

University of Groningen

A study of a frozen mummy of a wild horse from the Holocene of Yakutia, East Siberia, Russia

Boeskorov, Gennady G.; Potapova, Olga R.; Protopopov, Albert; Plotnikov, Valery V.; Maschenko, Eugeny N.; Shchelchkova, Marina; Petrova, Ekaterina A.; Kowalczyk, Rafal; van der Plicht, Johannes; Tikhonov, Alexey N.

Published in:
Mammal Research

DOI:
[10.1007/s13364-018-0362-4](https://doi.org/10.1007/s13364-018-0362-4)

IMPORTANT NOTE: You are advised to consult the publisher's version (publisher's PDF) if you wish to cite from it. Please check the document version below.

Document Version
Publisher's PDF, also known as Version of record

Publication date:
2018

[Link to publication in University of Groningen/UMCG research database](#)

Citation for published version (APA):

Boeskorov, G. G., Potapova, O. R., Protopopov, A., Plotnikov, V. V., Maschenko, E. N., Shchelchkova, M., Petrova, E. A., Kowalczyk, R., van der Plicht, J., & Tikhonov, A. N. (2018). A study of a frozen mummy of a wild horse from the Holocene of Yakutia, East Siberia, Russia. *Mammal Research*, 63(3), 307-314. <https://doi.org/10.1007/s13364-018-0362-4>

Copyright

Other than for strictly personal use, it is not permitted to download or to forward/distribute the text or part of it without the consent of the author(s) and/or copyright holder(s), unless the work is under an open content license (like Creative Commons).

The publication may also be distributed here under the terms of Article 25fa of the Dutch Copyright Act, indicated by the "Taverne" license. More information can be found on the University of Groningen website: <https://www.rug.nl/library/open-access/self-archiving-pure/taverne-amendment>.

Take-down policy

If you believe that this document breaches copyright please contact us providing details, and we will remove access to the work immediately and investigate your claim.



A study of a frozen mummy of a wild horse from the Holocene of Yakutia, East Siberia, Russia

Gennady G. Boeskorov^{1,2,3} · Olga R. Potapova⁴ · Albert V. Protopopov² · Valery V. Plotnikov² · Eugeny N. Maschenko⁵ · Marina V. Shchelchkova³ · Ekaterina A. Petrova⁶ · Rafal Kowalczyk⁷ · Johannes van der Plicht⁸ · Alexey N. Tikhonov⁶

Received: 16 November 2017 / Accepted: 8 March 2018 / Published online: 17 March 2018
© Mammal Research Institute, Polish Academy of Sciences, Białowieża, Poland 2018

Abstract

The paper presents a description of a rare finding of the partial frozen corpse of the Yukagir horse. Discovered from thawing deposits in northern East Siberia (Yakutia, Russia), its age is confirmed to be Mid-Holocene (about 4600 BP). The mummy had a preserved head with the neck and the back of the torso with the legs and tail. The Yukagir horse was relatively short, with short ears and tail. Compared to the modern breeds, including the Yakutian domestic horse, wild Przewalski's horse, and extinct Lena horse, *Equus lenensis*, the Yukagir horse was closest to the latter, which was also confirmed by studies of the hair microstructure. The pollen and plant remains from the horse's intestines indicated a preference to grasses. The late geological age of the Yukagir horse is an indication that this species survived the Pleistocene–Holocene crisis and lived through the Mid-Holocene in northern Eastern Siberia.

Keywords Lena horse · *Equus lenensis* · Remains of frozen corpse · Morphology · Yakutia · Holocene

Communicated by: Jan M. Wójcik

✉ Gennady G. Boeskorov
gboeskorov@mail.ru

¹ Diamond and Precious Metals Geology Institute, Siberian Branch of Russian Academy of Sciences (SB RAS), 39 Prospect Lenina, Yakutsk, Russia 677980

² Yakutian Academy of Sciences, 39 Prospect Lenina, Yakutsk, Russia 677007

³ North-Eastern Federal University, 48 Kulakovskogo str., Yakutsk, Russia 677013

⁴ Mammoth Site of Hot Springs, SD Inc., 1800 HWY 18 US, Hot Springs, SD 57747, USA

⁵ Borissiak Paleontological Institute, Russian Academy of the Sciences, 123 Profsoyuznaya str., Moscow, Russia 117997

⁶ Zoological Institute, RAS, 1 Universitetskaya quay, Saint Petersburg, Russia 199034

⁷ Mammal Research Institute Polish Academy of Sciences, 17-230 Białowieża, Podlasie Voivodeship, Poland

⁸ Center for Isotope Research, Groningen University, Nijenborgh 4, 9747 Groningen, AG, Netherlands

Introduction

In July 2010, the Yukagir tribe members found remains of the partial, frozen carcass of a presumably Pleistocene horse, named the “Yukagir horse” (Boeskorov et al. 2013), on the northern slope of the Oyagossky Yar on the coast of the Dmitry Laptev Strait in northern Yakutia (N72.690860°, E142.821769°) (Fig. 1).

