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Malikov, D. G., Shpansky, A. V., & Svyatko, S. V. (2020). New data on distribution of musk ox *Ovibos moschatus* in the Late Pleistocene in the south-east of Western Siberia and the Minusinsk Depression. *Russian Journal of Theriology*, 19(2), 183-192. <https://doi.org/10.15298/RUSJTHERIOL.19.2.09>

Published in:
Russian Journal of Theriology

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

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New data on distribution of musk ox *Ovibos moschatus* in the Late Pleistocene in the south-east of Western Siberia and the Minusinsk Depression

Dmitriy G. Malikov*, Andrey V. Shpansky & Svetlana V. Svyatko

ABSTRACT. New data on the timing of the maximum distribution and diet of *Ovibos moschatus* in south Siberia in the Late Pleistocene are presented. The southern border of the range of musk ox in the West Siberian Plain during the Karginian time (Denekamp Interstadial, DEN) was located in the Tomsk Ob' River region. During the maximum cooling of the Sartanian time (LGM), the southern boundary of the range was limited by the Minusinsk Depression and the foothill plain of the Altai Mountains. Musk oxen of Tomsk Ob' River region had a normal diet similar to that of Pleistocene musk ox and reindeer, and slightly different from the diet of modern musk ox. The diet of musk ox from the Minusinsk Depression was different from that of both the Pleistocene and modern musk oxen, and it was close to that of horses and woolly rhinos. It is possible that the diet of musk ox from the Minusinsk Depression had higher content of in grass and willow.

How to cite this article: Malikov D.G., Shpansky A.V., Svyatko S.V. 2020. New data on distribution of musk ox *Ovibos moschatus* in the Late Pleistocene in the south-east of Western Siberia and the Minusinsk Depression // Russian J. Theriol. Vol.19. No.2. P.183–192. doi: 10.15298/rusjtheriol.19.2.09.

KEY WORDS: musk ox, Late Pleistocene, Minusinsk Depression, West Siberian Plain, geographical distribution, stable isotope analysis, paleodiet.

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Новые данные о распространении овцебыка *Ovibos moschatus* на юго-востоке Западной Сибири и в Минусинской котловине в позднем неоплейстоцене

Д.Г. Маликов*, А.В. Шпанский, С.В. Святко

РЕЗЮМЕ. Приведены новые данные о времени максимального распространения и питании овцебыка *Ovibos moschatus* на юге Сибири в позднем неоплейстоцене. В каргинское время (интерстадиал Денекампа, DEN) южная граница ареала овцебыка в пределах Западно-Сибирской равнины располагалась в Томском Приобье. В максимальное похолодание сартанского времени (LGM) южная граница ареала ограничивалась Минусинской котловиной и предгорной равниной Алтая. Овцебыки Томского Приобья имели нормальный рацион, схожий с рационом плейстоценовых овцебыков и северных оленей, и немного отличный от рациона современных овцебыков. Диета овцебыка из Минусинской котловины отличалась от рациона как плейстоценовых, так и современных овцебыков и была близка к рациону лошадей и шерстистых носорогов. Возможно, в его рационе было высокое содержание травы и ивы.

КЛЮЧЕВЫЕ СЛОВА: овцебык, поздний неоплейстоцен, Минусинская котловина, Западно-Сибирская равнина, географическое распространение, анализ стабильных изотопов, палеодиета.

Introduction

Among the animals of the mammoth fauna, musk ox *Ovibos moschatus* Zimmermann, 1780 is of a particular interest. Along with reindeer and arctic fox, it represents

the arctic group of species which penetrated deep into south of Western and Central Siberia (Shpansky, 2018). Extralimital records of musk ox are a reliable indicator of harsh climatic conditions with shallow snow cover and low summer temperatures based on ecology of the extant *O. moschatus* as an extremely stenobiont species regarding humidity and temperature (Danilkin, 2005).

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Therefore, fossil records of musk ox are useful for paleoclimatic and paleolandscape reconstructions, assuming similar ecologies throughout the history of the lineage. Isotopic studies of fossils and recent musk oxen indicate that in the Pleistocene ecology of musk ox can be more diverse than at present (Raghavan *et al.*, 2014). For a better understanding of the ecology and history of the species, the study of a larger number of fossil remains from the pre-existing species range is essential.

In this respect the records of musk oxen from southern parts of Siberia with varying taxonomic and chronological identifications are of particular interest. An incomplete skull of the *Praeovibos* sp. is one of the oldest records of musk ox remains in the West Siberian Plain. It was discovered by Zinova (1972) on the Irtysh River shore upstream from the mouth of the Ishim River and attributed to the Late Eopleistocene (=late Early Pleistocene in modern terminology). A possible older record is the fragment of upper jaw of *Ovibovini* gen. indet. from the Bachat quarry of the Kuznetsk Basin; it was found in the Mokhovo Formation deposits and dates to the first half of Eopleistocene = Upper Villafranchian (Foronova, 2001; Vislobokova, 2008). For the Lower Pleistocene deposits, Bobkovskaya (2002) mentions the fragments of two skulls of *Praeovibos priscus* Staudinger, 1908 from the Gornofilino location (the right bank of the Irtysh River, near the Gornopravdinsk Village). Remains of *O. moschatus* were found in deposits of the second half (MIS 2–3) of the Upper Pleistocene (Shpansky, 2018; Stefaniak *et al.*, 2019).

Few papers have been focused on the boundaries of the maximum distribution and dynamics of the musk ox habitat in North Asia in the Late Pleistocene (Gromova, 1935; Kahlke, 2014; Markova *et al.*, 2015). The majority of musk ox remains in this area are located north of 56° N. Belyaeva (1933) mentions a single bone on the Irtysh River shore below Omsk City (above 55° N). In the Novosibirsk Ob' River area, musk ox remains were recovered from the beach of Chik River location, which is supposedly older than MIS 3 (Lobachev *et al.*, 2011). The most southern record of musk ox in Siberia comes from the Minusinsk Depression (Gromova, 1935).

