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The large mammals of North-Minusinsk basin in the Last Glacial period

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ABSTRACT

Twenty five species of large mammals are reliably established for the North-Minusinsk basin in the Last Glacial period. Another nine species of large mammal remains whose regular habitation is questionable are also known. The species biodiversity of mammals of open steppe landscapes is three times higher than the biodiversity of animals of closed and semi-closed forest biotopes. Species of closed and semi-closed forested landscapes are dominant in the modern fauna of the region. Most of the species who lived in open landscapes of the region became extinct. A possible reason for the extinction of large representatives of the mammoth fauna is the reduction of their migration ability. As a result of reduction of the area steppe landscapes beyond the depression, migration routes of large representatives of the mammoth fauna were disrupted. The steppe phytocoenoses, preserved in the territory of Minusinsk depression to the present, were not able to maintain the stability of the mammoth fauna. This may have led to the extinction of large animals. However, the stability of steppe ecosystems in the region promoted the preservation of most micro-mammals, as well as the later extinction of some large mammals in the region.

1. Introduction

The Minusinsk depression is situated in southern Middle Siberia. It is a part of the zoogeographic boundary between the West-Siberian and Mid-Siberian subdomains of the Euro-Siberian zoogeographic domain (Rogacheva, 1988). The Minusinsk depression consists of three basins: North-Minusinsk, Sydo-Erbinsk and South-Minusinsk basins. In this paper, the author analyzed the large mammals' fauna composition only in the territory of North-Minusinsk basin. In other parts of the Minusinsk depression, the large multispecies locations are known in small amounts. The natural boundaries of the North-Minusinsk basin are Eastern Sayans (in the east), Kuznetsk Alatau (in the west), Batenev (in the south) and Solgon (in the north) ridges (Fig. 1).

Research related to the fossil mammals was conducted many times in this region. However, they were mostly as a part of work of archaeological expeditions (Abramova et al., 1991; Ermolova, 1977, 1982; Abramova, 1979a,b), so the detailed study of fossil mammals has not been conducted. As a result, a comprehensive analysis of Pleistocene mammals' fauna of the region has not been carried out. Several papers by Ovodov (1992, 2009) are devoted to the solution of this problem. These publications described the species composition of mammals, mainly on the basis of cave sites from the territory of Khakass Republic. However, these data are also insufficient.

The author analyzed the large mammal fauna composition from the North-Minusinsk basin in the Last Glacial period. This time interval was selected because the extinction of many species of dominant mammals took place at the end of the last Ice Age. The study of the spatial distribution patterns of mammals can help in answering the question about the reasons of extinction at the Pleistocene-Holocene boundary.

2. Material and methods

The Last Glacial period (LGP) is the time of development of the last ice sheets and mountain-valley glaciations. The time interval for LGP is 24 000–10 300 BP (MIS 2). The deposits accumulated during this time range in the Minusinsk depression correspond to the Sartanian horizon of the West Siberian Regional Chart of Quaternary deposits (Volkova and Babushkin, 2000).

The list of fauna of large mammal species from this territory (Table 1) is based on materials that were collected by the author,

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studied in the collections of Paleontological museum of Tomsk State University, and Zoological museum of the Khakass State University, Abakan, and on published materials (Ermolova, 1982; Abramova, 1979a,b; Abramova et al., 1991; Ovodov, 1992; Motuzko et al., 2010; Kuzmin, 2011). The author refers the animals with body mass more than 2 kg (marmot and hare) to large mammals.

3. Localities

The literature and original materials from 36 localities of large mammals from the North Minusinsk basin are used in this study. All localities belong to MIS 2, confirmed by radiocarbon dating, geological structure, or archaeological artifacts. The fossil large mammal remains locations in the North-Minusinsk basin are presented by three types of taphocenosis: 1) Paleolithic sites; 2) alluvial locations; 3) cave locations (mainly zoogenic). Locations containing the remains of mammals of Sartanian age are mainly represented by Paleolithic sites. The analysis of the mammals focused on the most common species of Sartanian age. Individual findings are taken into account if they are rare species.

Kozhukhovo 1 and 2 (1 – hereinafter the figures correspond to the designation in Table 1 and Fig. 1), is situated between the Black and White Iyus Rivers (Khakass Republic), described by Shpansky and Malikov (2015). The Kozhukhovo 1 location is situated on the Black Iyus River (54°56′N, 89°46′E), and the Kozhukhovo 2 location is situated on the White Iyus River (54°54′N, 89°51′E). These outcrops are located above the 1st terrace above the floodplain, and contain stacked sandy-pebble alluvium of Sartanian age. The age is confirmed by an AMS radiocarbon date for *Ovis ammon* skull from Kozhukhovo 1, 17888 ± 110 BP (UBA-28341). Some material may be redeposited, as indicated by the AMS date on *Equus ovodovi* bone (>45 178, UBA-28340).

Tashtyk 1 (2) site is situated on the left bank of Krasnoyarsk reservoir on the Yenisei River (south of Krasnoyarsk region), at a distance of 50–60 m from the mouth of Tashtyk creek (54°42′N, 90°51′E). The site is formed with loess clay and sand deposits of 2nd terrace above floodplain. The cultural layers connected with the light-gray sandy loam. The radiocarbon date for the charcoal from the cultural layer is 12 180 ± 120 BP (LE-771). *Equus* sp. and *Rangifer tarandus* remains dominate in the fauna (Abramova, 1979a).

Tashtyk 2 (2) site is situated on the left bank of Krasnoyarsk reservoir on the Yenisei River (south of Krasnoyarsk region), on the left bank of Tashtyk creek, slightly upstream from Tashtyk 1 (54°41′N, 90°51′E). The site is formed with loess clay and sand deposits of the 2nd terrace above the floodplain. The cultural layers are large dark cross-bedded sand. The radiocarbon dates the bones and charcoal aconfirmed the age (Table 2). It is absolutely dominated by the reindeer remains, 82% of the total number (Abramova, 1979a).

Tashtyk 4 (2) site is situated on the left bank of Krasnoyarsk reservoir on the Yenisei River (south of Krasnoyarsk region), on the left bank of Tashtyk creek, 150 m upstream from the Tashtyk 2 (54°41′N, 90°51′E). The cultural layers are connected with sand deposits of the 2nd terrace above floodplain. Radiocarbon dates indicate the Sartanian age of the site (Table 2). Reindeer and bison remains are found in the site (Abramova et al., 1991).

Aeshka 2 (3) site is situated on the left bank of the Yenisei River, south of the former Aeshka village (54°52′N, 90°53′E). The cultural layers of site are located in reddish sandy loam and gray sand of the 2nd terrace above floodplain. The fauna include only the bones of reindeer (Abramova et al., 1991).

Ermolaevo (4) is situated on the right bank of the Yenisei River, at the mouth of Cheryomushki River, 3 km downstream of the Ermolaevo village (55°13′N, 92°12′E). The cultural layers are located in pebble deposits of terraces above the floodplain. Remains of woolly mammoth were found (Abramova et al., 1991).

