. 7. The Yukagir Bison mummy parts of the body: A – right side of the head; B, C – incisors in wear (yellow arrow shows the bulging gum over an unerupted canine); D – left horn (frontal side), E – right ear; F – lower belly with scrotum; G, H – fore limb hooves (dorsal and plantar views); I, J – hind limb hooves (dorsal and plantar views); K – tail. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Lab code	Sample	Age BP	$\delta^{13}\text{C}$ (‰)	C%	$\delta^{15}\text{N}$ (‰)	N%	C/N	Age cal BP
GrA 53290	Horn core tip	9310 ± 45 (±1σ)	-20.64	48.0	8.64	16.8	3.2	10,580–10,430 (±1σ)
GrA 53292	Hair	9295 ± 45 (±1σ)	-24.53	58.4	–	–	–	10,570–10,425 (±1σ)

Both samples, horn and hair, gave the same ^{14}C age within their uncertainty level, and can therefore be considered as excellent duplicate dates. The averaged value is 9300 ± 30 BP. The calibrated result for this averaged date is 10,565–10,490 (57% probability) and 10,455–10,440 (11% probability) cal BP (Fig. 6).

3.2. Yukagir Bison mummy description

Presumed rapid burial of the Yukagir Bison, and permafrost conditions facilitated the preservation of all the body parts, including internal organs; the head with intact fleshy snout, ears

and horns, the tail; complete extremities; genitalia, and the undamaged hide with patches of the dark-brown and black fur remaining (Figs. 2, 3 and 7). Examination of the external body surfaces revealed a complete absence of unoxidized (blue) vivianite mineral traces.

3.2.1. Body overall shape, size and weight

The Yukagir Bison retained the posture as found in the muddy shore landslide of the Chukchalakh Lake in 2011 and stored in Yakutsk since 2012 (Figs. 2 and 3). The mummy lies on its right side, its torso position is relatively straight, with the head lifted up and turned to the left. The spine is slightly curved up and has a gradual slope towards the neck. The proximal torso and neck positions, along with the lifted up and turned to the side head, do not allow for evaluation of the anterior shape and position of the hump over the frontal legs to compare it to the modern bison. The Yukagir mummy does not have a visible abrupt change in the spine contour between the last thoracic and lumbar vertebra, which is characteristic for the modern Wood bison (Van Zyll de Jong, 1986; Reynolds et al., 2003). The mummy's mouth is closed, but the lower lip is pulled down, exposing the entire row of the incisors (Fig. 7A–C). The front legs are bent at the elbow and antebrachio-carpal joints with hoofs tucked to the abdomen (Figs. 3 and 5). The hind legs are bent at the stifle (knees), tarsal (hock) and metatarsophalangeal joints with the lower parts of the limbs crossed and pushed to the body (Figs. 3 and 7F). The tail is in a raised position (Figs. 3, 5 and 7K).

ventral sides of the neck, breastbone, spine, pelvis, and ribs. The most significant deformation of the mummy is on the left abdominal side. Along with shrinkage of the internal organs that created voids under the abdominal wall, it was possibly caused by the sediment weight that pressed the flank down under the rib cage (Fig. 5). Thus, the measured torso circumference would underrepresent the size of the live animal and its conservative size estimation would be at least 10–15% more than that in the measured mummy.

The external genitalia of the bison are represented by the prepuce and scrotum (Fig. 7F). The scrotum is wrinkled and shrunken, and the testicles are not detectible. The distance from the posterior margin of the prepuce to the front of the scrotum is 33 cm and the distance from the posterior margin of the scrotum to the ventral end of the anus is 42.5 cm.

The body size of the Yukagir Bison was compared with that of the modern European and American bison (Table 1) from Halloran (1960) and Lobanov (1968), Meagher (1986), Van Zyll de Jong (1986), Skinner and Kaisen (1947), Krasinska and Krasinski (2002), and Danilkin (2005). The results showed that its body was shorter than that of same-aged American bison, and closer to the lower limit of the European bison. The withers and hip heights, as well as the chest girth of the Yukagir Bison is closer to the average of grown (>6 years old) bulls than to a 4.5-years old animal of both modern species, but its hind foot length falls within the lower limits of both European and American bison.

Table 1
The body sizes of *Bison* taxa. The additional data from: ¹Danilkin (2005); ²Lobanov (1968; Askania-Nova), Biosphere Reserve, Ukraine; ³Meagher (1986); ⁴Skinner and Kaisen (1947); ⁵McDonald (1981).

Measurements (cm)	Steppe bison <i>Bison priscus</i>	Modern bison (genus <i>Bison</i>)				
	Yukagir bison (this study)	European bison, <i>B. bonasus</i> (Free ranging)		American bison, <i>Bison bison</i>		
		Bialowieza National Park, Poland After Krasinska and Krasinski (2002)		American Plains Bison, <i>B. bison bison</i> After Halloran (1960)		American Wood bison, <i>B. bison athabasca</i> , Canada After Van Zyll de Jong (1986)
		4.1–4.5 years old	4-years old	≥6 years old	4.5 year old	≥6.5 year old
	limits (mean)	limits (mean)	limits (mean)	limits (mean)	limits (mean)	
Horn tips spread	est. 71 shealth	30–75 (45) shealth	39–61 (52) shealth	46–60 (53) shealth	46–74 (63) shealth	58.5–74 (66.5) ⁴ cores
Maximum horns spread (outside curve)	est. 76 shealth	54–70 (64) shealth	63–79 (71) shealth	65–70 (64.5) shealth	66–74 (70.9) shealth	645–750 (683) ⁴ cores
Length of ear	19	–	14–18 (16) ¹	–	15–21 (18) ²	–
Body length	196	208–246 (226)	245–300 (257)	285–291 (288)	287–317 (304)	274–335 (305.5)
Withers height	about 170	136–165 (150)	158–188 (172)	154–164 (157)	163–186 (174) 134–172 (161) ²	168–201 (182.2)
Hip height	165	–	–	–	–	144–181
Maximum rib cage circumference	206 [est. 226.6]	–	225–270 (245) ¹	–	198–270 (250) ²	–
Hind foot length	61	–	–	–	58–68 ³	62–71 (66.3)
Length of tail	44	–	54–74 (62) ¹	39.4	48–65 (57) ²	44–54 (49.6)
Weight, kg	616–943.6 (783)	260–430 (366)	436–840 (634)	420–590 (511)	461–721 (616) 880–990 (935) ²	759–1179 (943.6)

The overall body shape is somewhat deformed due to mummification and desiccation of the soft tissues that are significantly shrunken, allowing most of the skeleton to show through the skin (Fig. 5). These areas include the orbits, snout, dorsal and

Some relatively short body parameters of the subadult Yukagir Bison that seem closer to the grown European bison may reflect the “juvenile” proportions of the body, rather than demonstrating the conspecific morphology of the species. Two or more years of

growth Yukagir Bison might have enabled it to attain a longer body in its adulthood.