The majority of musk ox finds in Siberia have no stratigraphic references (Tikhonov, 1994). As such, the stratigraphy and paleoecology interpretation of these materials is difficult. This paper presents new data on time range and ecology of *O. moschatus* in the south-east of West Siberia and the Minusinsk Depression based on ¹⁴C dating and stable carbon (δ¹³C) and nitrogen (δ¹⁵N) isotope analysis.

Materials and methods

Musk ox fossil remains from the following museums were investigated: Minusinsk Martyanov Museum (Minusinsk, MMM) — MMM 7207/132, found in 1924 near the city of Minusinsk; Tomsk Regional Museum of Local Lore (Tomsk, TRM) — TRM 10300/168. Location: Tom River shore, above the Chernilshchikovo Village (56°36' N, 84°51' E), 30 km north-west from Tomsk, May 1958 (Fig. 1).

Skull measurements (Fig. 2) were taken point to point, using a caliper, with a precision to the nearest 0.1 mm according to the standard scheme of measurements of the bovine skull (Driesch, 1976), adapted for the *Ovibos* skull. AMS ¹⁴C dating and stable carbon (δ¹³C) and nitrogen (δ¹⁵N) isotope analysis were carried out in the 14CHRONO Centre for Climate, the Environment, and Chronology (Queen's University Belfast, UK), lab. code — UBA. For comparison, we used stable isotope data for mammals of the similar geological age from Europe (Bocherens *et al.*, 2015; Krajcarz *et al.*, 2016), Western and south of Central Siberia (Iacumin *et al.*, 2000, and our data) and recent musk ox from Greenland (Raghavan *et al.*, 2014). We evaluated our ¹⁴C and isotope data in the context of regional climatic stratigraphic horizons (Volkova & Babushkin, 2000) and climatic records following Markova *et al.* (2015).

Results

The nearly complete skull from Minusinsk (MMM 7207/132) belonged to an adult animal (Fig. 3). Its frontal sutures are fully obliterated, facial sutures are barely noticeable, and only nasal sutures are clearly visible. Only the premaxillary bones, teeth of the right side and left P2 are absent.

The skull is low, slightly elongated in the anterior-posterior direction, especially in the facial region. Maxillary bones are remarkably narrowed at the level of infraorbital foramen, with subsequent widening anteriorly. The posterior edge of the nasal bones reaches the level of the anterior orbit and M2. The lacrimal bone has a structure characteristic to *O. pallantis* H. Smith, 1827 (Tikhonov, 1994) in that it slightly narrows towards the orbit, without abrupt interceptions (Fig. 3). The pit on the lacrimal is shallow. The anterior upper protrusion of the squama temporalis forms a straight suture with the lacrimal bone, and in the posterior third the sutures between these bones are obliterated.

Orbits are round, widely spaced, their edges extend beyond the level of the lateral walls of the horn cores, their walls are thick, thinned in front, orbital wall with a small hole. The horncore bases are elongated in the anterior-posterior direction and are separated by a groove; width between horncore bases is 6 mm. The area approaching the position of the horncore tips is directed medially. Fossa temporalis is short and shallow. The sutura coronalis is not pronounced. The occiput is low, almost rectangular in shape. Occipital bone is slightly narrowed anteriorly, its posterior muscular tubercula are well defined and separated by cutouts on the sides of the mastoid processes. The occipital condyles are widely set apart, their articular surfaces do not merge, and the foramen magnum is narrow. Teeth of the left side (P3-M3) are preserved within the skull, with some damage on the buccal side. The masticatory surface is heavily worn, the P3 and M1 enamel loops (basal column) are almost completely worn down. Basal column on M2 and M3 is well expressed. The presence or absence of the basal column on M1 is impossible to determine due to the