Afanasyeva Gora (4) site is situated on one of the spurs of Batenevsky Hills, on the horizontal ledge of the mountain (54°33′N, 90°56′E). The findings are associated with a layer of light gray loam. The estimated age of the park is 20–22 thousand years (Lisitsyn, 1997).

Kokorevo 1 (5) site is situated from 0.5 km from the Kokorevo village, on the left bank of the Yenisei River (54°55′N, 90°55′E). The cultural layers are connected with floodplain alluvial deposits of the 2nd terrace above the floodplain of the Yenisei River. The radiocarbon age of cultural layers is 12 940–14 450 BP (Table 2). *Rangifer tarandus* and *Lepus* sp. dominate the fauna (Abramova, 1979a).

Kokorevo 2 (5), is situated 0.6–0.7 km from the bank of the Yenisei River, at the mouth of the Telejnyi log creek (54°56′N, 90°57′E). The cultural layers are associated with greenish-gray sandy loam deposits of 2nd terrace above the floodplain of the Yenisei River. Cultural layers correspond to the end of MIS 2 (Table 1). This site is the only one in the region where *M. primigenius* remains are dominated (Abramova, 1979a).

Kokorevo 3 (5) is situated in the alluvial cone of Kamenny Log, on the left bank of Telejnyi log creek (54°56′N, 90°57′E). *L. timidus* (59%) and *R. tarandus* (36%) remains dominate in the faunal complex. Radiocarbon age of the cultural layers is 12 690 ± 140 BP (LE-629) (Lisitsyn, 1997).

Kokorevo 4a (5) is situated 2 km downstream of the Yenisei River from the main Kokorevo group of sites. The site is located in the 180–250 m above the mouth of Kirpichnyi log, in the 2nd terrace above the floodplain of Yenisey River deposits (54°57′N, 90°57′E). According to geological data, the age of cultural layers of site is late Sartanian. The radiocarbon date confirms this age, 14 320 ± 330 B.P. (LE-469). Fauna in this site resembles other sites of the Kokorevo group (Lisitsyn, 1997; Kuzmin, 2011).

Kokorevo 4b (5) is situated on the left side of the Kipernyi log, 110 m from the Yenisey River (54°57′N, 90°57′E), in sediments of the 2nd terrace above the floodplain of this river. The age of the site is determined as 15 460 ± 320 BP (LE-540). Reindeer, red deer, roe deer, bison, rabbit, and wolf are present (Lisitsyn, 1997; Kuzmin, 2011).

Kokorevo 6 (5) is situated outside the Kokorevo group of sites, approximately 1.5 km from the mouth of Kipernyi log, downstream of the Yenisei River (54°57′N, 91°00′E). *L. timidus* (59%) and *R. tarandus* (36%) remains dominate the fauna of the site. The radiocarbon age of charcoal from the cultural layers is 12 690 ± 140 BP (LE-629) (Lisitsyn, 1997).

Novoselovo 4 (6) site is situated in the sediments of 1st terrace above the floodplain of the Yenisei River, on the left bank of this river. The site was situated at a former brick factory, near the oldest Novoselovo village (55°03′N, 91°04′E). The fauna is rich and includes animals of open habitats (Abramova et al., 1991).

Novoselova 6 (6) site is situated on the 1st terrace above the floodplain of the Yenisey River, on the left bank of this river (55°03′N, 91°04′E). The terrace includes loess deposits, and the cultural layer is associated with a pale gray, sandy loam. Dates from the cultural layer include charcoal: 11 600 ± 500 BP (GIN-403), and bone remains 18 090 ± 940 BP (LE-4807) and 13 570 ± 140 BP (LE-5045). Reindeer remains completely (9280 – 98%) dominate the fauna (Abramova, 1979b).

Novoselovo 7 (6) is situated on the 1st terrace above the floodplain of the Yenisey River, on the left bank, ~300 m north of Novoselovo 6, in a deep ravine (55°03′N, 91°04′E). The cultural layer was located in a white–gray, silty loam. A radiocarbon date from the cultural layer is 15 000 ± 300 BP (GIN-402). *Rangifer tarandus* dominates the fauna (Abramova, 1979b).

Novoselovo Zagotzerno (6) is situated on the left bank of Yenisei River, 12 km downstream from the eldest Novoselovo village (55°03′N, 91°11′E). Cultural layers occur in light-gray sand deposits of the 1st terrace above floodplain. The fauna has both forest species and animals of open habitats (Abramova et al., 1991).

Novoselovo alluvial (6) is located on the left shore of the Krasnoyarsk reservoir on the Yenisey River (South part of Krasnoyarsk

Table 1
Large mammals from the North-Minusinsk basin in LGP.

№	Name of site		Coordinates	*Lepus* sp.	*Marmota baibacina*	*Canis lupus*	*Vulpes vulpes*	*Alopex lagopus*	*Ursus arctos*	*Gulo gulo*	*Mustela putorius*	*Meles leucurus*	*Crocuta spelaea*	*Panthera spelaea*	*Mammuthus primigenius*
1	Kozhuchovo	1	54°55′N, 89°46′E												
		2	54°54′N, 89°50′E		1										
2	Tashtyk	1	54°42′N, 90°51′E	73	1	1		8						1	
		2	54°41′N, 90°51′E	4											
		4	54°41′N, 90°51′E												
3	Aeshka 2		54°52′N, 90°53′E												
4	Ermolaevo		55°13′N, 92°12′E												+
	Afanas'eva Gora		54°33′N, 90°56′E												+
5	Kokorevo	1	54°55′N, 90°55′E	1187		36		7							
		2	54°56′N, 90°57′E	36		35		1						24	148
		3	54°56′N, 90°57′E	215											
		4а	54°57′N, 90°57′E	+											
		4б	54°57′N, 90°57′E	+		+									
		6	54°57′N, 91°00′E												
6	Novoselovo	4	55°03′N, 91°04′E												+
		6	55°03′N, 91°04′E	11		27		8		12					
		7	55°03′N, 91°04′E	9		2		5							
		z –z. Al.	55°04′N, 91°11′E						+						
			55°05′N, 91°00′E		2	3						1			35
	Tarachikha		55°02′N, 91°01′E		+			+							+
	Yanovo 1		55°01′N, 91°00′E												+
7	Chegirak		55°03′N, 91°02′E												
8	Divny 1		55°05′N, 91°18′E			+									+
9	Kurtak 3		55°07′N, 91°29′E												
	Kashtanka 1		55°07′N, 91°25′E	+			+								
10	Shlenka		55°13′N, 91°54′E		+	+	+	+	+						+
11	Koma		55°01′N, 91°20′E												+
12	Anash		54°50′N, 91°00′E												+
13	Derbina	4, 5	55°19′N, 92°29′E	1							6		1		1
	Konzhul, Ust-Maltat 1, Maltat		55°20′N, 92°27′E	2			2								22
	Machlaevskii, Zelenyi, Lysyi ravine		55°19′N, 92°26′E										2		