Given the fact that American bison male acquires its maximum size at 6 years and weight around 13 years of age (Halloran, 1960), the Yukagir Bison weight, could reach up to 1000 kg and a withers height up to 200 cm, in its mature adulthood, which corresponds to the mean weight value of the modern Wood bison (Table 1), and a conservative estimate for bulls of the steppe bison, *Bison priscus*.

The tail length (44 cm) of the Yukagir Bison (Fig. 7 K) falls somewhere between the Wood bison (50 cm) and American Plains bison (42 cm; Van Zyll de Jong, 1986) sizes. Notably, the Blue Babe mummy had a short tail (20 cm; Guthrie, 1990); only half the size of the Yukagir Bison.

The Yukagir Bison mummy has not been weighed yet due to the lack of appropriate scales. The mass of the dry and sublimated mummy is estimated to be at least 400 kg. The methods for calculating mass of the bison species based on its body measurements, are absent, but the data on the body masses and sizes collected from the same specimens of the modern bison are available. If the withers and hip heights, as well as the chest girth of the Yukagir Bison places it within range of the 6 year old males of both modern species, its mass should have fallen within the similar parameters of these species. The mass of the Yukagir Bison can be calculated as an average of the modern bison: 6 year old European bison 634 kg (Krasinska and Krasinski, 2002), American Plains bison 616 and 935 kg (Halloran, 1960; Lobanov, 1968), and Wood bison 934.6 kg (Van Zyll de Jong, 1986), which equals 783 kg (Table 1). The bison mass calculations based on the domesticated cattle parameters: a cow (standard methods by Trukhanovsky and Kluwer-Strauch used in Russia, after Liskun, 1949) and heavy weight zebu (Abdelhadi and Babiker, 2009) body measurements give underestimated results (673–721 kg for cow, and average 464.4 kg for zebu) and should not be applied for mass calculation for this species.

3.2.2. Incisors

The pulled down lip exposed the mummy's front teeth (Fig. 7B, C) and allowed their examination.

I1 – Permanent first Incisor I1. Crown Height – 17.3 mm, width – 13.6 mm. The enamel is slightly worn, and the dentin is not exposed.

I2 – Permanent second Incisor I2. Crown height – 15.8 mm, width – 12.3 mm. Some wear is visible on the enamel which does not expose the dentin.

I3 – Permanent third Incisor I3. Crown height – 12.0 mm, width – 10.4 mm. No visible traces of wear on the enamel are present.

C1 – Permanent Canines – are absent, as well as the both deciduous canines. The gum surface behind the I3 is clear from scars and slightly bulged, indicating that the permanent canines possibly may have come out beyond the dental alveoli pushing out the soft tissues.

The state of the erupted permanent incisors of the Yukagir Bison is definitely older than group IV (3.5 years) and somewhat younger than the group V (I1–3, dC1 in place or gone with erupting C1), established for the modern American bison (*B. bison bison*; Frison and Reher, 1970). It fits into the group V (4.5 year olds) defined for the bison from the Late Prehistoric Glenrock Buffalo Jump, Wyoming (I1–I3 in place, dC1 in place, or gone with C1 erupting; Reher, 1970). However, at the 1500–1800 AD Vore Site (Wyoming)

the time of permanent canine eruption in *B. bison* is stated to be between 4.1 and 4.3 years of age (Fuller, 1959; Reher and Frison, 1980).

In modern European bison the permanent canines come in place sooner, at the age of 3.5 years (Krasinska and Krasinski, 2013). Thus, the canine eruption timetable in modern species places the Yukagir Bison between 4.1 and 4.5 years of age. The study of the mummy's cheek teeth, not yet available at the time of the study, may allow more precise age identification.

3.2.3. Horns and hoofs

The horns are projected laterally and turned upwards, characteristic for young adult and adult steppe bison. The right horn sheath is missing. The complete left horn sheath is black and is tightly attached to the horn core. The horn cores and horn are nearly circular in cross-section at the base and circular at the tip. The sheath surface is covered by longitudinal keels and grooves present between the base and middle section of the horn. The horn is not pierced by the new growing sheath, as normally occurs in 3–4-year old European bison and 7–8-year old American bison (Allen, 1876; Flerov, 1979). The sheath shows at least three scaly circular edges in its lower portion and slight wear on the tip (Fig. 7D). In the American bison, the growth rings give too low a value for young individuals and in American and European bison too high of a value to be 4 years old and older (Fuller, 1959), and therefore are not suitable to be used alone in the bison age determination (Fuller, 1959; Flerov, 1979).

The Yukagir Bison mummy had relatively long and wide spread horns, close to the maximum sizes of the modern adult males of the European and American bison (Table 1). Its sheath tips spread lies at the lower limits of bison from the Late Pleistocene (middle Würm/middle Wisconsin) of the Palearctic region designated by Flerov (1977) as *B. priscus occidentalis* with the horn core tips spread 670–800 mm, but over the maximum limits of bison from the Late Pleistocene of Eastern Siberia designated by Lazarev and Tomskaya (1987) as "*Bison priscus occidentalis*" with the sheath tips spread 624–660 mm. The Yukagir Bison sheath spread is very close to the horn core tips spread of the holotype *B. occidentalis* Lucas 1898 (702 mm) and falls within the lower limit of the horn core tips spread (670 mm–875 mm, mean 747 mm) of the Late Pleistocene bison from North America designated by Skinner and Kaisen (1947) as *B. (bison) occidentalis*. It also lies within the lower limit of the Late Pleistocene bison horn core tip spread designated as *Bison priscus* by McDonald (1981) (751–1064 mm, mean 888 mm) that comprised the bison from mid- and high latitudes of Eurasia and Beringia to a few sites in midlatitude and tropical North America.

When compared to the most complete specimens of the extinct species, the spread of the sheath tips of the Yukagir Bison appeared considerably smaller than that of the terminal Late Pleistocene (11,830 ± 45 BP) Tsiigehtchic Bison (940 mm) discovered in the Mackenzie River Valley, Yukon (Zazula et al., 2009) and the adult male Blue Babe (922 mm) from Alaska (~36,000 BP; Guthrie, 1990). If compared to the modern Wood bison, the Yukagir Bison sheath and horn core sizes and core lengths are between of 4.5 year old males and adult males of this species, but the horn's spread is significantly higher than that in average adult Wood bison, indicating the species differences (Table 2). If the animal lived and continued growing, it might have reached the horn lengths of 600 mm and 900 mm spread between the tips, at its maturity.