Oyagossky Yar is the longest Quaternary outcrop on the northern Yakutia, Siberia, Russia, stretching over 100 km from Svyatoi Nos Cape in the west to the Kondratieva River mouth in the east. The “Edoma” Pleistocene permafrost deposits are exposed along the Dmitry Laptev Strait and form terraces that are about 40–50 m high. The western part of the deposits is correlated with the Olyerian Formation (Lower Pleistocene; Velichko 1973; Tomirdiaro 1982), while the eastern part of the outcrop area corresponds to Karginian (47–26,000 BP) and Sartanian (17–16,000 BP) Formations, based on radiocarbon dates of mammal bones (Nikolsky and Basilyan 2003). The Oyagossky Yar yielded remains from almost all large mammal species characteristic of the Late Pleistocene in

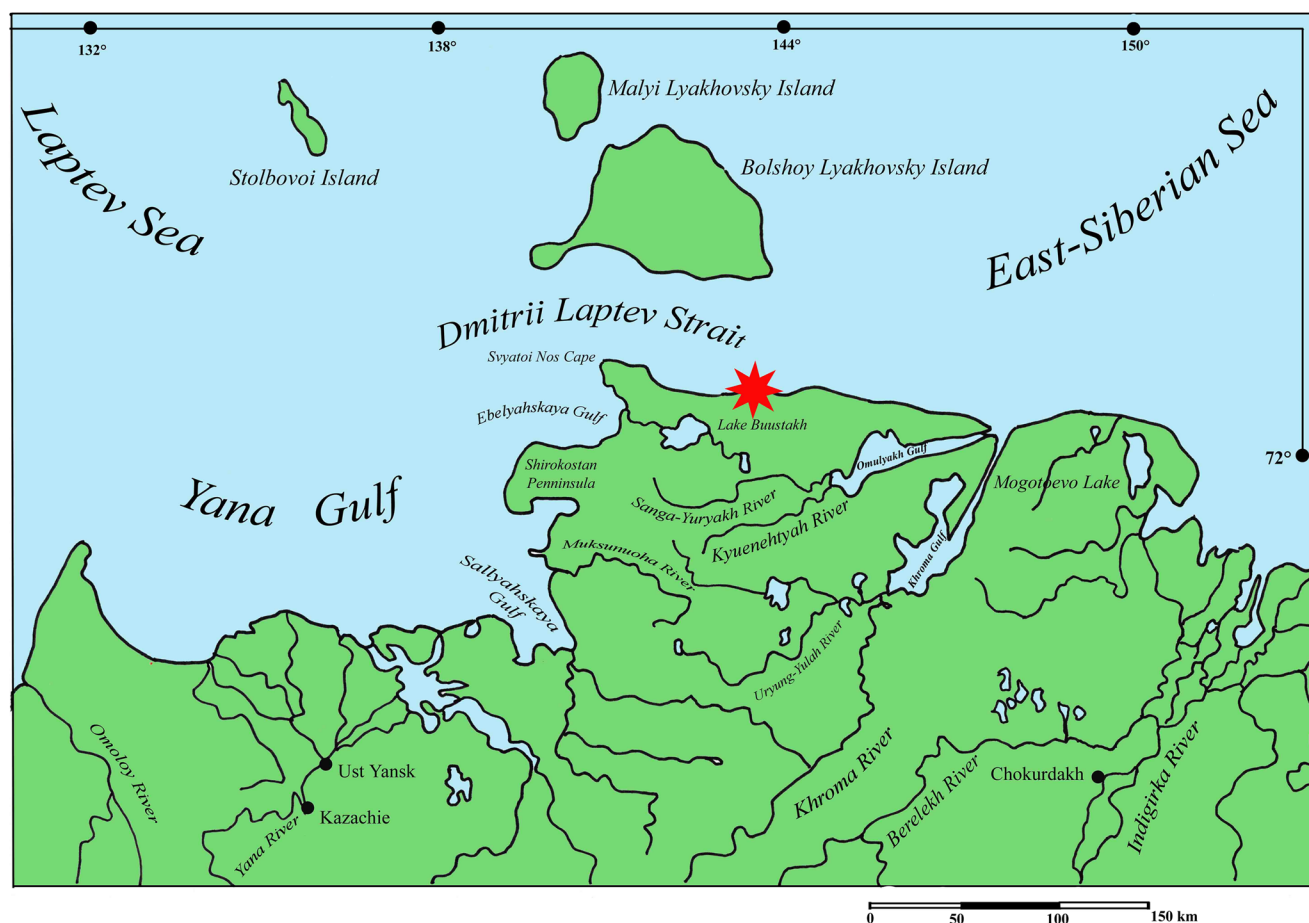


Fig. 1 The location of the Yukagir horse site in northern Yakutia

Yakutia, including *Canis lupus*, *Alopex lagopus*, *Gulo gulo*, *Ursus sp.*, *Panthera spelaea*, *Mammuthus primigenius*, *Coelodonta antiquitatis*, *Equus lenensis*, *Rangifer tarandus*, *Cervus cf. elaphus*, *Alces sp.*, *Bison priscus*, *Ovibos pallantis*, and *Saiga sp.* (Tomirdiaro 1982; Sablin 1991; Nikolsky and Basilyan 2003).