Equus sp. (large)	*Equus sp. (small)*	*Coelodonta antiquitatis*	*Sus scrofa*	*Cervus elaphus*	*Capreolus pygargus*	*Megaloceros giganteus*	*Alces alces*	*Rangifer tarandus*	*Bison priscus (+Bos sp.)*	*Saiga tatarica*	*Ovis ammon*	Age of site	Type of site
9		1					1		8		5	17 888 ± 110	Alluvial
8		5							3	1		Sartanian	Alluvial
169				28				370	6	19	100	12 880 ± 130	Paleolithic site
27								247	3	7	1	13 550 ± 350	Paleolithic site
								+	+			14 700	Paleolithic site
								+				Sartanian	Paleolithic site
												Sartanian	Paleolithic site
+								+			+	Sartanian	Paleolithic site
61	21			136	10			3242	38		170	14 450 −12 940	Paleolithic site
93				12			11	162	15	11	21	13 300 −12 100	Paleolithic site
2								131	7		6	12 690 ± 140	Paleolithic site
+								+	+		+	14 300	Paleolithic site
				+	+			+	+			15 460 ± 320	Paleolithic site
+								+	+			sartanian	Paleolithic site
+	+							+	+	+	+?	sartanian	Paleolithic site
				1				9280	142			18 090 −13 570	Paleolithic site
5								887	5	3		15 950 −14 220	Paleolithic site
				+	+			+	+			sartanian	Paleolithic site
189		24	1?	17	4	1	1?	21	76	4	11	Sartanian	Alluvial
+								+	+		+	18 900	Paleolithic site
	+								+			Sartanian	Paleolithic site
					+							Sartanian	Paleolithic site
							+	+	+			13 220 ± 150	Paleolithic site
								+	+			16 900 −14 300	Paleolithic site
+	+			+			+	+	+			24 800 −20 800	Paleolithic site
+	+			+					+		+	20 100 −18 600	Paleolithic site
								+				Sartanian	Paleolithic site
								+				Sartanian	Paleolithic site
115	8	14		26	1		11	8	36			21 320 −21 100	Paleolithic site
42	13	24			3			15	25			12 160 −11 980	Paleolithic site
43	2	18		18		5	6		6			~10 000	Paleolithic site

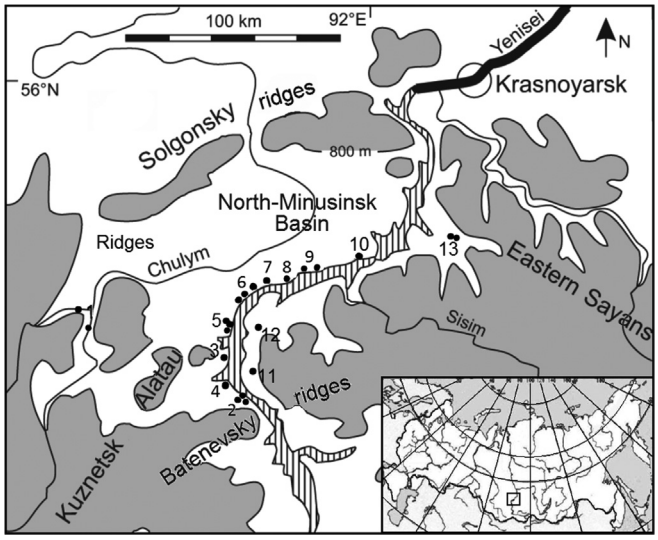

Fig. 1. Location Map of mammals remnants in LGP from North-Minusinsk basin. The numbers correspond to the numbers in Table 1.

region (55°05′N, 091°00′E)). The Quaternary deposits are represented by alluvium of the 1st terrace above floodplain, composed mainly of sand, sandy loams and loams. The mammal remains were collected on sandy beaches (Malikov, 2013). The material was not dated, but the radiocarbon dates obtained for Palaeolithic sites near Novoselovo (Abramova, 1979b) are: charcoal 22 000–11 600 BP; bone 15 950–11 700 BP (Kuzmin et al., 2011).

Yanovo 1 (6) site is situated on the left bank of the Yenisei River, 1.5 km north of the oldest Yanovo village (55°01′N, 91°00′E). Cultural layers occur in loamy loess sediments. Mammoth bones with traces of processing bone, and bison and "hemione-like" horses were found (Abramova et al., 1991).

Tarachiha (6) is situated on left bank of the Krasnoyarsk reservoir on the Yenisei River, 11 km downstream from the modern Novoselovo village, and 1–1.5 km above the Novoselovo group of sites (55°02′N, 91°01′E). Paleolithic finds and bone remains are associated with reddish sandy loam deposits. Radiocarbon dates on bones were 19 850 ± 180 BP (LE-3821), and 18 930 ± 320 BP (LE-3834). The fauna is quite rich and varied, represented by species of open landscapes (Lisitsyn, 1997).

Chegerak (7) is situated on left bank of the Krasnoyarsk reservoir on the Yenisei River, 6 km downstream from the modern Novoselovo village, at the mouth of the Chegerak River (55°03′N, 91°02′E). The cultural layer is located in the upper part of loess loam, which indicates the latest Pleistocene age of the site (Lisitsyn, 1997). The fauna is poor, with *Capreolus pygargus* remains.

Divnyj 1 (8) at the left bank of Krasnoyarsk reservoir on Yenisei River, is situated downstream from the Novoselovo group of sites, in the intermountain basin (55°05′N, 91°18′E). Cultural layers are arranged in a layer of light gray sandy loam. The radiocarbon age of fossil remains from cultural layer is 13 220 ± 150 BP (LE-4806). The fauna includes forest (elk) and steppe species (reindeer, bison, mammoth; Lisitsyn, 1997).

Kurtak 3 (9), site is situated at the left bank of the Krasnoyarsk reservoir on Yenisei River, 1 km downstream from the mouth of the Kurtak River, on a slope of the 100 m terrace (55°07′N, 91°29′E). The cultural layer lies in light gray sandy loam sediments. The age of charcoal from cultural layer varies: 14 300–16 900 BP (Table 2). The fauna is poor and is represented only by reindeer and bison (Lisitsyn, 1997).

Table 2
Radiocarbon dates for the Palaeolithic sites and natural locations of Sartan time (MIS 2) from North-Minusinkoy basin territory (Kuzmin et al., 2011).