Table 2
The horn sizes of *Bison* taxa. Additional data after: ¹Rusanov (1975), ²Skinner and Kaisen (1947), ³Flerov (1965), ⁴McDonald (1981), ⁵Shakelton et al. (1975) (4.5 year old males).

Measurements, mm	Extinct <i>Bison priscus</i>			Modern <i>Bison bison</i>	
	Yukagir Bison	<i>B. priscus occidentalis</i> Northeast Siberia, Late Pleistocene (n = 12)	<i>B. priscus occidentalis</i> , North America, Holocene (n = 31)	<i>B. bison athabascae</i> Canada (n = 12)	<i>B. bison bison</i> North America males
		After Lazarev and Tomskaya (1987)	After Van Zyll de Jong (1986)		After McDonald (1981)
		Limits (mean)	Limits (mean)	Limits (mean)	Limits (mean)
Horn sheath	Left				
Minimum distance between horn sheath tips	est. 710	624–660 (642)	–	585–740 (665) ²	–
Maximum width between horn sheaths (lateral sides)	760	522–900 (701.2)	–	–	–
Maximum (lateral curve) horn sheath length	420	500–560 (530)	–	–	–
Minimum (medial curve) horn sheath length	310	–	–	–	–
Minimum distance between horn sheaths bases	est. 355	210–340 (276)	–	–	–
Maximum circumference of the horn sheath base	276	360–370 (363.3)	–	–	–
Maximum (anteroventral-posterodorsal) diameter of horn sheath base	87	105–124 (113.2) ¹	–	–	–
Horn core	Right		⁴ n = 23–52	⁴ n = 9	n = 28–139
Minimum distance between horn core tips	est. 720	400–810 (622.1)	758.1	618–855 (700.8) 542–848 (680) ⁴ 505–650 (572) ⁵	510–778 (604)
Maximum (lateral curve) horn core length	258	160–380 (269.5)	285–416 (363) ⁴	162–323 (236) ⁴ 239–296 (256) ⁵	124–270 (191)
Minimum (medial curve) horn core length	210	–	275.4	178–235 (198) ⁵	–
Maximum circumference of horn core (base)	270	175–380 (240.4)	295.5	226–310 (286) ⁴ 207–225 (218) ⁵	199–324 (255)
Maximum (anteroventral-posterodorsal) diameter of horn core base	80	51–107 (75.2)	84–116 (98) ⁴	81–106 (92) ⁴ 69–75 (72) ⁵	69–99 (82)

The sizes of the steppe bison hoofs have never been analyzed in general or in detail due to the limited amount of the mummified remains, but this morphological feature potentially can provide

modern European bison (Flerov, 1979; Krasinska and Krasinski, 2013). Guthrie (1990) found that the hoof sizes of the Blue Babe mummy are also close to that of the American bison.

Table 3
The hoof sizes of *Bison* taxa. Data after: ¹Flerov (1979), ²Krasinska and Krasinski (2007), and ³Telfer and Kelsall (1979).

Measurements (cm)	Extinct <i>B. priscus</i>		Modern <i>B. bonasus</i>		Modern <i>B. bison</i>
	Yukagir Bison, male, 4–4.5 years old	Mylakhchyn Bison, female, 2.5 years old	European bison, <i>B. bonasus</i> , mature bulls		Wood bison, <i>B. bison athabascae</i> , mature bulls, Canada
	(this study)	(Flerov, 1977)	<i>B. bonasus bonasus</i>	<i>B. bonasus caucasicus</i>	
Maximum front hoof length	16	12.5	9–10.5 ¹ 11–18 ²	7–8.5 ¹	Up to 19
Maximum front hoof width	6.5	6	Up to 7 ¹	–	–
Maximum combined width of medial and lateral front hoofs	13	12	Up to 14 ¹ 10–14 ²	–	Up to 17.5 ¹ Up to 13 ³
Maximum length of hind hoof	14.6	–	10–11.5 ¹	7.5–9 ¹	–
Maximum width of hind hoof	6.4	–	–	–	–
Maximum combined width of medial and lateral hind hoofs	13.5	–	–	–	Up to 13 ³
Footprint weight bearing (g/cm ²)	1080–1141	–	1000–1300*	–	884.1 (mean) ³

valuable information on the ecology and habitats of the extinct species. The Yukagir Bison mummy hoofs (Fig. 7G–J) were preserved in good condition, and their states of preservation are very similar. The foreleg hoofs are loosely attached to the phalange bones. The upper (dorsal) parts of the hoofs are better preserved than the lower (volar) parts of the hind hoofs. Unlike the fore hoofs, the hind hoofs have somewhat overgrown and scaling edges extending beyond the sole levels (Fig. 7J).

The Yukagir Bison appeared to have large hoof sizes that are close to the maximum recorded for the modern European and Wood bison (Table 3) (Flerov, 1979; Telfer and Kelsall, 1979; Krasinska and Krasinski, 2002). Flerov (1977) determined the large size of the hoofs of the 2.5 year old Mylakhchyn Bison mummy (*B. priscus*). However, its sizes fall within the minimum range of the

The Yukagir bison had relatively longer forefoot hoofs than Mylakhchyn bison and significantly larger than the Struika Bison (single hoof length 98 mm, width 45 mm; Flerov, 1977) from the Late Pleistocene of the Indigirka River basin. The footprints of the Yukagir Bison measured 154.5 cm² for the front, and 178 cm² for the hind feet, with the total of 665 cm². If the bison was 783 kg (between 616 and 943.6 kg; see Table 1), it had a 1174 g/cm² (between 926 and 1419 g/cm²) footprint load, which is higher than that in the Wood bison (Telfer and Kelsall, 1979), but close to the average load range of the modern European bison (1000–1300 g/cm²; Flerov, 1977).