The horse was found within about 50 m of the Yuka Mammoth Site, dated to 39,440–38,850 cal BP. However, despite the vicinity of the sites, the horse age appeared to be much younger, about 4630 ± 35 BP (GrA-54209; Boeskorov et al. 2013). This date falls at the end of the second half of the Atlantic period, the warmest period during the Holocene that lasted from about 6000 to 4500 BP, and just before a significant cooling that was recorded in many sites in northern Eurasia (Velichko et al. 1997).

Material and methods

Material

Shortly after its recovery in the summer of 2010, the Yukagir horse mummy remains were brought to a

dugout ice storage in the Yukagir village where it was kept under freezing conditions. Later that year, the mummy, owned by the Yukagir Community and led by the Community leader Mr. Vassily Gorokhov, was loaned to the Yakutian Academy of Sciences, Yakutsk (catalog no. OYu 2; Department of Mammoth Fauna Studies,) for this study. In January 2012, the horse mummy remains (Fig. 2) were delivered to Yakutsk and tested for infectious diseases (foot and mouth disease, anthrax, brucellosis, rinderpest, etc.); all of which yielded negative results. The results of this paper are based on the studies of the exterior morphology of the horse mummy conducted in February, 2012, and February, 2014.

Determination of sex and age

The absence of canines in the lower jaw suggests that Yukagir horse was a mare. The state of the incisors' wear, according to the standard method of domestic horse age determination assumed in Russia (Liskun 1949), corresponds to a 5-year old individual (Fig. 3a). Therefore, the Yukagir horse was an adult mare.

Fig. 2 The remains of the Yukagir horse carcass



Descriptions and measurements

The horse mummy carcass was described and measured following the methods proposed for large, wild mammals by Gromov et al. (1963) and for domestic mammals by Liskun (1949).

For comparison, we measured body parts in seven modern domestic Yakut horses (*Equus caballus* spp.) bred in Khangalassky and Megino-Kangalassky Districts of Yakutia.

Radiocarbon dating

Radiocarbon analysis of the Yukagir horse bone was carried out by the University of Groningen, the Netherlands (code GrA). This laboratory uses AMS (Accelerator Mass Spectrometry) for measurements of the ^{14}C concentration. Radiocarbon dates are reported in BP, a defined timescale by

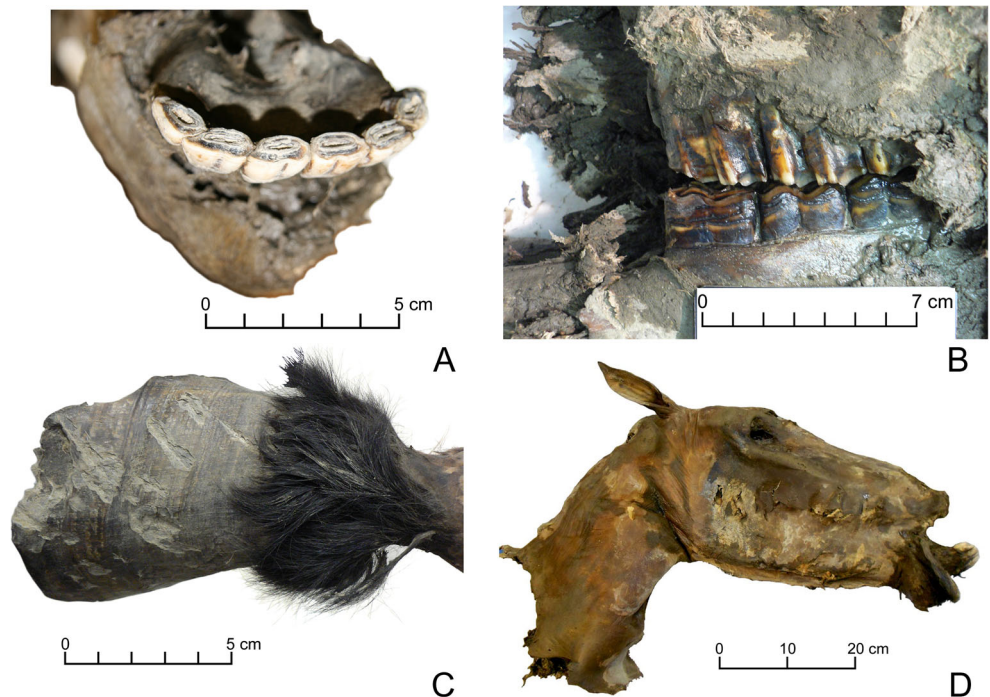
convention (Mook and van der Plicht 1999). The ^{14}C dates need to be calibrated to obtain absolute ages. This is done using the internationally accepted calibration curve IntCal13 (Reimer et al. 2013). This then results in the final calendar dates for the fossil. They are reported in cal BP, which is calendar years before 1950 AD.