№	Site	Material	14C date	Error	Lab code
1	Derbina 4	Charcoal	21 930	220	SOAN-4955
2	Derbina 5	Charcoal	32 430	1540	SOAN-4201
3	Derbina 5	Charcoal	31 480	1650	SOAN-4202
4	Derbina 5	Charcoal	29 230	940	SOAN-4200
5	Derbina 5	Charcoal	21 440	450	SOAN-4797
6	Derbina 5	Charcoal	21 320	300	SOAN-4346a
7	Derbina 5	Charcoal	21 100	120	SOAN-4346
8	Derbina 5	Charcoal	20 460	465	SOAN-4796
9	Derbina 5	Charcoal	18 960	220	SOAN-6007
10	Divnyj 1, lay. 2	Bone	13 220	150	LE-4806
11	Kashtanka 1, lay. 2	Charcoal	29 400	400	GIN-6969
12	Kashtanka 1, lay. 1	Charcoal	24 805	425	SOAN-2853
13	Kashtanka 1, lay. 1	Charcoal	24 400	1500	IGAN-1048
14	Kashtanka 1, lay. 1	Charcoal	23 830	850	IGAN-1050
15	Kashtanka 1, lay. 2	Charcoal	21 800	200	IGAN -1049
16	Kashtanka 1, lay. 2	Charcoal	20 800	600	GIN-6968
17	Kokorevo 1, lay. 3	Charcoal	15 900	250	IGAN-104
18	Kokorevo 1, lay. 3	Charcoal	14 450	150	LE-628
19	Kokorevo 1, lay. 3	Charcoal	13 000	500	IGAN-102
20	Kokorevo 1, lay. 2	Charcoal	15 200	200	IGAN-105
21	Kokorevo 1, lay. 2	Charcoal	13 300	50	GIN-91
22	Kokorevo 1, lay. 2	Charcoal	13 100	500	IGAN-103
23	Kokorevo 1, lay. 2	Charcoal	12 940	270	LE-526
24	Kokorevo 2	Charcoal	13 300	100	GIN-90
25	Kokorevo 2	Bone	12 090	100	LE-4812
26	Kokorevo 2	Bone	11 550	220	LE-5362
27	Kokorevo 3	Charcoal	12 690	140	LE-629
28	Kokorevo 4a, lay. 3	Charcoal	14 320	330	LE-469
29	Kokorevo 4b, lay. 3–5	Charcoal	15 460	320	LE-540
30	Kokorevo 6	Bone	10 800	240	LE-5366
31	Konzhul	Bone	12 160	175	SOAN-4954
32	Konzhul	Bone	11 980	155	SOAN-4953
33	Kozhuchovo 1	Bone	17 888[a]	110	UBA-28341
34	Kurtak 3	Charcoal	16 900	700	GIN-2102
35	Kurtak 3	Charcoal	14 390	100	LE-1456
36	Kurtak 3	Charcoal	14 600	200	GIN-2101
37	Kurtak 3	Charcoal	14 300	100	LE-1457
38	Kurtak 4, lay. 11–12	Charcoal	27 470	200	LE-2833
39	Kurtak 4, lay. 11	Charcoal	27 770	310	AA-68668
40	Kurtak 4, lay. 11	Charcoal	25 160	280	AA-68669
41	Kurtak 4, lay. 11	Bone	24 890	670	LE-3357
42	Kurtak 4, lay. 11	Charcoal	24 800	670	GIN-3357
43	Kurtak 4, lay. 11	Charcoal	24 170	320	LE-3351
44	Kurtak 4, lay. 11	Bone	24 000	2950	LE-4156
45	Kurtak 4, lay. 11	Charcoal	23 800	900	LE-4155
46	Kurtak 4, lay. 11	Charcoal	23 470	200	LE-2833a
47	Kurtak 4, lay. 11	Charcoal	21 270	160	AA-72147
48	Kurtak 4, lay. 11	Charcoal	20 690	240	AA-72146
49	Kurtak 4, lay. 11	Charcoal	17 740	120	AA-68670
50	Novoselovo 6	Bone	18 090	940	LE-4807
51	Novoselovo 6	Bone	13 570	140	LE-5045
52	Novoselovo 6	Charcoal	11 600	500	GIN-403
53	Novoselovo 7	Bone	15 950	120	LE-4802
54	Novoselovo 7	Charcoal	15 000	300	GIN-402
55	Novoselovo 7	Bone	14 220	170	LE-4803
56	Novoselovo 7	Bone	13 800	140	AA-68674
57	Novoselovo 7	Bone	13 480	140	AA-68672
58	Novoselovo 7	Bone	11 700	110	AA-72561
59	Novoselovo 13	Bone	21 580	480	LE-3739
60	Novoselovo 13	Bone	15 030	620	LE-4896
61	Novoselovo 13	Bone	13 630	200	LE-4805
62	Sazhency	Charcoal	22 175	195	SOAN-7439
63	Shelenka	Bone	17 660	700	GIN-2862a
64	Shelenka	Bone	18 600	200	GIN-2862
65	Shelenka	Bone	20 100	100	GIN-2863
66	Shelenka	Bone	19 700	200	GIN-2861
67	Tarachiha	Bone	19 850	180	LE-3821
68	Tarachiha	Bone	18 930	320	LE-3834
69	Tashtyk 1	Bone	13 300	100	LE-5235
70	Tashtyk 1, lay. 1	Bone	12 090	100	LE-4980
71	Tashtyk 1, lay. 1	Charcoal	11 550	220	LE-5362
72	Tashtyk 2	Bone	13 550	320	LE-4801
73	Tashtyk 4, low layer	Charcoal	14 700	150	GIN-262

Table 2 (*continued*)

№	Site	Material	14C date	Error	Lab code
74	Ust-Maltat 1	Charcoal	12 010	140	SOAN-5366
75	Volchika 2	Bone	20 085	80	OxA-20251

[a] From Shpansky and Malikov, 2015.

Kashtanka 1 (9) site is situated at the left bank of the Krasnoyarsk reservoir on the Yenisei River, between the Bezguza and Kurtak Rivers (55°07′N, 91°25′E). The site is connected with a decrease in the slope of the 70–80 m terrace, and the cultural layers are located in the red sandy loam and light brown loams. The first cultural layer is of Sartan age (20 800 ± 600 BP (GIN-6968), 24 805 ± 425 BP (SOAN-2853)), and the second corresponds to the fossil soil of Karga age (Lisitsyn, 1997).

Shelenka (10) site is situated 1 km southeast of Primorsk village (55°13′N, 91°54′E). The cultural layer of site is associated with light gray loam deposits. Radiocarbon ages of mammoth remnants from the cultural layer are 20 100 ± 100 BP (GIN-2863) and 19 700 ± 100 BP (GIN-2861). Reindeer, mammoth and horse remains dominate the fauna, but there are many other species (Lisitsyn, 1997).

Koma (11) site is situated on the right bank of the Krasnoyarsk reservoir on the Yenisei River, near Koma village (55°01′N, 91°20′E). At the sediments of terrace above the floodplain of Koma River, reindeer and mammoth bones were found (Abramova et al., 1991).

Anash (12) is situated on the right bank of Yenisei River, near Anash village (54°50′N, 91°00′E). The material comes from the deposits of the 2nd terrace above the floodplain. Mammoth and the reindeer remains were found (Abramova et al., 1991).

Derbina 4 (13) site is situated on the right bank of the Derbina Gulf, Krasnoyarsk reservoir (55°19′N, 92°29′E). The cultural layer is located in grayish-brown loam sediments. Radiocarbon age of charcoal from the cultural layer is 21 930 ± 220 BP (SOAN-4955). Fauna include horse remains (Motuzko et al., 2005).