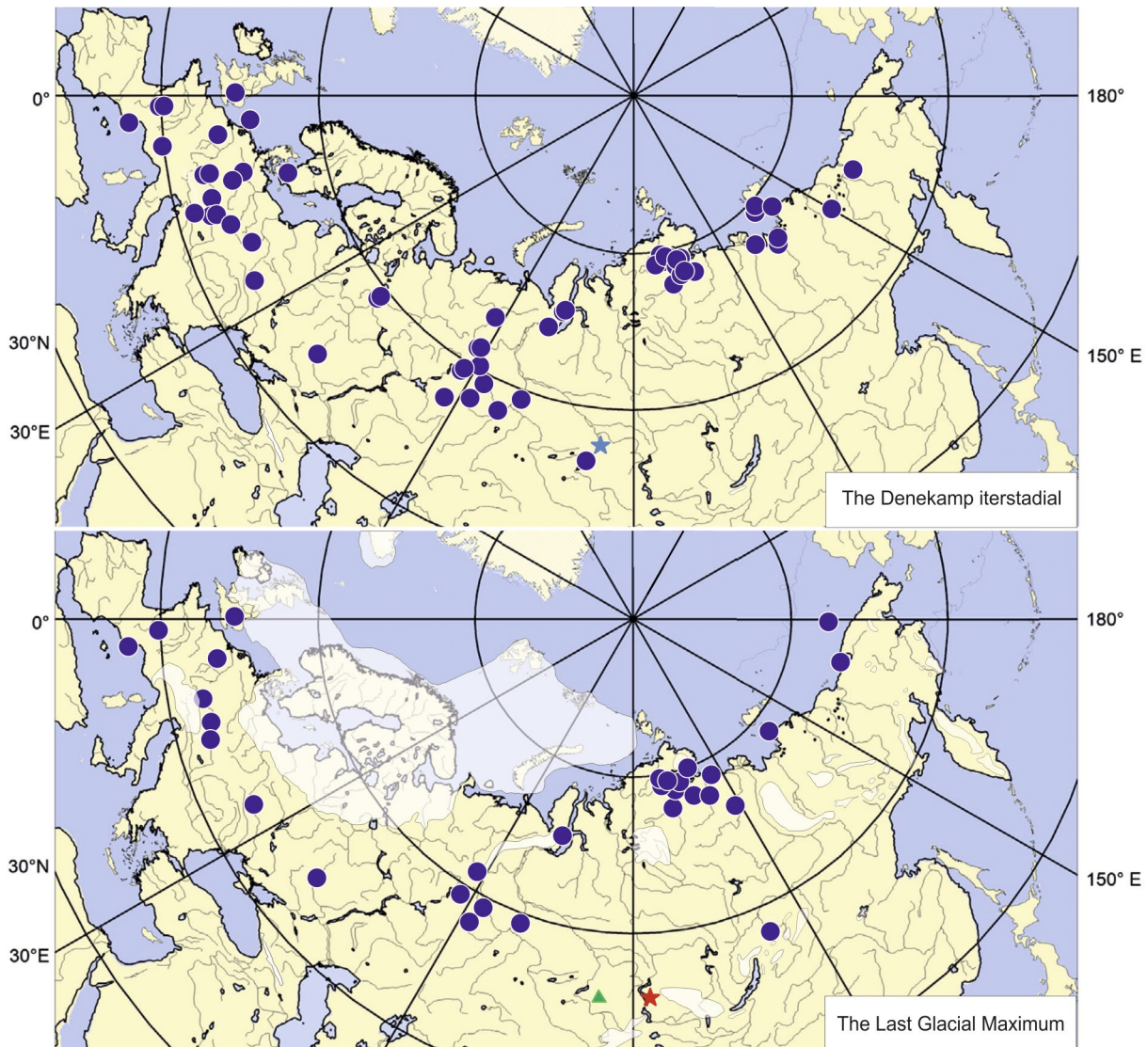


Fig. 1. Geographical distribution of dated musk oxen in Europe and North Asia (adapted from Markova *et al.*, 2015): blue star — Chernilshchikovo, red star — Minusinsk, green triangle — Chumysh River (Vasiliev *et al.*, 2018).

severe tooth wear. The presence of the basal column is a characteristic feature for *O. pallantis* (Tikhonov, 1994).

In the skull from Chernilshchikovo (TRM 10300/168; Fig. 3) frontal sutures are obliterated, facial sutures are clearly visible, nasal sutures are open and ossa nasale are absent. The facial section bones (prae-maxillare and nasale) are broken off; the buccal wall of the left maxillare is damaged; the horncore tips are broken off. Teeth are missing from alveoli. The forehead surface is flat. The orbit walls are thick and round. On the front wall of the orbit there is a fossa, on the frontal surface side there is a well-developed tuberculum. Fossa temporalis is oval. The horncore base is saddle-shaped, wide, square, bent as if embracing the neurocranium, going down vertically below the zygomatic bone. The outer horncore surface is rough, uneven. Occipital foramen is round.

The size of the skull from the Minusinsk specimen is rather small; in most parameters it is exceeded by the animals from Siberia and the European Plain (Tab. 1). At the same time, the length of dentition of the individual from the Minusinsk Depression is slightly larger than that of samples from Siberia and Eastern Europe (Tab. 1). This is especially obvious from premolars. The skull from Chernilshchikovo is the largest among the known Eurasian musk oxen (Tab. 1); the horncores, orbital width, width between the buccal walls of the teeth and the occiput are especially massive.

The morphological structure of the studied musk ox skulls corresponds to the *O. pallantis* species. However, analysis of both ancient and modern musk ox DNA revealed the genetic homogeneity of fossils and modern forms (Campos *et al.*, 2010). Therefore, we classify our materials as *O. moschatus*.