For the Yukagir horse, the measured ^{14}C date is 4630 ± 35 BP (GrA-54209). The calibrated date is 5450–5310 cal BP (1-sigma), in the second part of the Atlantic period.

Results: description of exterior morphology

The Yukagir horse carcass was preserved in two large pieces: the head with the neck, a part of the torso with some internal organs, hind limbs, and tail (Figs. 2 and 3). The missing part of the snout appeared to be ripped off the fore limbs with the

Fig. 3 The Yukagir horse mummy parts of the body: **a** lower jaw incisors in wear, **b** upper and lower molars, right side view, **c** left hoof, hind limb, **d** right side of the head



frontal part of the torso had numerous torn holes, and gaps and stripes on the hide indicated that the horse was hunted and/or scavenged by a large predator, possibly a bear or wolf.

The frozen mummy's skin was intact on the hind limbs, on a large part on the head, on the back of the, neck and on the sides of the torso. The predominant color of the skin was dark brown, and the skin was mummified and very stiff. The skin thickness varied from 1 to 5.1 mm in different parts of the body. The thinnest skin measured on the top of the head (1.0–1.4 mm, average 1.16 mm), and the thickest skin was found on the belly (3.7–5.1 mm, average 4.52 mm), gluteal region (3.3–5.1 mm, average 3.9 mm), thigh (3.4–4.1 mm, average 3.82 mm), and front of the neck (2.6–3.0 mm, average 2.76 mm). In the domestic horse breeds, the skin thickness in the different parts of the body varies between 1 and 7 mm (Akaevsky 1975).

The mummy had both the ears and eye sockets preserved. The left ear was deeply dried out and had lost its natural shape, while the right side was well-preserved with a characteristic, relatively long, funnel-shaped ear with a pronounced tip (Fig. 3d). The right ear opening was relatively narrow with protruding front and rear edges. The length of the ear from the lower edge of the ear notch to its apex was 14 cm; the maximum width of the ear was 7 cm. If compared to the *E. przewalskii* and modern domestic Yakut horse (Table 2), the Yukagir horse ear was shorter.

The dimensions of the right eye socket were anterior-posterior length of 44 mm and height of 19 mm. The left eye socket measured anterior-posterior length of 49.6 mm and height of 20 mm. Both sockets had mummified eyeballs, which were palpable under the skin.

Short (45–70 mm), dark-brown and, in some places, black hair was preserved only on the distal parts of the limbs, below the tarsal-phalanx joint (Fig. 3c). Mammoth, bison, and horse carcasses frozen in permafrost usually have most of the body hair detached from the skin, but often, the hair on the distal parts of the limbs is retained.

The microstructure of the Yukagir horse hair was examined using a scanning electron microscopy and was compared with the microstructure of modern domestic horse hair (including the Yakut domestic horse), as well as with the hair collected from the mummies of the extinct Lena horse (*Equus lenensis* Russanov, 1968) found in Yakutia: Selerikanskaya horse, Maksunuohskaya horse, Dyukarskaya horse, and Cherskaya horse (Chernova et al. 2015). These mummies were recovered from the deposits of the Late Pleistocene Karginian interstadial (38,500–29,500 BP; Arslanov and Chernov 1977; Vereschagin and Lazarev 1977; Lazarev 2002; Lazarev 2008). The hair test confirmed that, while having had general similarities to other breeds, the Yukagir horse hair microstructure is closest to that of the Lena horse. The hair core is shifted to the side of the rod and is characterized by a cellular-mesh structure, with the presence of polymorphic cavities and thick, rough septa with short

outgrowths and large perforations. All of these structures extend along the stem rather than across it (Chernova et al. 2015), confirming that the Yukagir horse belongs to the Lena horse species, *E. lenensis*.

We managed to estimate some of parameters of the horse's skull by measuring the un-skinned and un-fleshed horse head. Most of the Yukagir horse skull measurements fall within the variation range of *Equus lenensis* Russanov, 1968, which was studied by Lazarev (1980) and Kuzmina (1997). However, the Yukagir horse was relatively large-headed and possessed a relatively large dentition (Fig. 3b, Table 1).

The estimated height at the hip of the Yukagir horse is similar to average *E. przewalskii*'s hip height (Table 2), but slightly shorter than that of the Selerikan horse mummy, *E. lenensis* from the Upper Indigirka River basin (about 38,000 BP) (Table 2) and average hip height of the modern Yakutian mares from the Verkhoyansk District (134.34 cm) and Sredne-Kolymsk District (138.12 cm) (Gabyshev 1957). The distal parts of the Yukagir horse hind legs were relatively large.

The tail was preserved intact but was missing hair. Tail length from the base to the tip was 36.5 cm. The thick base of the tail gradually tapered towards the tip. The circumference of the base of the tail was 19 cm, in the middle 12 cm, and at the end (5 cm from the tip) 6 cm. The width of the tail base was 8 cm. It was relatively short in comparison to Przewalski's horse and modern Yakutian one (Table 2).