Among some ungulates, relatively wide hoofs in comparison to modern forms were characteristic for extinct Late Pleistocene wild horses (possibly belonging to a single and variable species

(Eisenmann, 1991)) that coexisted with the steppe bison in Eurasia, and represented by the Wide-hoofed (*Equus latipes* Gromova, 1949), Lena (*Equus lenensis* Russanov, 1968), and Ural (*E. uralensis* Kuzmina, 1975) horses. The wide hoofs were interpreted to be an adaptation for movement in the deep snow, or over landscapes with taller grasses and softer substrates (Vereschagin and Kuzmina, 1982). The hoofs of animals with relatively smaller footprint sizes and high sole loads, such as Antelope saiga, *Saiga tatarica* (600–800 g/cm²; Geptner et al., 1961), which widely occupied north Eurasia in the Late Pleistocene (Kahlke, 1999) may indicate an adaptation to arid savanna, steppe or prairie environments with very sturdy substrates (Bannikov et al., 1961). The footprint load of the steppe bison, including the Yukagir Bison, differs substantially with the weight load of reindeer (140–180 g/cm²), musk ox (325–400 g/cm²), and moose (420–560 g/cm²), which are more adapted to boggy environments, and the latter has special morphological adaptations to foot withdrawal from deep substrates (Guthrie, 1990). The reindeer, musk ox and the domestic horse use hoofs to dig through the snow when feeding in winter (Baskin, 1976; Danilkin, 2005). The modern European bison uses hoofs for digging if snow does not exceed 30 cm depth (Sokolov, 1959), but American bison are reportedly not capable of digging snow with hoofs, and both species prefer using the head for such purposes, pushing the snow with a circular movement of the head (European bison), or swinging it from side-to-side (American

intact with no tears or noticeable scratches detected. It was covered by a fine layer of grey loam with no traces of blue vivianite dusting.

The mummy's skin was measured in several locations where the samples of microflora and soft tissues were collected, as well as along the body ventral cut (Fig. 5). The first set of measurements was taken at the skin cut made along the central line of the ventral part of the body, the middle portions of the neck and breastbone, and the cranial and caudal sections of the abdomen. The other set was taken from the cut along the middle line of the upper occipital and caudal frontals, along the caudal edge of the mandible ascending ramus, the left side of the abdomen, and the sampling hole remaining on the left side of the croup. All areas except the head and croup had flexible skin. The skin on the croup looked drier, and the skin on the back of the head and mandible had tissue bundles stuck to the skull surface and was very difficult to detach.

The collected data was compared to measurements from the modern European bison and the extinct *B. priscus* specimen from Alaska (Blue Babe) (Table 4). The skin thickness of the European bison bulls is similar between young animals (3–14.2 mm) and adults (3–12.7 mm) (Flerov, 1979). The thickest skin develops on the front and back of the head, breastbone area, abdomen, and sides of the torso. The skin of cattle is thickest on the frontals and croup and thinnest on the neck, varying between 3 and 13 mm in different parts of the body (Yudichev et al., 2003).

Table 4
The skin thicknesses of *Bison* taxa.

Skin thickness (mm)	Extinct <i>B. priscus</i>		Modern <i>B. bonasus</i>					
	Yukagir Bison, young male, 4–4.5 years old		Blue Babe adult male, 8–9 years old		Young males, 2–4 years old		Adult males	
	This study		After Guthrie (1990)		After Flerov (1979)			
	Limits	mean	N		Limits	mean	N	
Mandible	1.7–2	1.84	5	10	–	–	–	
Parietals	4.1–4.3	4.2	3	–	12	1	8.7	1
Lower (upper) neck	7.2–9.1	8.18	5	12–13	5.3–12	5	9–12	4
Breastbone	4.4–8	5.44	7	6–8	–	–	8.9–12	3
Cranial and middle abdomen	4.2–7.7	6.06	5	5	7.5–14.2	5	6.1–8	3
Caudal abdomen	4.7–5.1	4.44	5	5	10.0	7	6–7.4	4
Torso side	3.6–4.1	3.58	5	6	5.7–11	3	5–7.9	3
Croup	3.1–3.5	3.32	5	12	4–7	5	4.8–7	4
					6.0		6.2	

bison) to access forage, and utilizing systems of trenches broken in a deep snow for location (McHugh, 1958; Baskin, 1979; Guthrie, 1990). The relative small sizes of hoofs of the Yukagir Bison and other steppe bison specimens (Flerov, 1977; Guthrie, 1990) in comparison to these species may reflect the general adaptation of the steppe bison to relatively firm soils in dry environments. The observed difference in hoof sizes of the rare mummified steppe bison specimens can be attributed to age-related and sex-related individual variations.

3.2.4. Skin

Upon the mummified carcass delivery to Yakutsk and first examination in 2012, the buffy-brown skin appeared completely

Similar to the European bison, the Yukagir Bison had the thickest skin in the breastbone area and abdomen. The thin skin observed on the head and the side of the torso is possibly due to a higher level of mummification of these parts of the body. If the latter is not considered, the thickness of the Yukagir bison skin (4.2–9.1) would be very similar to the young European bison.

The Blue Babe Bison from Alaska had the skin thickness on the main part of its body vary between 3 and 14 mm, which generally falls within the range of cattle and the European bison (Table 4). However, the Blue Babe had unusually thick skin in several regions, including the frontals (22 mm), cheeks (20 mm), and upper neck (16 mm) (Guthrie, 1990). Guthrie interpreted his observations as a male protection enhancement against injuries that might have occurred during bull fights (head butting). These fights were

probably more dangerous in steppe bison, which had longer and more forward-oriented horns in comparison to modern species. The Yukagir Bison would also develop thicker skin in the same regions when it reached full maturity.

3.2.5. Hair

The studies of the Mylakhchin Bison and Rauchua River Bison skin and hair showed that the steppe bison possessed sebaceous glands and the hair was denser and more differentiated by higher number of categories of the guard and underfur hair than its modern counterparts (Sumina, 1977; Chernova and Kirillova, 2013). The description of the East Siberian steppe bison (*B. priscus occidentalis* (Lucas)) pelage is given by Flerov (1977) and is based on hair from several specimens: the female Mylakhchin Bison; the hair samples, photos and slides of the Fairbanks Creek mummy and the “different materials” from the Vilui and Yana Rivers, of which the age differs, the location of the hair origin on the body is guessed, and the season of death is unknown, thereby not providing reliable comparative data. However, the data on the modern bison and the Blue Babe pelage, which died in late fall-early winter (Guthrie, 1990) allows direct comparisons with the Yukagir Bison.

At the time of the Yukagir Bison mummy's discovery, a significant part (at least 40% of the left side) of its body was covered by hair, which had subsequently fallen off during the removal from the site, transportation, and storage in the temporary building in the Yukagir village. The “*in-situ*” mummy had some hair at the bases of both horns and a belt of hair (predominantly brown and dark-brown color) covering most of the neck, throat, basal part of the head (lower jaw), cheeks and areas around the orbits and horn bases (dark-brown/black). The upper part of the head had relatively short under-fur and guard hair in comparison to its lower part. The largest patch of brown hair was covering most of the left side of the torso from the spine line to the frontal part of the lower abdomen, between the shoulder and lumbar areas. Large patches of the hair were present under the tail and on the groin, between the anus and scrotum, and very small haired areas were on the left lateral surface of the left thigh. Relatively stiff hair was covering both fore-legs from the elbows down to the hoofs. The hind legs still retained hair around the hoofs.