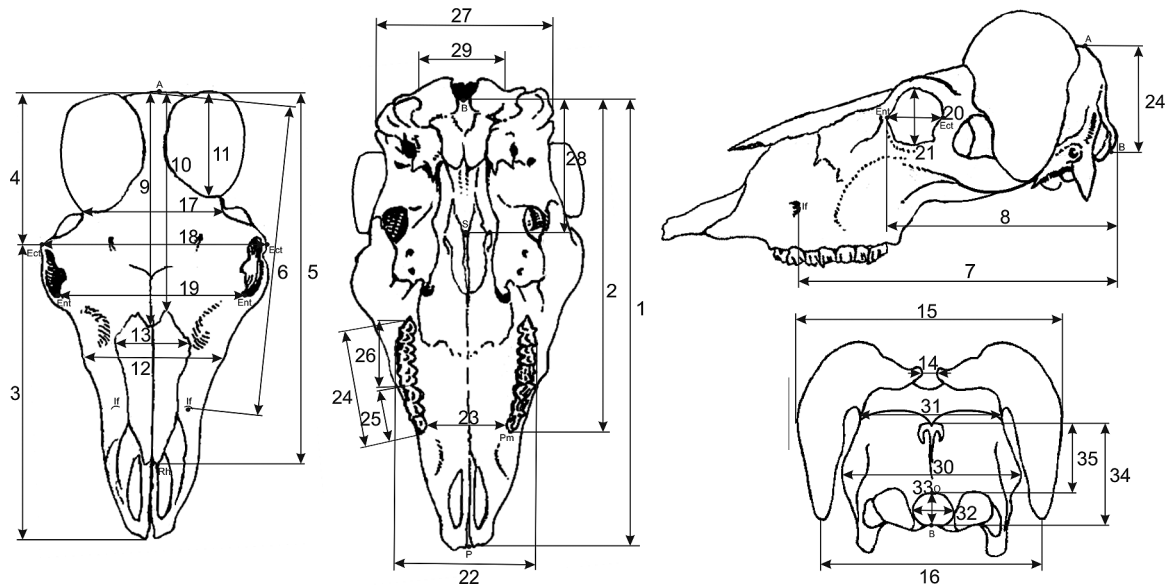


Fig. 2. Scheme of skull measurements in *Ovibos moschatus* (modified after Danilkin, 2005, measurements adapted from Driesch, 1976): 1 — basal length (basion — prosthion); 2 — short skull length (basion — premaxilla); 3 — facial length (ectorbitale — prosthion); 4 — cranial length (akrocranial — ectorbitale); 5 — short upper cranial length (akrocranial — rhinion); 6 — length from akrocranial to infraorbitale of one side; 7 — length from occipital condyles to infraorbitale of the same side; 8 — length from basion to entorbitale of the same side; 9 — median frontal length (akrocranial — nasion); 10 — small frontal length (from akrocranial to median point of intersection of the line joining the oral points of the frontals); 11 — greatest (oro-aboral) diameter of the horncore base; 12 — facial breadth (across the facial tuberosities); 13 — greatest breadth across the nasal; 14 — least breadth between the bases of the horncores; 15 — greatest tangential distance between the outer curves of the horncores; 16 — least distance between the horncore tips; 17 — least frontal breadth (breadth of the narrowest part of the frontal aboard of the orbits); 18 — greatest frontal breadth (between ectorbitale); 19 — least orbital breadth (between entorbitale); 20 — greatest inner length of the orbit (ectorbitale — entorbitale); 21 — greatest inner height of the orbit (perpendicular to m.20); 22 — greatest palatal breadth — across the outer borders of the alveoli; 23 — least palatal breadth — across the inner borders of P2 alveoli; 24 — upper cheek teeth row length P2-M3; 25 — upper premolars row length on alveoli P2-P4; 26 — upper molars row length on alveoles M1-M3; 27 — greatest mastoid breadth (between otion); 28 — basicranial axis (basion — synsphenion); 29 — greatest breadth of occipital condyles; 30 — greatest breadth at the bases of the paraoccipital processes; 31 — smallest width of occiput; 32 — greatest breadth of the foramen magnum; 33 — height of the foramen magnum (basion — opisthion); 34 — greatest height of occiput (akrocranion — basion); 35 — least height of occiput (akrocranion — opisthion).

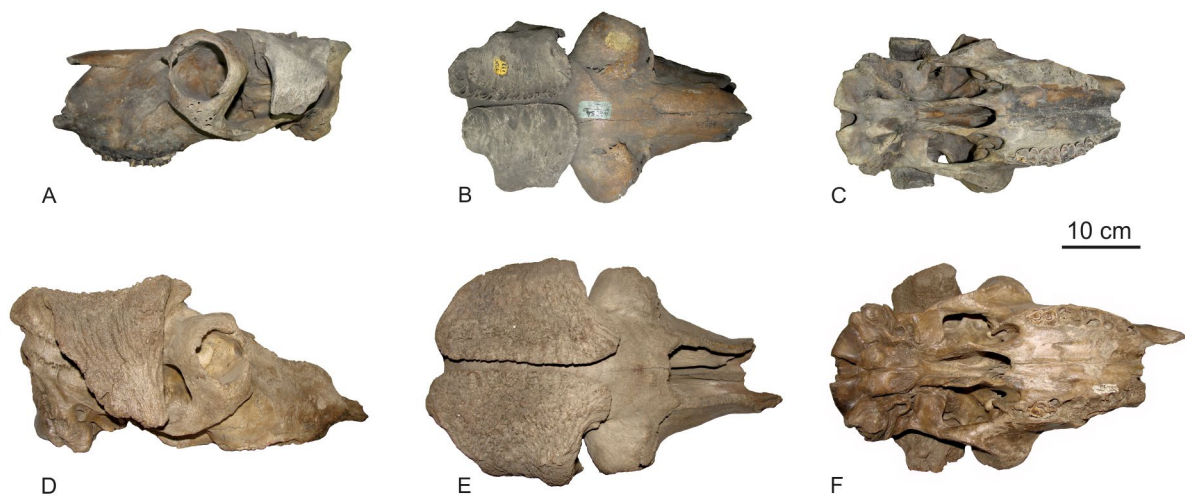


Fig. 3. *Ovibos moschatus* skulls: Minusinsk skull (MMM 7207/132) — A, B, C; Chernilshchikovo skull (TRM 10300/168) — E, F, D. The lateral (A, E), dorsal (B, F) and basal (C, D) views.

Table 1. The measurements (mm) for the fossil *Ovibos* skulls from Northern Eurasia.