The left hoof (Fig. 3c) was larger and wider than hoofs reported for the Late Pleistocene horse (*E. lenensis*), *E. przewalskii*, and the domestic Yakutian breed (Table 2). Development of wide hoofs is an adaptation in terrestrial mammals to reduce weight load and allow them to move comfortably in lowland wetlands and boggy tundra, as well as enhance their ability to dig down to the grass under snow during snowy winters (Formozov 1946).

Discussion and conclusions

The Yukagir horse species affiliation

There are several records of the extinct Pleistocene horse remains (possibly *E. lenensis*) from the Holocene (ca. 4600–2000 BP) in Central and Eastern Siberia, indicating that this species inhabited the wide area from Western Taymyr Peninsula to the Indigirka River in the east and from Bolshoi Lyakhovsky Island in the north to the Verkhoyansk Mountain Ridge in the south (Table 3).

The Pleistocene horse remains have never been dominant in the Holocene assemblages, and this likely indicates that the species survived through the Late Holocene in small populations in scattered and isolated steppe refugia.

Table 1 Head sizes of the Pleistocene and Holocene horse remains from Siberia

Measurements (mm)		Yukagir horse, Holocene (this study)	<i>Equus lenensis</i> , Late Pleistocene (Lazarev 1980; Kuzmina 1997) <u>Limit</u> Mean
Skull and maxilla teeth			
Parietal length		~ 540	511.6–542.5 528.7
Height of the maxilla in front of P2		~ 95	96.4–106.6 99.9
Width at the back edges of the orbits		~ 200	201.2–224.0 204.8
Width at the mandibular articular processes		~ 195	180.6–208.0 193.1
Maximum width of the neurocranium		~ 120	110.1–117.7 113.5
Length of the upper premolar crowns row P2–P4		~ 90	83.5–92.5 89.5
Upper P2	Length	39	37–42 38.4
	Width	26.8	23.5–27 25.8
Upper P3	Length	31	27–31 28.8
	Width	29.1	28–30 29.0
Upper P4	Length	30.1	25.3–28 27.1
	Width	29.8	27.5–33 29.5
Mandible with teeth			
Length (projected) from the tip of pars incisiva to caudal edge of angulus mandibulae		> 400 (Estimated)	394.2–422.5 398.1
Length of the mandible from caudal edge of articular process to the frontal side of the incisors		~ 450 (Estimated)	413.8–451.8 398.1
Length of diastema		~ 100 (Estimated)	70–100 90.9
Height of the mandible at the articular process		~ 200 (Estimated)	188.3–240.1 221.0
Width between lateral incisor crowns (I3)		72.6	54.8–67.1 62.1
Minimum width of the mandible (in diastema)		~ 50 (Estimated)	37.7–46.3 42.2
Length of the lower premolar crowns row (P2–P4)		~ 105 (Estimated)	77–104.1 87.4
Lower P2	Length	31.3	29–37 32.6
	Width	16.5	14.5–19 16.1

Some Russian scholars (Cherskiy 1891; Gabyshev 1957; Lazarev 1980) believed that the short-stature, domestic Yakut horse represented the survived Late Pleistocene Lena horse. However, this astounding morphological similarity between these horses could be a result of the parallel, independent

evolution of adaptation to cold climate (Kuzmina 1997; Boeskorov 2000). In the 1990s, the method of protein mobility electrophoresis ruled out affiliation between these horses and confirmed the modern Yakut horse kinship to some Central Asian breeds of the domestic horse *Equus caballus*

Table 2 Comparison of the size of the body parts of Yakutian horse mummies to those of some modern species of horses

Measurements (cm)	Fossil horse <i>Equus lenensis</i>		Modern horses			
	Yukagir horse, ♀ (this study)	Selerikan horse, ♂ adult, 38,000 years BP (Vereschagin and Lazarev 1977)	Przewalski's horse <i>Equus przewalskii</i> , ♂♂ and ♀♀ adult (Bannikov 1954; Balaschov 1961; Vereschagin and Lazarev 1977)	Modern domestic Yakutian horse <i>Equus caballus</i> spp., ♀♀ adult (this study)	<i>n</i>	
			Limit Mean	Limit Mean		
Ear length	14	–	14.8–18.6 16.68 (<i>n</i> = 21)	13–17 15.0 ± 1.06	4	
Hip height	132	136	125–143 132.75 (<i>n</i> = 4)	130–147* 138.12 ± 0.246	133	
Tail length (hair on the tail tip not included)	36.5	~34 (Estimated, this study)	38–60 –	39–63 51.07 ± 4.03	7	
Length of the distal rear limb (from the heel to the back side of the hoof)	59	50	48–52 –	52–59 56.08 ± 1.21	6	
Metatarsus diaphysis circumference	24.5	24	17.5–19 –	–	–	
Phalanx III (coffin bone), rear limb	Dorsal length	4.5	5.5	5.6	5.4**	1
	Maximum width	8.3	7.15	7.0	7.3**	1
	Plantar length	~8.0 (Estimated)	6.81	7.1	6.38**	1
Rear limb hoof	Sole surface length	19	13	12.5	11–14 12.64 ± 0.45	7
	Maximum width	15	12	11.3	10.5–14.5 12.67 ± 0.71	6

*After Gabyshev 1957; **After Vereschagin and Lazarev 1977

L. (Guriev 1998; Tikhonov et al. 1998.). The lack of genetic relationship between the Lena Pleistocene horse and modern Yakut breed was finally proven recently by DNA analyses (Librado et al. 2015).