At the time of this study in 2012, hair was retained on approximately 15% of the left side of the body (Fig. 3), mostly being frozen to the skin. The right side of the mummy was completely hairless.

The Yukagir Bison retained some hair at the bases of both horns (very light brown) and a belt of hair covering most of the neck (brown), throat (almost black mane about 10–15 cm long), basal part of the head (black/dark-brown), cheeks (dark brown/black about 15–20 cm long) and areas around the orbits (about 5 cm long, dark brown/brown, with some light brown under-fur on upper parts). Most likely, the area between the horns (“bonnet”) had the same fur color covering the horn bases, matching the color of the Blue Babe in this area (Fig. 8). The upper part of the head had relatively short under-fur and guard hair in comparison to its lower part. At the time of this study, the head hair was preserved in very small isolated patches on the right upper side of the snout in front of the orbit and in the area at the base of the right horn and ear, behind the right orbit. A few black guard hairs were retained in the middle part of the left mandible. It is unclear, if the Yukagir Bison had a neck mane.

The sparse patches of hair on the head of the Yukagir bison had a similar pattern of color and general length with the Blue Babe (Fig. 8). However, the latter had a darker frontal part of the head. The reconstructed pelt of the Yukagir Bison head would have had the relatively uniform dark brown/brown hair on its upper part, very light brown bonnet, and an almost black (with dark brown under-fur) mane. This image differs by its overall lighter hair from the adult males of the Wood and Plains bison, which have almost blackish brown hair on the head (Allen, 1876; Reynolds et al., 2003).

The largest patch of relatively uniform in color and length, dense hair (brown/reddish brown, dark brown, black) covered most of the left side of the torso from the spine line, approximately between the shoulder and lumbar areas, and the frontal half of the abdomen. It was felted and crumpled in the neck and abdomen areas. The frontal part of the torso consisted of soft undercoat hair 5–8 cm long interspersed with a large amount of long (12–15 cm) coarse black guard hair located between the front leg line, shoulder tip and the midline of the torso/abdomen. The middle part of the torso was covered by brown and dark brown/black hair. The very rear side, along the mid-thoracic-mid abdomen line, of the remaining torso

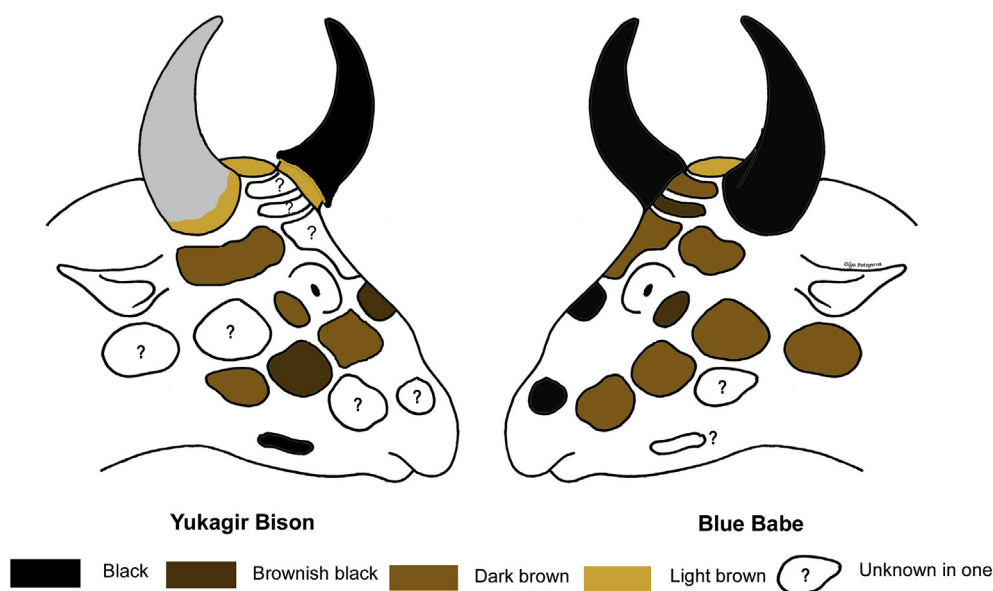


Fig. 8. The hair pattern of the Yukagir Bison (left; this study) and Blue Babe (right; the data from Guthrie, 1990) heads. The data is restricted to few locations. The shown colors are close to descriptions in the text, but do not precisely reflect the actual hair shades (drawing by Olga Potapova). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

pelt, had brown and light brown colored underfur, and it is unknown if the long guard hair (black or brown) in this area was initially present, shed, or simply was not taphonomically preserved. There were areas of frozen bunches of short brown hair and longer dark brown, almost black hair on the belly between the legs, which was not clearly definitive for presence of the breast mane.

Large amounts of the detached hair were collected and saved for this study from the sediments at the Yukagir Bison site, as well as the hair detached from the body during the mummy transportation and storage. This collected hair is represented by the soft underfur hair (3 to 7 cm long, predominantly light brown to brown), and the coarse guarding hair (30–55 cm long, almost black). The longest hair strands most likely came from the frontal body sides (shoulders or hump) where it is longest in all the modern bison species.

The clear boundary formed between the “shoulder cape” and the rest part of the torso by different color (yellow-ochre in summer) and hair lengths, which is typical for the Plains bison (Van Zyll de Jong, 1986; Reynolds et al., 2003), was absent in the Yukagir Bison mummy. In this feature, the Yukagir Bison is very similar with the Wood and European bison with gradual torso hair shortening in the caudal direction, and absence of the clear cape demarcation posterior to the shoulders (Fig. 9).

The hair in the rear part of the Yukagir Bison was almost completely gone with an abrupt “thick hair/bare skin” boundary across the middle of the abdomen separating the front part of the body from the hindquarters. The latter indicates that this part of the body was probably exposed from thawing sediments earlier than the rest of the body, losing the fur that detached at the roots and was not recovered.

A large patch of hair (dark brown) was present on the hips just behind the tail (very dark brown/black), under the tail and on the groin (between anus and scrotum; very dark brown). Very small brown haired areas were on the left lateral surface of the left thigh. Coarse and stiff 5–8 cm long hair (very dark brown/almost black) was covering both forelegs from the elbows down to the hoofs. The extended chaps (leggings) on the forelegs were not present in the Yukagir Bison, and were similar to the short-haired forelegs of the Blue Babe mummy and the modern European and Wood bison. The steppe bison's numerous images depicted in the Paleolithic caves (Guthrie, 1990, 2005) also lack hairy chaps,

probably setting this specimen apart from the American Plains bison, and the Mylakhchin female from eastern Siberia, identified by Flerov (1977) as *B. priscus occidentalis*, both with moderately grown chaps (Flerov, 1977). The short and stiff hair, 5–8 cm long and dark brown, almost black in color was preserved on the Yukagir Bison's lower legs. The hind legs retained coarse and stiff hair around the hoofs.