	European Plain (Petrova, 2009)				Western Siberia				Yakutia (Petrova, 2009)			
	Measurements GMM KSU 362	NW European Plain ZIN 26691	Verkhnekamsk phosphate mine	NE European Plain ZIN 8693	Minusinsk MMM 7207/132	Chemilshchikovo TRM 10300/168 (Shpansky, 2000)	TSU 2155 (Aleksieva, 1980)	Tolstrinoe ZIN 6489 (Petrova, 2009)	Udzha ZIN 32176	Bykovsky Peninsula ZIN 25621	Laptev Strait ZIN 30134	
1	–	–	–	–	>393.0	>503.0	–	–	–	–	–	
2	360.0	–	–	–	340.0	–	–	340.0	–	350.0	–	
3	–	–	–	–	~255.0	–	–	–	–	252.6	–	
4	270.0	237	–	–	225.0	–	–	230.0	–	–	–	
5	–	400	–	–	403.0	–	–	–	–	–	–	
6	365.0	–	–	–	350.0	–	–	335.0	–	–	–	
7	340.0	–	–	–	258.0	–	–	330.0	–	–	–	
8	280.0	292.0	–	–	229.0	–	–	–	–	–	–	
9	265.0	237.2	–	244.8	223.0	–	–	257.0	284.2	265.0	–	
10	283.0	252.2	–	262.4	244.0	–	–	277.0	322.0	–	–	
11	–	–	–	–	178.0	242.0	160.0	–	–	–	–	
12	165.0	–	–	–	160.0	–	–	138.3	–	–	–	
13	83.0	73.4	–	68.9	77.0	–	–	–	76.4	70.6	–	
14	–	5.7	–	15.7	6.0	12.0	11.0	7.2	11.7	7.1	12.4	
15	–	228.0	–	–	238.0	–	–	254.0	–	251.0	268.6	
16	260.0	–	–	–	~220.0	297.0	–	–	–	–	233.0	
17	–	124.3	–	146.5	143.0	163.5	126.0	141.2	164.0	143.6	148.0	
18	264.6	247.4	252.0	239	255.0	295.0	–	252.4	269.2	253.5	~266.8	
19	170.0	–	–	–	190.0	–	–	158.0	–	~159.5	–	
20	62.3	68.0	70.0	–	64.0	66.5	–	54.6	–	61.2	–	
21	53.7	–	61.2	–	66.0	57.5	–	60.3	–	58.4	–	
22	–	–	–	–	143.0	154.0	–	–	–	–	–	
23	–	–	–	–	66.0	93.5	–	–	–	–	–	
24	131.2	–	–	–	147.0	151.5	–	135.4	–	144.7	–	
25	55.3	–	–	–	50.5	–	–	46.9	–	–	–	
26	94.4	–	–	–	95.0	–	–	90.3	–	–	–	
27	187.2	176.8	191.0	–	–	–	–	179.1	198.2	165.5	177.2	
28	–	–	–	–	125.0	–	–	–	–	–	–	
29	114.3	108.1	–	–	107.0	–	–	114.1	117.9	98.1	124.4	
30	–	–	–	–	174.0	203.0	190.0	–	–	–	–	
31	144.5	125.3	–	136.1	141.0	–	148.0	127.8	138.6	126.3	136.4	
32	26.5	26.5	27.8	26.7	27.0	31.0	–	24.6	26.9	25.0	31.1	
33	27.9	37.1	29.5	30.9	33.0	37.0	–	30.5	31.1	32.2	35.8	
34	139.2	117.2	–	129.7	105.0	164.0	102.0	121.2	144.3	124.0	121.1	
35	125.4	100.7	–	107.8	83.0	134.0	–	95.1	122.5	101.6	97.4	
Tooth												
P3	Length	18.2	–	15.3	–	22.0	–	–	17.3	–	–	–
	Width	17.1	–	20.0	–	17.0	–	–	15.9	–	–	–
P4	Length	18.9	–	–	–	17.0	–	–	17.1	–	–	–
	Width	22.5	–	–	–	18.3	–	–	18.4	–	–	–
M1	Length	24.8	–	20.7	–	21.0	–	–	23.9	–	–	–
	Width	24.2	–	20.0	–	23.0	–	–	22.1	–	–	–
M2	Length	30.5	–	26.8	–	27.0	–	–	30.9	–	–	–
	Width	25.8	–	–	–	23.3	–	–	19.5	–	–	–
M3	Length	38.8	–	36.3	–	45.0	–	–	37.5	–	–	–
	Width	24.6	–	24.7	–	23.7	–	–	21.7	–	–	–

The skull from the Minusinsk Depression does not have exact geographic and stratigraphic provenance (Malikov, 2015). The Pleistocene mammal bone remains found in the Minusinsk Depression are usually light gray and gray-yellow, but the musk ox skull is brown. Based on other remains with similar preservation found with bones of *Mammuthus primigenius* Blumenbach, 1799 in the Malaya Minusa Village (Minusinsk District, Krasnoyarsk Region), we assume that the studied musk ox skull maybe was found near the same village, in sediments of the Minusinka River (~53°43' N, 91°47' E).

The obtained radiocarbon (^{14}C) date for this skull (Tab. 2) corresponds to the maximum cooling of the last glaciation (LGM). The date of the Chernilshchikovo skull indicates that this animal lived during the Karginian interstadial (DEN).

Stable isotope analysis

The stable nitrogen and carbon isotope analysis of the skulls revealed interesting results. The isotopic composition of the skull from Chernilshchikovo (Fig. 4) is close to that of the reindeer *Rangifer tarandus* L., 1758 and

musk ox *O. moschatus* remains from Europe (Bocherens *et al.*, 2015; Krajcarz *et al.*, 2016). A similar type of subsistence and selectivity of fodder are characteristic to both species. Thus, isotopic data suggests the presence of normal conditions for the Chernilshchikovo musk ox. Stable isotope data for some large mammals from the south of Western Siberia obtained by authors and others (Iacumin *et al.*, 2000; Raghavan *et al.*, 2014; Jürgensen *et al.*, 2017) show high degree of similarity with the isotopic composition of *O. moschatus*, *R. tarandus*, and *Saiga tatarica* L., 1766 (Tab. 3). The differences have been recorded for *Coelodonta antiquitatis* Blumenbach, 1799 and *M. primigenius* with higher variability of the isotopic composition in Western Siberia than in conspecifics in Europe (Fig. 4). This may indicate regional features in the nitrogen and carbon isotopic ratios, or differences in the animal's palaeodiet.

On the contrary, the musk ox from the Minusinsk Depression revealed a deviation from the norm, as its diet was closer to that of horses and woolly rhinos and different from fossil musk oxen (including one from Chernilshchikovo), recent *O. moschatus* and reindeer (Fig. 4). It remains an outlier even when compared with data for the Pleistocene European (Bocherens *et al.*,

Table 2. AMS ^{14}C dates for remains of *Ovibos moschatus*.