Derbina 5 (13) is situated on the right bank of the Derbina Gulf, Krasnoyarsk reservoir, on a promontory jutting out below the mouth of Maltat Gulf (55°19′N, 92°28′E). Two cultural layers are present at this site. The first layer relates to fossil soil horizons (29 230–32 430 (Table 2)) and the second cultural layer is an ancient alluvial fan deposit (18 960–21 440 (Table 2)). The tundra-steppe species dominate the fauna of the second cultural layer (Motuzko et al., 2010).

The materials of the fauna of Ust-Maltat 1, Maltat and Konzhul (13) locations are described together (Motuzko et al., 2010), and are considered comprehensively. The age of this location matches the end of Sartan time (11 980–12 160 (Table 2)). The species of open habitats (steppes and tundra-steeps) dominate.

In the deposits of low terraces of the Derbina Gulf (Machlaevskii, Zelenyi, Lysyi log (13)), fauna from the end at Sartan time or early Holocene was found (Motuzko et al., 2010). Steppe species dominate in this fauna (56%), with tundra-steppe (20%) and forest (24%) species about equal.

An overview of radiocarbon dates on the location of the territory of Siberia is given in Kuzmin et al. (2011). Table 2 shows the radiocarbon dates.

4. Systematic review

The spatial distribution of large mammals during the Late Glacial Period is analyzed in this section. Also discussed are the possible reasons of extinction of the mammoth fauna and taxonomic status of some species. Species that do not inhabit the region today are marked with «†».

Lepus tolai Pallas, 1778† and *Lepus timidus* Linnaeus, 1758

Hares were abundant and widely distributed in the North-Minusinsk basin in Sartanian time. A large number of hare remains in some Paleolithic sites confirms the high abundance of hares: Kokorevo 1 (23%), and Kokorevo 3 (59%) (Abramova, 1979b). The bulk of the hare remains found in the region does not have a definition of species. In the literature, these materials are described as *Lepus* sp.

The hares known in the region can be divided into two species – *L. tolai* and *L. timidus*. The remains reliably attributable to these species are known from a number of cave localities and some of the Paleolithic sites (Ovodov, 2006; Ovodov and Martynovich, 2008b). Currently, the region has extant *L. timidus* (in the 20th century, *L. europaeus* has been introduced). Tolai hare became extinct in the Late Holocene, as indicated by its remains in the Holocene deposits of many caves (Ovodov, 2009). The absence of radiocarbon dates from *L. tolai* precludes discussion about the time of its extinction.

Marmota baibacina Kastschenko, 1899†

Marmot was widespread in the Minusinsk depression during the LGP. Remains are found in various parts of the region, but always in small quantities.

Marmot remains are isolated in all known locations. Probably this is due to the fragility of the samples, rather than a small number of individuals in the region. In contrast to most representatives of the mammoth fauna the marmot remained in North-Minusinsk basin until the second half of the Holocene. In the Holocene deposits of many caves –Proskuryakova Grotto, Archaeological Cave, Fanatic Cave, Kashkulak Cave (Ovodov, 2009), marmot remains was found, but without radiocarbon dates. At present, it is extinct.

Canis lupus Linnaeus, 1758

Wolf remains in Sartanian age deposits are represented by isolated specimens in the North-Minusinsk basin, predominantly from Palaeolithic sites situated in the flat part of the basin. At present, the wolf population is situated mostly in steppe-forest, although wolves are found in all landscape zones (Sokolov, 1979).

Vulpes (Alopex) lagopus Linnaeus, 1758†

Arctic fox lived throughout the territory of North-Minusinsk basin in the Sartanian. Remains are known from many Paleolithic site (Table 1).

Arctic fox remains are known now within the Minusinsk depression only in its northern part (North-Minusinsk basin). On this basis, we can assume that the southern boundary of the range of this species was located on the Batenevsky hills. However, the lack of finds in the southern regions of the basin may be due to insufficient study. This is indirectly confirmed by the habitat in the southern regions of the species are considered typical periglacial forms, mammoth, woolly rhinoceros, musk ox and reindeer. Presently extinct.

Vulpes vulpes Linnaeus, 1758

Fox remains in deposits of Sartanian age were found only in the foothills of the Eastern Sayan, in Derbina Archaeological region localities (Table 1). In other parts of the Minusinsk depression, fox remains of the Sartanian age are also known from a few localities, Dvuglazka (Ovodov and Martynovich, 1992), Ui 1, and Maina (Vasiliev, 1996). Presently, the species is widely distributed in the region. Fox inhabits both forest and steppe landscapes (Nepomnyaschy, 2010).

Ursus arctos Linnaeus, 1758

Brown bear remains are known only from one location in the North-Minusinsk basin, “Novoselovo Zagotzerno.” In other parts of the depression, brown bear remains of the Sartanian age are well known from two localities, Dvuglazka (Ovodov and Martynovich, 1992), and Irba-2 (Polyakov et al., 2014). At present, bear inhabits

the forest zone and subalpine meadows and high mountain tundra, visiting the steppe-forest zone only when driven by a deficiency of food (Sokolov, 1979).

Gulo gulo Linnaeus, 1758

Wolverine remains to the LGP at present are known only in Novoselovo 6 (Abramova, 1979b, p. 166).

Wolverine has lived in the Minusinsk depression from Karga time (MIS 3) continuously to the present. This is confirmed by the presence of its remains in the localities of Karga age throughout the territory (Ovodov and Martynovich, 1992; Ovodov, 2009): in North-Minusinsk basin (Proskurjakova Grotto, Malaya Syia), in Sydo-Erbinskaya basin (Dvuglazka), and in South-Minusinsk basin (Fanatikov Cave). The presence of wolverine remains in the Novoselovo 6 (North Minusinskaya) and Maina (South Minusinskaya) localities confirms that it continued to dwell in the region during the LGP. The small quantity of wolverine remains is probably due to the relative remoteness of the forest from the majority of locations of this age in the region. Presently, the species prefers of dark coniferous forests in mountainous terrain in the region (Sokolov, 1979).

Meles leucurus Hodgson, 1847

Badger remains are known in one location of Sartanian age in the central part of the basin (Novoselovo alluvial). A cranium with mandible (ZM KHSU 278) was found.

The absence badger remains is likely explained as for wolverine (see above). At present, badger has a fairly large range in the Khakass Republic. It is a background species in the steppe and forest communities (Kudryavtseva and Smirnov, 2005).

Mustela sp.

Mustela sp. (*M. putorius*? (Motuzko et al., 2010)) remains are known only in the foothills of the Eastern Sayan (Derbina 4, 5).