The environment

The Yukagir horse lived in a period characterized by a moister climate due to the ongoing marine transgression. The annual

precipitation level was 200 mm more than the present precipitation in Yakutia, which caused an expansion of moisture-demanding conifers (*Pinus sibirica*, *Abies sibirica*, *Picea obovata*) to the north, where currently, only drought-resistant conifers (*Larix* spp.) exist (Monserud et al. 1998; Pisaric et al. 2001). The local vegetation consisted of open larch woodland with shrub alder, alternating with dwarf birch and dwarf willow growths (Kaplina and Lozhkin 1982; Velichko et al. 1997; Andreev et al. 2011). A significant cooling at the end of this

Table 3 The Holocene remains of the wild horses, *Equus* from the northern Eastern Siberia, Russia

Locations	Absolute age (years ago, Lab)	Dated material	Description	References
1 Bolshoy Lyakhovsky Island, Yakutia	2220 ± 50 (GIN-10687)*	Bone	Isolated bone	Kuznetsova et al. 2001
2 Moychoon Lake, Khromskaya Gulf, Yakutia	2310 ± 80 (LU-1084)**	Bone	Adult mare, frozen mummy remains	Lazarev 1980
3 Kotelny Island, Yakutia	3000 ± 45 (GIN-13237)	Bone	Isolated bone	Kuznetsova and van der Plicht 2009
4 Agapa River, east of the mouth of the Yenisei River	3250 ± 60 (GIN-3243)	Bone	Isolated bone	Sulerzhitsky and Romanenko 1997
5 Batagay, Verkhoyansk District, Yakutia	4400 ± 35 (GrA-48709)***	Bone	Foal, frozen mummy	Lazarev et al. 2011
6 Bykovsky Peninsula, east of the mouth of the Lena River, Yakutia	4610 ± 40 (GIN-10256)	Bone	Isolated bone	Kuznetsova et al. 2001
7 Oyagosskii Yar, coast of the Dmitry Laptev Strait, Yakutia	4630 ± 35 (GrA-54209)	Bone	Adult mare, ~5 years old, partial frozen mummy	Boeskorov et al. 2013

*GIN Geological Institute, RAS, Moscow, Russia; **LU Leningrad University, Leningrad (now St. Petersburg), Russia; ***GrA Groningen University, Groningen, The Netherlands

period (4000–3000 BP) implied the southern shift of vegetation zones and a retreat of the forest vegetation (*Picea*, *Larix*, *Pinus*) to the south (McDonald et al. 2000).

In contrast to the composition of the vegetation, the palynological spectrum of the samples from the Yukagir horse colon shows a predominance of grass (97.4%), with a low percentage of tree (1.9%) pollen and spores (0.6%). The grass is represented by true grasses (91.6%), sedges (4.5%), and others. The analyses of macroremains, which included fragments of leaves and stems of monocots, with rare remains of mosses (genus *Bryales*) and grass seeds (family Poaceae), confirmed that the Yukagir horse strongly preferred grasses for its diet (Gravendeel et al. 2014). The Yukagir horse diet included more “grasses” than the diet of the early Holocene Yukagir and “Chukotka” Bisons (Boeskorov et al. 2016; Kirillova et al. 2013), which lived in unfavorably changing landscapes and vegetation that were shifting towards forest and swampy tundra.

The Yakutian Holocene horses lived not in the characteristic Arctic steppe with dense soil and dry climate, but, rather, in the moist grassy tundra. The Yukagir horse had specific adaptations for living in conditions of tundra with its softer ground and a high level of snow in winter based on the wide hooves with large areas of weight support and long sections of the distal parts of the limbs. The short ear and tail reflected the general trend in mammals of the Far North as expressed in the ecogeographical “Allen’s Rule.” Thus, on the basis of morphological similarity and identification of skull size and the microstructure of hair, we can state that the horse belonged to the extinct Lena horse species that survived the Pleistocene-Holocene crisis.

Some morphological adaptations such as relatively small body size, long limbs, and large hooves, and possibly smaller than *Bison priscus* size herds, were important factors for the survival of the Pleistocene horse during the Late Holocene.

Acknowledgements The authors thank Julia Mossman (Hot Springs, SD, USA) for editing the text.