Site	Collection No.	Lab. code	^{14}C age BP	Cal BP 95.4%	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	C/N _{atm}
Minusinsk	MMM 7207/132	UBA-37843	20725±156	25410–24480	–20.1	4.8	3.17
Chernilshchikovo	TRM 10300/168	UBA-38454	29603±451	34623–32814	–19.0	3.2	3.26

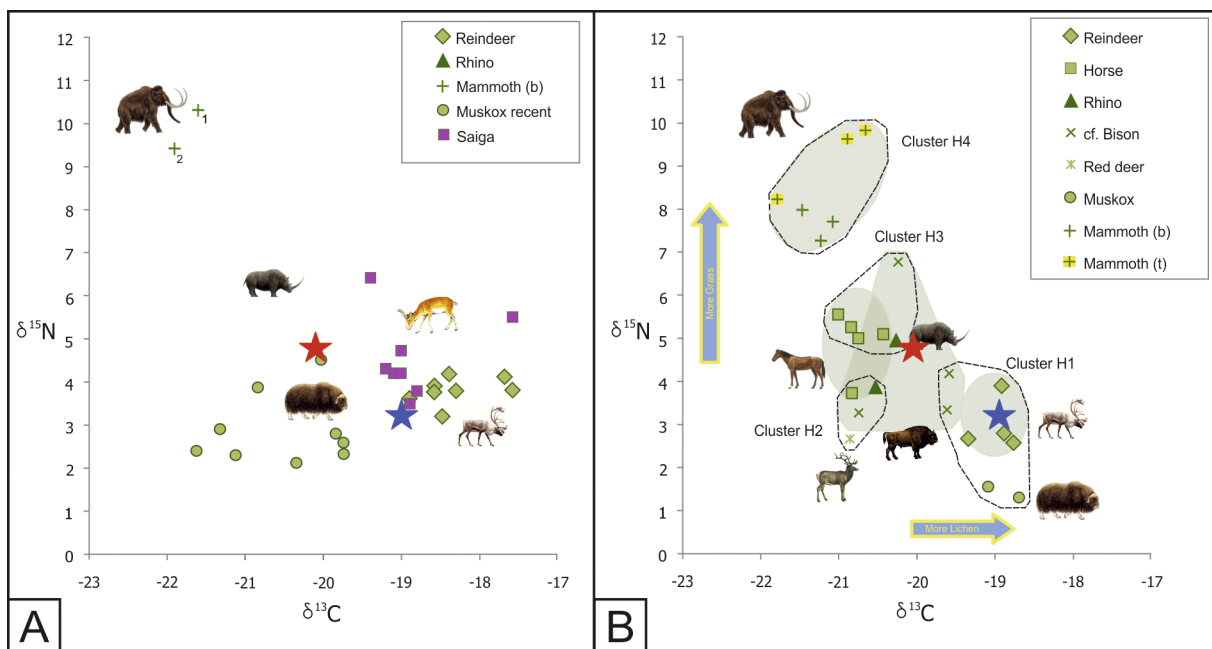


Fig. 4. Ratios of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of bone collagen of Siberian *Ovibos moschatus* (Chernilshchikovo — blue star, Minusinsk — red star) compared to mammals of Western Siberia, recent musk oxen from Greenland (Raghavan *et al.*, 2014) (A) and Central Eastern Europe (B) (Bocherens *et al.*, 2015).

Table 3. Results of stable isotope analysis of fossil herbivorous mammals from Siberia.

Museum abbreviations: MMM — Minusinsk Martyanov Museum, Minusinsk; TRM — Tomsk Regional Museum of Local Lore, Tomsk; TSU — Tomsk State University, Tomsk; PM TSU — Paleontology Museum of the Tomsk State University, Tomsk; GMM KSU — Geological and Mineralogical Museum of Kazan State University, Kazan; ZIN — Zoological Institute, Russian Academy of Sciences, Saint Petersburg; GIN — Geological Institute of the Russian Academy of Sciences, Moscow.

Site and collection No.	Lab. code	%coll	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	C:N _{at}	Reference
<i>Ovibos moschatus</i>						
Minusinsk (Minusinsk depr.) — MMM 7207/132	UBA-37843	8.7	-20.1	4.8	3.17	this paper
Chernilshchikovo (Tomsk reg.) — TRM 10300/168	UBA-38454	4.6	-19.0	3.2	3.26	this paper
<i>Coelodonta antiquitatis</i>						
Sergeevo (Tomsk reg.) — PM TSU 18/1	UBA-38452	9.3	-20.6	7.2	3.18	this paper
Krasnoturansk (Minusinsk depr.) — MMM 9437/5	UBA-39179	5.2	-20.2	5.6	3.15	this paper
<i>Mammuthus primigenius</i>						
Asino (Tomsk reg.) — TRM 10300/3	UBA-38453	7.7	-21.6	10.3	3.25	this paper
	UBA-39395	11.8	-21.9	9.4	3.08	this paper
<i>Saiga tatarica</i>						
Aydorakh (Minusinsk depr.) — ZIN 15097	OxA-22638		-19.0	4.2	3.4	Jürgensen <i>et al.</i> , 2017
Askiz (Minusinsk depr.) — GIN-661	OxA-22671		-19.4	6.4	3.3	Jürgensen <i>et al.</i> , 2017
Ushaika river (Tomsk reg.) — ZIN 32727	OxA-22641		-19.1	4.2	3.4	Jürgensen <i>et al.</i> , 2017
Krasniy Yar (Tomsk reg.) — ZIN 32728/1	OxA-22520		-19.2	4.3	3.4	Jürgensen <i>et al.</i> , 2017
Krasniy Yar (Tomsk reg.) — ZIN 32728/2	OxA-22612		-18.8	3.8	3.3	Jürgensen <i>et al.</i> , 2017
Kutznetzk depression — ZIN 32725/1	OxA-22613		-19.0	4.7	3.4	Jürgensen <i>et al.</i> , 2017
Kutznetzk depression — ZIN 32725/2	OxA-22614		-17.6	5.5	3.3	Jürgensen <i>et al.</i> , 2017
Kutznetzk depression — ZIN 32750	OxA-22615		-18.9	3.5	3.3	Jürgensen <i>et al.</i> , 2017
<i>Rangifer tarandus</i>						
Kashtanka (Minusinsk depr.)	1	15.2	-18.4	4.2	3.3	Iacumin <i>et al.</i> , 2000
Kashtanka (Minusinsk depr.)	2	10.9	-17.7	4.1	3.2	Iacumin <i>et al.</i> , 2000
Kashtanka (Minusinsk depr.)	3	9.5	-18.6	3.8	3.2	Iacumin <i>et al.</i> , 2000
Kashtanka (Minusinsk depr.)	4	12.3	-18.5	3.2	3.2	Iacumin <i>et al.</i> , 2000
Kashtanka (Minusinsk depr.)	5	14.2	-18.6	3.9	3.5	Iacumin <i>et al.</i> , 2000
Kashtanka (Minusinsk depr.)	6	12.8	-17.6	3.8	3.5	Iacumin <i>et al.</i> , 2000
Kashtanka (Minusinsk depr.)	7	11.7	-18.9	3.6	3.4	Iacumin <i>et al.</i> , 2000