The modern range of *M. putorius* is situated in Europe, and east of the Urals the species is not found (Aristov and Baryshnikov, 2001). Four species of the genus *Mustela* are present in the fauna of the Minusinsk depression. Three species (*Mustela erminae, M. nivalis, M. sibiricus*) inhabit in steppe-forest and forest biotopes, and live mostly in middle mountain areas (Sokolov, 1979). One species *M. eversmanni* inhabits steppe biotopes (Aristov and Baryshnikov, 2001). Two species are most similar to *M. putorius* in size, *M. sibiricus* and *M. eversmanni*. Probably, the *Mustela* sp. remains from Derbina sites belong to one of these species.

Crocuta spelaea Goldfuss, 1823†

Cave hyena remains in the North-Minusinsk basin are found only in the deposits of low terraces in the area of Derbina gulf, in the foothills of the Eastern Sayan (Motuzko et al., 2010). Cave hyena remains are known from Sartanian deposits (layer 4—17 420 ± 330 BP (SOAN-4317)) of Dvuglazka grotto (Ovodov and Martynovich, 1992). Discussion about the time of the hyena extinction is premature, because there are no direct radiocarbon dates for hyena remains.

Panthera spelaea Goldfuss, 1810†

Cave lion was quite widespread within the North-Minusinsk basin in LGP. Its remains are found in many Paleolithic sites of the region. These sites are located mostly in the central lowland part of the region.

The youngest radiocarbon dating of lion bone is 20 085 ± 80 BP (OxA-20251), from this region (Stuart and Lister, 2011). However, the younger late Paleolithic site (Tastyk 1—12 880 ± 130 (LE-4980), Kokorevo 2—12 090 ± 100 (LE-4812)) also contain the remains of the cave lion (Abramova, 1979a,b). Presently extinct.

Mammuthus primigenius Blumenbach, 1799†

Mammoth was quite widespread within the North-Minusinsk basin in LGP. The mammoth remains are known in the localities is situated in the central lowland, parts of the region, and in the foothills. In the Paleolithic sites, mammoth remains are rare (below 2%), but in the natural locations mammoth bones constitute up to 9% of all remains (Malikov, 2013).

The question of time and reasons for the mammoth extinction in the Minusinsk depression is not resolved (Malikov, 2014). It was previously thought that the mammoth become extinct in the region between 20 000 and 15 000 years ago (Ermolova, 1977). However, later radiocarbon dates are derived from the woolly mammoth bones from Konzhul (Akimova, 2010): 11 980 ± 155 (SOAN-4953) and 12 160 ± 175 (SOAN-4954). Thus, like most of the large mammals, the mammoth existed to the end of the Pleistocene in the Minusinsk depression. Presently extinct.

Equus sp. large and small form

As horses live in large groups and consume large amounts of food, survival of several species with similar requirements is difficult in a small area. Likely to, the existence of two groups of genus *Equus* in the region to explain of their different ecological features. Therefore, horses are conditionally divided into a group of "widely-ungulate" horses *Equus* ex gr. *germanicus-gallicus* or *E. ferus*) and "hemione-like" (*E. hemionus* or *E. ovodovi*).

Equus large form†

"Widely-ungulate" large horse is one of the dominant species of mammoth fauna in the North-Minusinsk basin. Their remains are known in almost all known localities in the region (Table 1).

Equus small form†

The remains of small "hemione-like" horses, quite regularly and in large quantities, are found in the region in LGP. However, their number is less than the remnants of large "widely-ungulate" horses.

Genetic research has shown that "hemione-like" horse from Minusinsk depression does not belong to the species *E. hydruntinus*, and constitutes a separate species, *E. ovodovi* (Eisenmann and Vasiliev, 2010). Therefore, the author attributes to *E. ovodovi* all remains of horses described in the literature as *E. hydruntinus*. The remains of horses attributed in the literature to *E. hemionus* are attributed by the author proposes to a group of gracile horses with *E. ovodovi,* in the absence of genetic analysis.

Late Pleistocene *E. hemionus* from Altai and Minusinsk depression differed from other Asiatic wild (Gromova, 1949). Distinctive features include: more large and thick metatarsal bones; lower cheek teeth are narrower, shallow lingual grooves, elongated double knots; and deep vestibular grooves (Gromova, 1949, P. 220). Those symptoms are observed in the diagnosis of *E. ovodovi* (Eisenmann and Vasiliev, 2010).

Few descriptions and measurements of horses from the Minusinsk depression exist. From the available sources, known metatarsal horses from Kokorevo 2 are described as *E. hemionus* (Abramova et al., 1975). However, this bone is larger and bulkier than the Pleistocene Asiatic wild ass and more consistent with the Ovodov horse. Such a bone, but larger, is described from Malaya Syia (Muratov et al., 1982).

Probably that to the end of the Pleistocene, the territory of Minusinsk depression was inhabited by only one species of gracile horses — *E. ovodovi*. The radiocarbon dating of the *E. ovodovi* remains from geologically young localities may confirm this supposition.

The wild horses have not survived in the Minusinsk depression.

Coelodonta antiquitatis Blumenbach, 1799†

Woolly rhinoceros was widespread in the region in LGP. The remains of the species are found in the foothills and in the lowland parts of the basin.

Woolly rhinoceros was not the object of Paleolithic hunting in the North-Minusinsk basin. This is confirmed by the almost complete absence of remains in Paleolithic sites (Table 1). It was therefore suggested that by Sartanian time the woolly rhinoceros had already become extinct in the region (Ermolova, 1977, 1982).

However, in the natural locations and Paleolithic sites from the Derbina region, the remains of this animal are fairly common and account for up to 5.6–16% of the total composition of the fauna (Motuzko et al., 2010; Malikov, 2013). Presently extinct.

Cervus elaphus Linnaeus, 1758

Red deer was a usual species of fauna of the North-Minusinsk basin in Late Glacial Period. Remains are found everywhere, but always in small quantities from 0.1 to 9% (Abramova, 1979a,b; Akimova et al., 1992; Malikov, 2013).

Red deer inhabited the whole territory of the Minusinsk depression in Sartanian time. Likely, the bulk of the animals lived in the foothills, in forest landscapes. This is confirmed by a regular increase in the number of deer remnants from flat terrain, Kokorevo-Novoselovo groups of sites (0.1–4.9%), to the foothills of the Eastern Sayan, in Derbina Archaeological region localities (9%). The maximum percentage of deer remains (20.3%) is observed in the Maina site (South-Minusinsk basin), located in the foothills of the Western Sayan (Vasiliev, 1996). Red deer are lived in the region in Sartanian time in mostly forest-steppe landscapes, as does modern *C. elaphus*. Presently, the deer inhabit the forested areas of the slopes of Kuznetsk Alatau, Western and Eastern Sayan. They live everywhere, but rarely move into the steppe zone (Sokolov, 1979).

Capreolus pygargus Pallas, 1771

Roe deer remains are very few in number in LGP, as are the remains of most species associated with forest habitats. Its remnants are found both in lowland as well as in foothill parts of the basin. That points to widespread roe deer in the region. At present, it inhabits mostly the subtaiga zone, mainly abundant in the Western Sayan (Sokolov, 1979).