References

- Akaevsky AI (1975) Anatomiya domashnikh zivotnykh. Izdatelstvo Kolos, Moscow (in Russian)
- Andreev A, Schirmermeister L, Tarasov P, Ganopolski A, Brovkin V, Siegert C, Hubberten H-W (2011) Vegetation and climate history in the Laptev Sea region (Arctic Siberia) during Late Quaternary inferred from pollen records. *Quat Sci Rev* 30:2182–2199
- Arslanov HA, Chernov SB (1977) Ob absolyutnom vozraste Selerikanskoy loshadi. In: Vereschagin NK (ed) Fauna i Flora Antropogena Severo-Vostoka. Nauka, Leninrad, pp 76–78 (in Russian)
- Balaschov NT (1961) Die Zucht der Przewalski-Pferde in Askania-Nova. In: Veselovsky Z (ed) Equus. Proceedings of the 1-st Intern. Symp. on Przewalski Horse. Nakladatelstvi Československe Akademie ved, Praha, ss 59–84
- Bannikov AG (1954) Mlekopitayushie Mongolskoy Narodnoy Respubliki. Izdatelstvo Vysshaya Shkola, Moscow (in Russian)
- Boeskorov GG (2000) K istorii taksonomicheskikh issledovaniy pozdneplejstocenovyyh loshadej Vostochnoy Sibiri i vklad professora A.A. Braunera v jeto napravlenie. In: Lobkov VA (ed) Chleniya pamjati A.A. Braunera. Materialy Mezhdunarodnoi Konferentsii. Astroprint, Odessa, pp 76–85 (In Russian)
- Boeskorov GG, Protopopov AV, Mashchenko EN, Potapova OR, Kuznetsova TV, Plotnikov VV, Grigoryev SE, Belolyubskii IN, Tomshin MD, Shchelchkova MV, Kolesov SD, van der Plicht J, Tikhonov AN (2013) New findings of unique preserved fossil mammals in the permafrost of Yakutia. *Dokl Biol Sci* 452:291–295
- Boeskorov GG, Potapova OR, Protopopov AV, Plotnikov VV, Kirikov KS et al (2016) The Yukagir bison: analysis of a complete frozen mummy of the bison, *Bison priscus* from the early Holocene of Northern Eurasia. *Quat Int* 406:94–110
- Chernova OF, Boeskorov GG, Protopopov AV (2015) Identifikatsiya volos golocenovoi mumii Jukagirskoi loshadi, *Equus* spp. *Dokl Akad Nauk. Obshchaya Biol* 462(3):373–375 (In Russian)
- Cherskiy ID (1891) Opisanie kolleksii posletretichnykh mlekopitayushchikh zivotnykh, sobrannykh Novo-Sibirskoyu ekspeditsiyey v 1885–1886 gg. *Zapiski Akademii Nauk* 65(1):1–706 (In Russian)
- Formozov AN (1946) Snezhnyi pokrov kak faktor sredy, ego znachenie v zhizni mlekopitayushchikh I ptic SSSR. Materialy k poznaniyu fauny I flory SSSR. Moscovskoye obshchestvo ispytateley prirody, Moscow (In Russian)
- Gabyshv MF (1957) Jakutskaya loshad. Jakutskoe Knizhnoe Izdatelstvo, Jakutsk (in Russian)
- Gravendeel B, Protopopov A, Bull I, Duijm E, Gill F, Nieman A, Rudaya N, Tikhonov AN, Trofimova S, van Reenen GBA, Vos R, Zhilich S, van Geel B (2014) Multiproxy study of the last meal of a mid-Holocene Oyogos Yar horse, Sakha Republic, Russia. *The Holocene* 24:1288–1296. <https://doi.org/10.1177/0959683614540953>
- Gromov IM, Gureev AA, Novikov GA, Sokolov II, Strelkov PP, Chapskii KK (1963) Fauna SSSR. Mlekopitayushie. Opredelitel mlekopitayushchikh. Chast 2. (Kitoobraznye, Khishnye, Lastonogie, Napanopalye, Parnopalye). Moscow-Leningrad, Akademiya Nauk SSSR (in Russian)
- Guriev IP (1998) Evolutsiya domashnei loshadi. *Nauka i Obrazovanie* 1: 51–57 (in Russian)
- Kaplina TN, Lozhkin AV (1982) History of the development of vegetation in the coastal lowlands during the Holocene of Yakutia. Development of Nature in the Pleistocene and Holocene. Nauka, Moscow, pp 207–220 (in Russian)
- Kirillova IV, Zanina OG, Kosintsev PA, Kulkova MA, Lapteva EG et al (2013) First find of the Holocene bison (*Bison priscus* Bojanus, 1827) frozen carcass on Chukotka. *Dokl Ross Akad Nauk* 452: 466–469 (in Russian)
- Kuzmina IE (1997) Loshadi Severnoi Evrazii ot Pliocena do Sovremennosti. Zoological Institute, RAS Press, Sankt-Petersburg (in Russian)
- Kuznetsova TV, van der Plicht J (2009) Pozdneplejstotsenovyye i golotsenovyye loshadi Severnoy Yakutii. In: Barskova IS, Nazarova VN (eds) 200 Let Otechestvennoy Paleontologii. PIN RAN, Moscow, pp. 65–66 (in Russian)
- Kuznetsova TV, Sulerzhitsky LD, Siegert Ch (2001) New data on the “mammoth” fauna of the Laptev Shelf Land (Arctic Siberia). Proceedings of the First International Congress “The World of Elephants”. Rome 16–20 October 2001, pp. 289–292
- Lazarev PA (1980) Anthropogeovye loshadi Yakutii. Nauka, Moscow (in Russian)