In summary, the Yukagir Bison body was uniformly covered by relatively thick and short hair on most parts of its body. It had significantly shorter hair than the modern adult American bison, which reportedly has hair length of 2.5 cm on flanks and rear, 5–9 cm on rump and hips, 6.5–16 cm on shoulders and hump, 15–19 cm on chaps, and 30 cm on beard (Meagher, 1986). Hair strands similar to the Yukagir Bison (6–40 cm long, with majority of 7–16 cm long) containing the under-fur and guard hair from unknown body locations was recorded for the Rauchua Bison partial mummy (Chernova and Kirillova, 2013). The overall pattern of the body hair places the Yukagir Bison as similar in appearance to the Wood and European bison.

4. Discussion and conclusions

4.1. Environment and diet

The Yukagir Bison died about 10,500 calendar years ago at the early Holocene–Later Dryas abrupt climatic warming (Khotinsky, 1977; Severinghaus et al., 1998). In northeastern Siberia and Oyagossky Yar particularly, this period is characteristic for thermokarst processes that included thawing and reworking of the permafrost deposits, which were accumulated during the preceding Sartanian glaciation in the eastern section of the arctic shelf (Wetterich et al., 2009).

The bison diet based on the samples identified from the rumen showed that it consisted of a considerable variety of plants dominated by pollen and spores of Poaceae (70–72%), Apiaceae (4.5–13.2%) and mosses with horsetails (4.5–4.5–18.8%) (Geel et al., 2014). Among those are species (*Daucus* sp., *Crithmum maritimum*, Fam. Apiaceae) that are absent in the modern flora of the Yakutian Republic and adjacent territories. The other plants from this Family (*Angelica* sp., *Heracleum* sp., *Peucedanum* sp.),

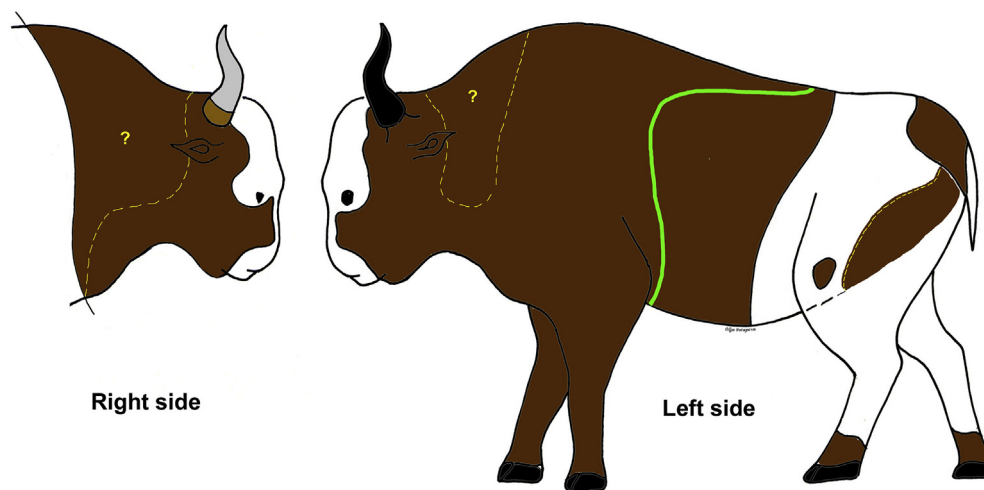


Fig. 9. The hair coverage of the Yukagir Bison: *Brown* (not reflecting the actual color) – the areas where the hair was present (combined data from 2011 to 2014; the “in-situ” and the lab examination photos); *Yellow dashed lines* with question marks—the hair presence at the time of the specimen discovery are uncertain; *Green line*—the area of definite separation in hair composition and color in the American Plains bison but absent in Wood bison (based on the data from Van Zyll de Jong, 1986 and Reynolds et al., 2003) (drawing by Olga Potapova). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

and *Lepidium* sp. (Brassicaceae), *Cirsium* sp., *Tragopogon* sp. (Asteraceae), and *Plantago* sp. (Plantaginaceae)) are predominantly confined to edaphic conditions of the mesophytic meadows, commonly found in river valleys (Perfileva et al., 1991) and found south from the Yukagir Bison Site. The other group of the identified plants *Comarum palustris* (Rosaceae), *Menyanthes trifoliata* (Menyanthaceae) and genus *Utricularia* (Lentibulariaceae), are obligate hydrophytes (Kuznetsova and Zaharova, 2012). The moss, *Calliergon giganteum* (Amblystegiaceae) prefers a similar biotope. The mentioned above vascular plants inhabit the river banks with a steady flow or standing water bodies, such as lakes or deep micro depressions in polygonal tundra, which are widely represented in the modern tundra zone (Perfileva et al., 1991; Aiken et al., 2007; Kuznetsova and Zaharova, 2012; Yakshina, 2012).

Similar data on the gastric content (Kirillova et al., 2013) was obtained from the analysis of the partial mummy of the steppe bison (*B. priscus*) discovered in the Holocene deposits of the Rauchua River in the vicinity of Bilibino, Eastern Siberia. Living at slightly lower latitude (69N, 166E) and being a little younger in geological age (about 8900 BP) than the Yukagir Bison, the Rauchua Bison also preferred feeding mostly on Poaceae grasses, which dominated in pollen spectra along with sedges, forbs (dominant in microremains) and a significant portion of mosses in its diet. The large intestine content of the Mylakhchin Bison from the Indigirka River, dated to about 29,000 BP, showed predominance of herbs (Cypripaceae, Caryophyllaceae, Asteraceae totaling 29%) pollen, with mosses (43%) and spores (Ukraintseva, 1993). The silt samples associated with the Blue Babe Bison also showed the dominance of graminoids and mosses, accompanied with high numbers of birch (*Betula*) and pine (*Pinus*) pollen (Guthrie, 1990).

The environmental conditions of the early Holocene or Preboreal chronozone about 10,300–9000 years ago in Eastern Siberia were manifested by climate warming (Khotinsky, 1977) followed with even more significant warming of the Boreal chronozone (9000–8000 years ago). It led to the expansion of tree and bush vegetation that reached the northernmost boundary ever recorded in Siberia since the last interglacial period (Eemian), with birch species reaching the New Siberian Islands (Kaplina and Lozhkin, 1982; Sher, 1997a,b; Wetterich et al., 2009).