Megaloceros giganteus Blumenbach, 1799†

Remains of a giant deer are known only in two localities from North-Minusinsk basin in LGP: Machlaevskii(?) ravine and Novoselovo alluvial. There is only one find of *M. giganteus* known from the South-Minusinsk basin (Polyakov et al., 2014).

The small number of finds precludes discussion of the time and reasons for of extinction of this species. However, the finding a fragment of giant deer antler in the Irba-2 site suggests that this species was present at least until the end of the Pleistocene. The fossil remains of mammals (without specifying a species) from this site was dated to 12 550 ± 120–11 300 ± 190 BP (Polyakov et al., 2014). Presently extinct.

Alces alces Linnaeus, 1758

Elk remains from the LGP are found in the lowland and foothill parts of the basin. This indicates it was a widely disseminated species in the region. Elk remains are always represented by single specimens, in Paleolithic sites well as in natural localities. This is probably due to its adaptation to forest conditions, thereby reducing the likelihood of burial. The largest percentage (4%) of *A. alces* remains is found in foothill areas, and likely forest landscapes were present in this territory (Vasiliev, 1996; Motuzko et al., 2010). At present, the elk population is unevenly spread. They are found in dark coniferous forests of the Kuznetsky Alatau and Sayan (Sokolov, 1979).

Rangifer tarandus Linnaeus, 1758

Reindeer was widespread in the North-Minusinsk basin in LGP. Its remains are known in almost all localities of this age, in the plains and the foothills.

During the Late Pleistocene, reindeer was a typical representative of fauna in the Minusinsk depression. Even when extinction of many large mammals (mammoth, wooly rhino, saiga antelope, giant deer) occurred, this species went on to play an important role in the fauna of the region. The relative abundance of reindeer during the Holocene is indicated by images of rock art in the plains (Kyzlasov and Leontiev, 1980). At present, small populations of reindeer live in the high mountains zone of Kuznetsky Alatau and West Sayan (Red data book…, 2014).

Bos sp.†

Fossil bull remains in the North Minusinskaya depression are found in some locations in conjunction with *Bison priscus* remains (Abramova, 1979a,b). However, because of the lack detailed description of the material, it is difficult to assess their taxonomic status. Some of these remains possibly belong to *Bison priscus*. However, in the Karga age deposits in Proskurjakova and Dvuglazka grotto, remains of *Bos* (*Phoephagus*) *baikalensis* are specified (Ovodov, 1992, 2009). The Khakass National Museum (Abakan) has two pieces of horn cores of *Bos primigenius* (KHNM 7116/2, 2110/7), but unfortunately there is no exact information about the locations of these findings. Therefore, it is assumed that the remains attributed in the literature to *Bos* sp. are the remains of the wild ox or Baikal yak. Presently extinct.

Bison priscus Bojanus, 1827†

During the whole of the Late Glacial Period, bison was widespread in the North-Minusinsk basin. Its remains are found in most natural locations and Paleolithic sites (Table 1). Bison fossil remains are found in large numbers, indicating the abundance of the species in the region. However, despite the massive of finds of bison remains, discussion of the time and cause of extinction of this species is not possible, because of the absence of direct radiocarbon dating of the bone remains of *B. priscus*. Presently extinct.

Saiga tatarica Linnaeus, 1766†

Saiga fossil remains are known only from the central plains of the North-Minusinsk basin (Tashtyk, Kokorevo and Novoselovo group of sites). Only one find of saiga remains in the foothills of Kuznetsky Alatau was found, along the Aydorah river, of Sartanian age (Baryshnikov and Tikhonov, 1994). Saiga remains are more frequently represented in cave locations of the Kuznetsky Alatau in the Karga age deposits (Ovodov, 2009).

Saiga remains are few in number in all localities of the North Minusinsk basin. They make up about 0.3% of the total number of remains of large mammals (Abramova, 1979a,b; Malikov, 2013). This is probably due to the ecological characteristics of this species. Low water demand, unlike other animals, led to the fact herds stay away from the rivers and therefore are less subject to natural burial. Their high speed, to 75–80 km/h (Jirnov, 1982), made them difficult subjects for hunting by Paleolithic humans. The small number of saiga remains could be due to seasonal migrations, and for this reason the Paleolithic hunters rarely hunted saiga. Presently extinct.

Ovis ammon Linnaeus, 1758

Argali sheep was widespread in the region during the Last Glacial period. It inhabited mainly the central, most lowland parts of the basin. At present, argali is not found in the North-Minusinsk basin. The nearest large population of argali sheep is situated on the Mongun-Taiga ridge in Tuva (Red data book…, 2014). Argali sheep visits may have occurred in the Western Sayan.

Twenty-five species of large mammals lived in the North-Minusinsk basin in Sartanian time. The mammals are classified are 6 orders: Lagomorpha – *Lepus tolai*†, *Lepus timidus*; Rodentia – *Marmota baibacina*†; Carnivora – *Canis lupus*; *Vulpes* (*Alopex*) *lagopus*†; *Vulpes vulpes*; *Ursus arctos*; *Gulo gulo*; *Meles leucurus*; *Mustela* sp.; *Crocuta spelaea*†; *Panthera spelaea*†; Proboscidea† – *Mammuthus primigenius*; Perissodactyla† – *Equus* large form; *Equus* small form; *Coelodonta antiquitatis*; Artiodactyla – *Cervus elaphus*; *Capreolus pygargus*; *Megaloceros giganteus*†; *Alces alces*; *Rangifer tarandus*; *Bos* sp.†; *Bison priscus*†; *Saiga borealis*†; *Ovis ammon*.

Apart from species which doubtless lived in the North-Minusinsk basin, other mammal remains may indicate casual visits rather than permanent occupation. These specimens are

represented by isolated samples, and often they did not have stratigraphic control: *Cuon alpinus*, *Ursus savini rossicus*†, *Uncia uncia*, *Felis manul*, *Sus scrofa*, *Moschus moschiferus*, *Ovibos moschatus*†, *Ovis nivicola*†, and *Capra sibirica*. The comments about these species are given below.

Cuon alpinus Pallas, 1811

Currently in the region there is only one location with fossil remains of red wolf, Tohzaskiy grotto (Ovodov, 2009). The geological age of the deposits in the cave is unknown. Perhaps the deposits in the grotto are synchronous to deposits of the Proskuryakova grotto of Karga (MIS 3) age (Ovodov, 2009). However, it is possible that the deposits in the Tohzaskiy grotto are younger. Most probably, this find indicates a single visit of the red wolf in the territory of basin. Such visits by modern red wolves are common. Currently, the red wolf does not live in the region, and are known only a few visits in the southern parts of South-Minusinsk basin (Red data book…, 2014). The main area of the red wolf is situated in South-East and Central Asia, in the Altai, Western Sayan, and Transbaikal (Aristov and Baryshnikov, 2001).

Uncia uncia Schreber, 1775

The fossil remains of snow leopard are found only in the Proskurjakova grotto in the North-Minusinsk basin (Ovodov, 2009). The deposits in the grotto formed in Karga age (MIS 3). It is possible that in the Sartan time (MIS 2) some individuals continued to live in the region. At present, the snow leopard is found in the region in the upper reaches of the Abakan river (Western Sayan), with transitory visits to Kuznetsky Alatau (Red data book…, 2014).