2015; Krajcarz *et al.*, 2016) and Siberian (Iacumin *et al.*, 2000; Jürgensen *et al.*, 2017) faunal representatives, and recent musk oxen (Raghavan *et al.*, 2014). The presence of a dietary outlier may suggest a different habitat for the musk oxen from Minusinsk, relative to musk oxen from Tomsk Ob' River and Europe. Further testing of additional specimens will be needed to clarify whether this is an individual anomaly or a regional trend.

Discussion

Apart from Chernilshchikovo, within the West Siberian Plain, *O. moschatus* remains from the later part of Late Pleistocene (11.7–57 ka cal. BP) are also known in the multi-species sites of Sergeevo, Krasniy Yar in Krivosheino district (Tomsk Region), Yurovsk (Khanty-Mansi Autonomous Area), Evalga (east of the Sverdlovsk Region), yet no remains have been found to the south of 56° N (Shpansky, 2018). Many localities containing the Pleistocene fauna remains are known

within the Minusinsk Depression (e.g. Ovodov, 2009). However, after more than a hundred year history of study, only a single record of musk ox is known in this area (Gromova, 1935; Malikov, 2015) This may indicate that the region was not a permanent habitat for the species. We suggest that in the later Late Pleistocene, musk ox dispersed into the Minusinsk Depression only during the LGM, when climatic conditions were most optimal for this species. Given this hypothesis, we anticipate further discoveries of musk ox records in the region, from localities of the similar age (Kurtak 4, Kashtanka, Shlenka, Derbina-4, Novoselovo alluvial, and Pervomayskoe; see Graf, 2009; Motuzko *et al.*, 2010, Malikov & Ovchinnikov, 2019). Unfortunately, most of these locations are presently submerged by the Krasnoyarsk Reservoir. Therefore, new sites are needed to test the presence of *O. moschatus* in the region during the later part of Late Pleistocene. The fourth cervical vertebra of musk ox was found on the beach of the Chumysh River near the Titovo Village in the Pre-Altai Plain (53°24' N).

The date of $16\,989 \pm 183$ BP (BINP-NSU-1295) obtained at the experimental accelerator mass spectrometer of the Budker Institute of Nuclear Physics SB RAS in Novosibirsk (Vasiliev *et al.*, 2018) suggests the Sartanian age of this fossil. This record (Fig. 1) suggests that the range of *O. moschatus* had a maximal southward expansion during the LGM. The records from Minusinsk and Chumysh are good indicators that the southernmost expansion of the range of musk ox in the LGM reached the latitude of 53° N. Increase in humidity and, as a result, depth of snow cover in the foothills of the Eastern Sayan and Altai Mountains possibly became a limiting factor for the further distribution of the species to the south. Modern musk oxen avoid rugged terrains, and do not live in areas with the snow depth exceeding 20–30 cm, with 40–50 cm at maximum (Danilkin, 2005). This is associated with the specific anatomical features of this animal with short legs, low height of the chest, and a considerable body mass. Landscape features, namely the predominance of low-hill and low-mountain relief mixed with plains and peneplains in the foothill regions, could be another factor limiting musk ox distribution in Southern Siberia (Mistryukov, 1991). The same factors limited the expansion of *S. tatarica* in the Minusinsk Depression (Malikov, 2018).

Paleoecology of musk ox

The nitrogen and carbon isotope ratios are highly dependent on the ecosystem. The $\delta^{15}\text{N}$ values of herbivore tissues from arid regions are higher than those in humid regions. As such, an increase in $\delta^{15}\text{N}$ in bone collagen can be interpreted as an indication of drier conditions and a diet based on grassy vegetation (Bocherens *et al.*, 2015). The lower $\delta^{13}\text{C}$ may indicate an increase in the amount of precipitation, or feeding on plants subjected to the “canopy effect” (Kohn, 2010; van der Merwe & Medina, 1991). For example, modern wet cereals have an average $\delta^{13}\text{C}$ of 29.1‰, while in dry habitats they average around 26.9‰ in $\delta^{13}\text{C}$ (Wooller *et al.*, 2007); therefore, herbivores that feed on the latter will exhibit higher $\delta^{13}\text{C}$ values.