- Lazarev PA (2002) Kadastr mestonakhozhdeniy fauny mlekopitayushchikh pozdnego kaynozoya Yakutii. Nauka, Novosibirsk (in Russian)
- Lazarev PA (2008) Krupnyye mlekopitayushchiye antropogena Yakutii. Nauka, Novosibirsk (in Russian)
- Lazarev PA, Grigoriev SE, Plotnikov VV, Savvinov GN (2011) Nakhodki unikalnykh ostatkov trupov loshadi I bizona v Verkhoyanskom rayone Yakutii. *Probl Reg Ecol* 4:13–18 (in Russian)
- Librado P, Der Sarkissian C, Ermini L, Schubert M, Albrechtsen A, Fumagalli M et al (2015) Tracking of the origins of Yakutian horses and the genetic basis for their fast adaptation to Subarctic environments. *PNAS* 112(50):E6889–E6897. <https://doi.org/10.1073/pnas.1513696112>
- Liskun EF (1949) *Exterier sel'skokhozyaystvennykh zhyvotnykh. Gosudarstvennoye izdatel'stvo sel'skokhozyaystvennoy literatury, Moscow* (in Russian)
- McDonald GM, Velichko AA, Kremenetski CV, Borisova OK, Goleva AA et al (2000) Holocene treeline history and climate change across Northern Eurasia. *Quat Res* 53:302–311
- Monserud RA, Tchepakova NM, Denissenko OV (1998) Reconstruction of the mid-Holocene palaeoclimate of Siberia using a bioclimatic vegetation model. *Palaeogeogr Palaeoclimatol Palaeoecol* 139:15–36
- Mook WG, van der Plicht J (1999) Reporting ^{14}C activities and concentrations. *Radiocarbon* 41:227–239
- Nikolsky PA, Basilyan AE (2003) Mys Svyatoy Nos—opomyi razrez chetvertichnykh otlozheniy Yano-Indigirskoy nizmennosti. In: Balakireva (ed) *Estestvennaya istoriya Rossiyskoy vostochnoy Arctiki v Pleistocene I Holocene*. GEOS, Moscow, pp 5–13 (in Russian)
- Pisaric MFJ, MacDonald GM, Velichko AA, Cwynar LC (2001) The late-glacial and post-glacial vegetation history of the northwestern limits of Beringia, from pollen, stomata and megafossil evidence. *Quat Sci Rev* 20:235–245
- Reimer PJ, Bard E, Bayliss A, Beck JW, Blackwell PG, Bronk Ramsey C, Buck CE, Cheng H, Edwards RL, Friedrich M, Grootes PM, Guilderson TP, Haflidason H, Hajdas I, Hatté C, Heaton TJ, Hoffmann DL, Hogg AG, Hughen KA, Kaiser KF, Kromer B, Manning SW, Niu M, Reimer RW, Richards DA, Scott EM, Southon JR, Staff RA, Turney CSM, van der Plicht J (2013) IntCal13 and Marine13 radiocarbon age calibration curves, 0–50,000 years cal BP. *Radiocarbon* 55:1869–1887
- Sablin MV (1991) Vozmozhnoye sootnoshenie vidov krupnykh mlekopitayushikh v faune tundra-stepi Severnoy Yakutii. Abstracts 6th Soveshaniya “Izucheniye Mamontov I Mamontovoi Fauny”. Zoological Institute, St. Petersburg, pp 48–49 (in Russian)
- Sulerzhitsky LD, Romanenko FA (1997) Vozrast I rasprostraneniye “Mamontovoy fauny” v polyarnom regione Azii. *Kriosfera Zemli* 1(4):12–19 (in Russian)
- Tikhonov VN, Kotrjen EG, Knyazev SP (1998) Populyatsionno-geneticheskie parametry aborigennykh Yakutskikh loshadei v svyazi s filogeniey sovremennykh porod domashnei loshadi *Equus caballus* L. *Genetika* 6:796–809 (in Russian)
- Tomirdiaro SV (1982) Arkticheskiy i subarkkticheskiy tipy merzlotnogo lessa I vydeleniye edomnykh formaciy shelfovogo I kontinentalnogo tipov. Nauka, Moscow (in Russian)
- Velichko AA (1973) *Prirodnyi process v Pleistocene*. Nauka, Moscow (in Russian)
- Velichko AA, Andreev AA, Klimanov VA (1997) Climate and vegetation dynamics in the tundra and forest zone during the Late Glacial and Holocene. *Quat Int* 41/42:71–96
- Vereschagin NK, Lazarev PA (1977) Opisaniye chastey trupa i skeletnykh ostatkov selerikanskoy loshadi. *Trudy Zoologicheskogo Instituta, AN SSR* 63: 85–185 (in Russian)