Similar to the Yukagir Bison site (9300 BP, or 10,500 cal BP), the shrub- and forest-tundra landscapes with the lowest representation of steppe-grass vegetation were identified for significant north Siberian region: Taymyr Peninsula around 10,000 BP (Klimanov, 2002), the Laptev Sea shelf about 9300 BP (core samples PZ-2 and PZ-3; Naidina, 2006), the Oyagosskii Yar on the Laptev Sea arctic coast between 11,500 and 8400 BP (particularly dominated by bush alder (*Alnaster fruticosa*), and dwarf birch (*Betula nana*), and willow (*Salix* sp.) (Wetterich et al., 2009; Andreev et al., 2011), and Eastern Siberia about 10,500–8000 years ago (El'gygytgyn Lake; Tarasov et al., 2013).

The comparison of pollen data from the bison digestive tract with those of sediment data directly confirmed that the steppe bison was a selective steppe grazer species, which has been advocated before (Guthrie, 1990). The relatively high ratio of mosses and hydrophilic vegetation plants in the “last meal” of the Yukagir, Mylakhchin (Ukraintseva, 1993) and Rauchua River (Kirillova et al., 2013) Bison might have had behavioral bias, or “before the death” consumption of available vegetation in vicinity of the “death site”. Based on the data of the digestive tract contents of the bison mummies, the animals probably met their deaths close to the water bodies within the mesophytic or lacustrine floodplain meadows and cotton grass-sedge marshes interspersed within deep micro depressions or small lakes that dominated the arctic Siberia highland steppe environment at that time.

4.2. Season of death

The season of death is demonstrated by two sources of data. The analyses of the rumen content indicates occurrence with seasonal vegetation (spring-fall), which was not narrowed down due to a high probability of a strong bias in the pollen representation (Geel et al., 2014). The state of the frontal teeth eruption and wear age indicate the Yukagir Bison to be not older than 4.1–4.5 years, placing its death between spring (April/May) and fall (October/November), assuming it was born in spring.

4.3. Possible causes of death

As mentioned previously (Boeskorov et al., 2013, 2014), the lack of skin damage by predators and the characteristic posture of the Yukagir Bison are indications that the animal died due to a natural cause. The “death” posture of the Yukagir Bison appeared to be similar to the postures of the Blue Babe (legs tucked under the belly) carcass, and particularly the Anyuy Bison mummy that also had the raised and turned to the side head, both of which were reportedly hunted or scavenged (Guthrie, 1990; Nikolskiy and Shidlovsky, 2014). In contrast to these mummies, the Yukagir Bison mummy is intact and death caused by predation has been dismissed. The rapid death of this young and obviously injury-free animal, which had access to food before its death based on the rumen being filled by partly processed vegetation, remains enigmatic.

A natural cause of death of large ungulates is often tympanitis, which is frequently observed in free-range cattle hungry for green and fresh vegetation in spring (Vilner, 1966). Among modern bison, the cases of death caused by tympanitis and lethal poisoning by toxic meadow buttercup (*Ranunculus acris*) and white hellebore (*Veratum* sp.) have been registered in the Caucasus region (Kalugin, 1968).

In northern latitudes, many boreal forest and tundra plants are toxic to large mammalian herbivores. This strategy is applied by plants facing nutrient restricted resources, allocating some resources for growth, and others to toxic chemical defenses (Guthrie, 1990).

Among plants recovered from the Yukagir Bison rumen were the wormwood (*Artemisia* sp.), marsh marigold (*Calpha palustris*, buttercup Family) and horsetail (*Equisetum* sp.), which were represented by a relatively large percent of spores. Each of these plants are lethal for cattle if eaten in early spring in significant quantities, paralyzing the central nervous system, and often causing death within a few hours (Vilner, 1966; Panter et al., 2011). However, several poisonous plant species may cause death if consumed in smaller quantities (Vilner, 1966). Two plants, the marsh marigold and horsetail, are hydrophytes and grow in the wet meadows, waterlogged lowlands and river floodplains, like others that were recovered from the Yukagir Bison rumen (*Menyanthes trifoliata* (Menyanthaceae), *Utricularia* sp. (Lentibulariaceae), *Calliergon giganteum* (Amblystegiaceae), as well as some invertebrates (*Daphnia* sp.)) indicating that before its death the bison grazed on the shore of the pond, or in its vicinity. Among the plant associations of the tundra marshes, ponds and lakes is the well-known water hemlock, *Cicuta virosa* that belongs to the Family Apiaceae (Peshkova, 1996), which comprises six taxa of plants identified from the Yukagir Bison rumen (Geel et al., 2014). Identified in the Holocene deposits of the Indigirka, Yana, and Omoloy Rivers (Giterman, 1963; Tomskaya, 1981), the water hemlock, most likely was also present in the Yana-Indigirka Lowland. Small amounts of this highly poisonous plant consumed in early spring can cause death of a ruminant within two hours (Vilner, 1966; Panter et al.,

2011). There is a possibility that the death of the Yukagir Bison was caused by digesting the mentioned above poisonous plants.

4.4. Species extinction

During the Middle-Late Pleistocene, the extinct species of *Bison priscus* populated vast steppe territories from Western Europe to Beringia. Before this, in the Middle Pleistocene (MIS 8 to 6, ca. 300,000 to 130,000 ka BP), it occupied eastern Beringia and penetrated into central North America during the last interglacial period (130,000–75,000 ka) (McDonald, 1981; Guthrie, 1990; Harrington, 2010). In Beringia, starting approximately 136 ka, this species started to diversify (Shapiro et al., 2004). The subsequent asymmetric genetic exchanges between Eurasian and North American clades gave rise to ancestral *Bison*, which eventually, about 20,000 BP gave rise (through (?) *B. antiquus*; Wilson et al., 2008) to two modern subspecies; the Wood bison (*B. bison athabascae*) and Plains bison (*B. bison bison*). In Eastern Europe, *B. priscus* gave rise to the European bison (*B. bonasus*) that survived there until historic times in a few populations (Flerov, 1979). Both European and American modern species that survived through the severe population bottleneck in the late 18 – beginning of 19th centuries (Roe, 1970; McDonald, 1981) are phenotypically and osteologically distinct (Olsen, 1960; Guthrie, 1970, 1990; Flerov, 1979; Van Zyll de Jong, 1986; Stephenson et al., 2001), but genetically very close (Polziehn et al., 1996; Wilson and Strobeck, 1999).