As it has been mentioned, the carbon and nitrogen isotope ratios in the Chernilshchikovo musk ox are close to those of Pleistocene musk oxen and reindeer from Europe and Siberia, and is slightly different from modern oxen in Greenland. The $\delta^{13}\text{C}$ of Chernilshchikovo musk ox and reindeer from the Minusinsk Depression are within the interval between -19.0‰ and -17.6‰ , and their $\delta^{15}\text{N}$ are between 3.2‰ and 4.2‰ (Fig. 4). In modern Greenland musk oxen, $\delta^{13}\text{C}$ vary between -21.7‰ and -19.8‰ , and $\delta^{15}\text{N}$ between 2.1‰ and 2.9‰, which implies their habitation in more humid conditions than those of the Pleistocene musk oxen in Siberia. Only two modern specimens have the similar high $\delta^{15}\text{N}$ ratios — 3.9‰ and 4.6‰ (Raghavan *et al.*, 2014). The higher $\delta^{13}\text{C}$ values of this group as compared to modern Greenland oxen suggest their habitation in more arid conditions than those of modern Greenland. Another possible reason for the higher $\delta^{13}\text{C}$ in the Pleistocene musk ox is the higher lichen content in its

diet, similar to the diet of reindeer (Bocherens *et al.*, 2015), as compared to modern animals.

Unlike the Chernilshchikovo musk ox, the Minusinsk specimen differs both from Pleistocene animals of Siberia and modern Greenland musk oxen (Fig. 4). In most modern musk oxen $\delta^{15}\text{N}$ ratios are half as high as those in the Minusinsk musk ox. Only one modern specimen from Greenland has carbon and nitrogen isotopic levels (-20.1‰ and 4.6‰) similar to those of the Minusinsk musk ox (-20.1‰ and 4.8‰). By $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ ratios, the specimen from Minusinsk is closest to woolly rhino and horse (Fig. 4).

As the animals living in arid environments are characterized by increased both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, and the Minusinsk individual is elevated only in $\delta^{15}\text{N}$ (its $\delta^{13}\text{C}$ are similar to modern animals), it is possible that this is not related to different living conditions.

Perhaps *Salix* sp., characterized by relatively high $\delta^{15}\text{N}$ (Michelsen *et al.*, 1998) and low $\delta^{13}\text{C}$ values due to the «canopy effect», were a significant part of the Minusinsk musk ox diet. This is in good agreement with the selectivity of modern musk oxen regarding *Salix* sp. (Kazmin *et al.*, 2011). Few palynologically characterized Pleistocene sections in the region are generally poor in the pollen of willow. In the Karginian (MIS 3) and Sartanian (MIS 2) deposits of the Kurtak archaeological region (160 km north from Minusinsk) pollen of *Salix* sp. has been observed only occasionally and in small quantities (Drozdov *et al.*, 2005). Thus, the available palynological data is not yet sufficient to consider willow as a widespread fodder in the region in the Late Pleistocene. However, this species was actually found in the region during the period of *O. moschatus* existence, suggesting its possible contribution to the ox diet.

Particularly interesting is the isotopic difference between the Minusinsk specimen and reindeer from the Kashtanka site, also located in the Minusinsk Depression (Tab. 3). The majority of the remains from Kashtanka date to the early Sartanian time, 24400–20800 BP (Lisitsyn, 1997; Drozdov *et al.*, 2005), making this data the most appropriate for the comparative analysis. Even more surprising is the isotopic difference between the musk ox and reindeer that lived in the same region at approximately the same time. Although our sample size from Minusinsk is small, we hypothesize that the diet of reindeer included more lichen, which resulted in an increase in $\delta^{13}\text{C}$ and decrease in $\delta^{15}\text{N}$ values in their bones. At the moment, this is only a hypothesis that requires additional materials and results of stable isotope analysis. Pollen spectra obtained from the Kashtanka site indicate humid conditions with large shares of forest and tundra vegetation (Drozdov *et al.*, 2005). Further isotopic data for various local species will be essential for a more detailed interpretation of the diet of fossil mammals in the region.

Conclusions

We studied musk ox skulls from close geographical areas of the Minusinsk Depression and Tomsk Ob' Riv-

er region dating to the Sartanian and Karginian period respectively. Our data are consistent with the earlier hypothesis (Markova *et al.*, 2015) that during the maximum cooling interval of LGM, *O. moschatus* in Eurasia reached maximal distribution. The southern boundary of the musk ox range in North Asia was limited to 53° N. Maximum penetration of the species to the south, to the Minusinsk Depression and Pre-Altai Plain, is recorded for the Sartanian time. This is concurrent with the maximum development of cryo-arid landscapes in the northern half of Western and Middle Siberia (Velichko *et al.*, 2007). The southern border of the musk ox habitat within the West Siberian Plain during the Karginian time (DEN) was located significantly further to north, at 55–56° N, in the Omsk Irtysh River and Tomsk Ob' River regions.

Stable isotope analysis indicates that musk ox diet in the Tomsk Ob' River region was similar to that of Pleistocene reindeer and musk oxen. Our data suggest that during the Karginian time the landscape and climatic conditions in the Tomsk Ob' River region were suitable for musk oxen. Isotopic analysis of the skull from the Minusinsk Depression, on the contrary, suggests a different diet than that of the Tomsk musk ox. The results are similar to isotopic values found for horses and woolly rhinos. In addition, isotopic data may indicate a diet based on willow *Salix* sp. and grassy vegetation. Lichens were probably absent in the diet of the Minusinsk musk ox. It is possible that the dietary change reflected the transformation of the vast tundra-steppe zone, and its disintegration into the actual tundra zone in the northern and dry steppe in the southern part, or associated with individual dietary preferences of the Minusinsk musk ox on the edge of the species distribution area. The small number of available materials precludes unambiguous answers to these questions. The search for new materials is necessary to address the existing issues.

ACKNOWLEDGMENTS. The authors would like to acknowledge the administration and staff of the Minusinsk Martyanov Museum for the opportunity to work with the material. The ¹⁴C dating of the Minusinsk sample was funded by the Russian Foundation for Basic Research project No. 18-35-00118. Work is done according to the State assignment of IGM SB RAS. This study was supported by the Tomsk State University competitiveness improvement program (research grant No. 8.1.48.2018). The authors thank reviewers for valuable comments and corrections.

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