In Eastern Beringia, the bison of the Clade 4 and 2 survived through the early Holocene, with some specimens dated as late as few hundred years ago in Alaska and Canada (Shapiro et al., 2004; Wilson et al., 2008; Zazula et al., 2009), which are more likely the descendants of the steppe bison. In Western Beringia, a significant relative scarcity of the steppe bison remains was registered for the Bølling-Allerød warm interstadial (about 12400–10800 BP), providing the first indirect evidence of the distribution range collapse (Markova et al., 2015), which previously covered this part of northern Eurasia. Approximately between 11,500 and 8000 BP, this region that was characterized by warmer and high precipitation climates, but the steppe bison that was adapted to live in open landscapes dominated by graminoids (sedges and grasses), persisted largely in unfavorable habitats dominated by the shrub- and forest-tundra vegetation with the treeline (*Alnus*, *Betula*, *Larix*) about to reach the modern arctic coast (MacDonald et al., 2000; Andreev et al., 2004). In the Far East Russian arctic, the interval between 10,500 and 8000 BP revealed the lowest cold steppe (STEP) biome score for the period between 24,000 and 2000 BP (Tarasov et al., 2013). Several finds of the Holocene bison remains in northeastern Asia present valid evidence that the species survived the Pleistocene-Holocene boundary and remained within a vast territory from the Taimyr Peninsula in the west, to the Chukotka Peninsula in the east, and Wrangel Island in the north, in the early Holocene between 8 and 10,000 BP (MacPhee et al., 2002; Vartanyan, 2007; Lazarev et al., 2011; Kirillova et al., 2013) (Table 5, Fig. 10).

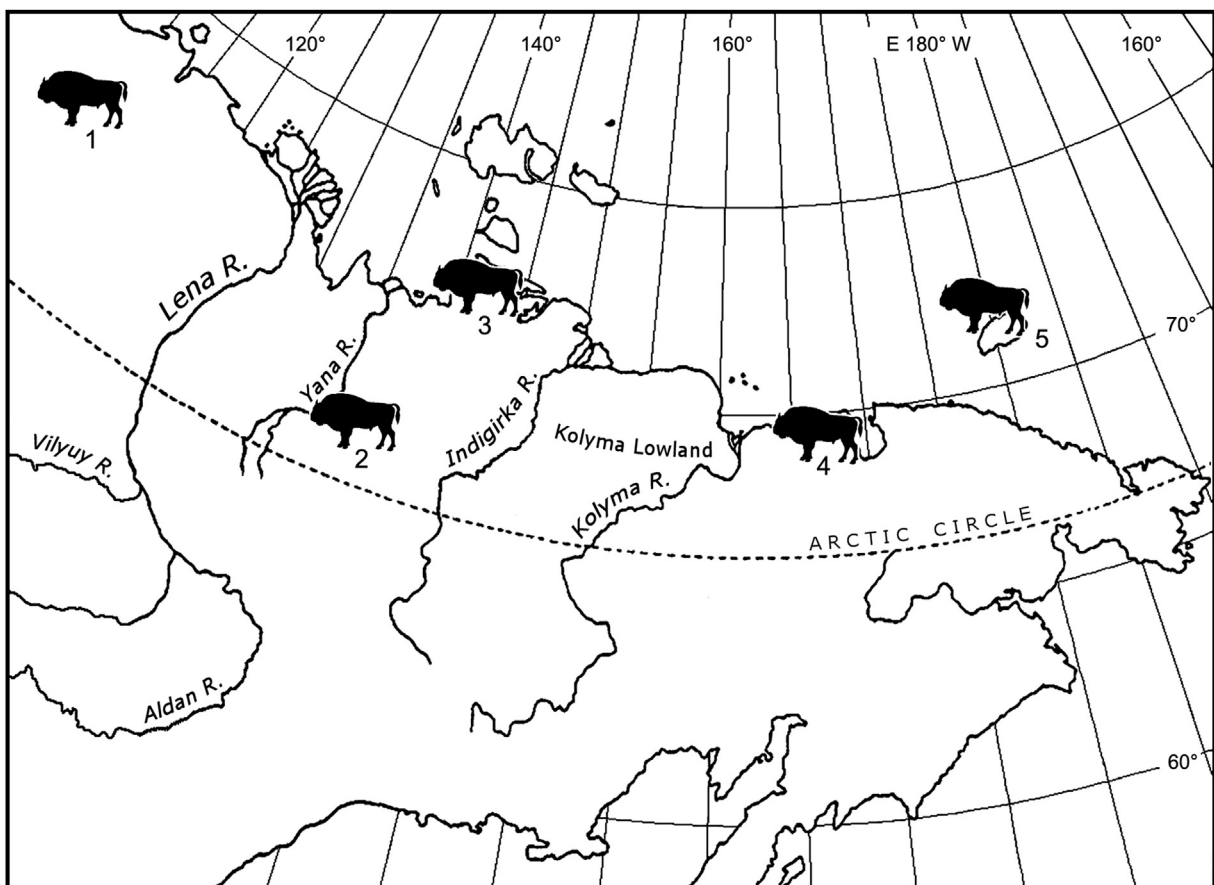


Fig. 10. The localities of the extinct steppe bison, *Bison priscus* found in the Holocene deposits of Eastern Beringia; 1 – Popigay River, 2 – Batagai Bison calf, 3 – Yukagir Bison, 4 – Rauchua Bison, 5 – Wrangel Island (See Table 5).

Table 5
The Holocene remains of steppe bison, *Bison priscus* from Eastern Siberia.

Locations	Absolute age (years ago, Lab)	Dated material	Description	References
1 Popigay River, Taimyr District, Russia	8860 ± 40 (Beta 148623)	Bone	Isolated bone	MacPhee et al., 2002
2 Batagay, Verkhoyansk District, Yakutia	About 8215	Bone	2 months old, frozen mummy	Lazarev et al., 2011; Mammoth Museum data
3 Yukagir bison, Chukchalakh Lake shore, Ust-Yansk District, Yakutia	9310 ± 45 (GrA-53290)	Horn core bone	4–4.5 years old male, frozen mummy	Boeskorov et al., 2013, 2014
4 Rauchua River, Western Chukotka District, Russia	8030 ± 70 (SPb-743)	Skin	6–8 years old, mummy	Kirillova et al., 2013
	9497 ± 92 (AA-101271)	Rib		Kirillova et al., 2014
5 Wrangel Island, Russia	9450 ± 100 (LU-2801)	Rib	Isolated bone	Vartanyan, 2007

This data may indicate that in the Siberian high Arctic the dramatic decrease of the suitable habitats and pastures for the steppe bison during the early Holocene climatic optimum was a major factor causing vegetation change that lead to irreversible population fragmentation and decline. Similar changes of climate such as higher temperatures and precipitation, along with the change of vegetation in the northern Palearctic characterized by boggy tundra in the north and forestation in the mid- and higher latitudes, led to the species' extinction elsewhere. With the beginning of the Boreal chronozone (about 8000 years ago), the isolated populations of the steppe bison survived in the mild climatic optimum and gradually disappeared in changing landscapes and developing forested and tundra belts in northern Siberia.

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