Sus scrofa Linnaeus, 1758

The North-Minusinsk basin has only one known finding of wild boar, supposedly of Pleistocene age. A right M3 was found in the «Novoselovo alluvial» locality. The sample does not have geological control. However, the location contains remains of mammals mostly of Sartanian age. As well, significant fossilization could indicate a relatively ancient age of this sample.

The majority of the Pleistocene wild boar finds are concentrated in Europe and the Caucasus (Bibikova, 1960). Single finds of remnant wild boar are known from Altai caves, but the exact geological age of these findings is not known, the Pleistocene age indirectly indicated by finds of extinct species (Galkin and Ovodov, 1975). Kurtun-1 cave, near Baikal, is the only place in Siberia where the wild boar remains of Pleistocene age are known. The Karga age deposits (MIS 3) of this cave contain a small amount of *Sus scrofa* remains in association with *Coelodonta antiquitatis*, *Mammuthus primigenius*, *Crocuta spelaea*, *Panthera spelaea* and other extinct forms (Filippov et al., 2012).

Presently, wild boar is not a permanent representative fauna of the region. However, its population in the region is gradually increasing. Wild boar lives in forests, but always visited steppe areas in the valleys of rivers and streams (Sokolov, 1979).

Moschus moschiferus Linnaeus, 1758

Tohzaskiy grotto (valley of Belyi Iyus River) has a single find of Pleistocene musk deer (Ovodov, 1980). The geological age of the deposits in the Tohzaskiy grotto is unknown reliably. At present, the species inhabits mostly taiga areas of the Western Sayan, occasionally present on the Abakan ridge and the Kuznetsk Alatau (Red data book…, 2014).

In the southern part of the Minusinsk depression (Sydo-Erbinsk and South-Minusinsk basins) in the localities was dated to MIS 2, the remains of *Ovis nivicola* Eschscholtz, 1829 (Ovodov, 2003), *Capra sibirica* Pallas, 1776 (Vasiliev, 1996), *Felis* (*Otocolobus*) *manul* Pallas, 1776 (Ovodov and Martynovich, 2008a), *Ovibos moschatus* Zimmermann, 1780 (Malikov, 2015) were found. These species also could inhabit the North-Minusinsk basin. In addition, *Ursus savini rossicus* Borissiak, 1930 could survive here until Sartanian time, although the youngest remains of this bear are known from MIS 3 (Ermolova, 1982).

5. Discussion

LGP (Sartanian horizon, MIS 2) of North Minusinsk Depression was characterized by a rich diversity of species of large mammals from a large number of locations. The total number of revealed taxa is 34 species, assuming the same age of identified remains, considerably larger than in adjacent regions. For example, 16 species of large mammals in the Kuznetsk Basin (Foronova, 2001) and 12 species in south Western Siberia (Kosintsev and Vasiliev, 2009) were revealed. Such a diverse faunal composition of the territory of the basin can be explained by the transitional position of the fauna due to the geographical location of the basin at the boundary of the West-Siberian and Mid-Siberian zoogeographical subdomains. As a result, the presence of the Arctic species (*Vulpes lagopus*, *Rangifer tarandus*, *Ovibos moschatus*) and Central-Asian species (*Lepus tolai*, *Saiga borealis*, *Ovis ammon*, *Cuon alpinus*, *Uncia uncia*, *Felis manul*, *Capra sibirica*) is observed in the region.

5.1. Relative abundance of large mammals of North-Minusinsk basin in the LGP

The large mammal species of the Sartanian time from the North-Minusinsk basin may be divided in three groups based on frequency of occurrence of their remains: 1) the abundant species, the remains of which are numerous; 2) the species of relatively high quantity, but represented by small amount of remains; 3) the species represented by few specimens, whose regular habitat in the region is questionable.

The first group includes large herd animals: mammoths, horses, bison, reindeer, and argali sheep. The abundance of these animals' remains can be explained by several reasons: firstly, by really high populations of animals, which increased the possibility of their burial, secondly, these species (an exception for mammoth) were a convenient object of hunting for Paleolithic humans. Their abundance is supported by their presence in Paleolithic sites (Abramova, 1979a,b; Motuzko et al., 2010): reindeer (up to 98% of the all faunal remains in Novoseolovo 6), horses (up to 55.4% in Derbina 4 and 5), argali (up to 15% in Kokorevo 1, layer 4), and bison (up to 16.8% in Ust-Maltat, Maltat, Konzhul). The third reason is a high water requirement for these animals (with the exception of reindeer), and therefore in natural burials percentages of remains of these species are high as well (Malikov, 2013; Shpansky and Malikov, 2015).

The second group is represented by relatively numerous species: all predators, deer, rhinos, oxen, and saiga. The small amount of mammal remains of this group could be explained by the ecological characteristics of these species. The small number of predator remains is due to the fact that predators are much less numerous than herbivores in the ecosystem. That is why the probability of preservation of predator remains in taphocenosis is lower than for herbivores. The small number of predator remains in Paleolithic site can be explained by the fact that predators are rarely used for food.

The small amount of deer remnants can be explained by the fact that they mostly lived in the forests, where burial conditions were less favorable. This is supported by the increase in the number of remains in the foothills in the forest area in comparison with lowland areas. For example, in the Kokorevo-Novoselovo group of sites the remains of *Cervus elaphus* comprise up to 0.1–4.9% of all mammal remains (Abramova, 1979a,b). In the foothills of the Eastern Sayans, for Derbin Archaeological region, this value is 9% (Motuzko et al., 2010). The maximum percentage of red deer remains was discovered in the Maina site (South-Minusinsk basin), which is situated in the foothills of the Western Sayans, where the remnants of deer reach up to 20.3% (Vasiliev, 1996). A similar pattern is observed in the elk remains. The highest percentage of *A. alces* remains (up to 4%) is found in the foothills (Vasiliev, 1996; Motuzko et al., 2010), whereas

on the plain they represent 0.6% (Novoselovo alluvial) to 1.8% (Kokorevo 2) (Abramova, 1979a,b; Maikov, 2013).

Coelodonta antiquitatis remains are rare because they are solitary, and therefore the population of animals was not too high. Being a fairly large and dangerous animal, the woolly rhinoceros probably was not of interest for Paleolithic humans. Although modern saiga live in large herds, fossil *Saiga borealis* remains are not numerous due to ecological characteristics of the species. Seasonal migrations and high speed limited the attractiveness of saiga to Paleolithic hunters.

The third group includes the mammals with habitat marginal to the Minusinsk depression: *Cuon alpinus*, *Uncia uncia*, *Felis manul*, *Ovibos moschatus*, *Ovis nivicola* and *Capra sibirica*. Because of the low population of these animals, the remains of these species are represented by isolated specimens. In the same way, the limited amount of remains of these mammals can be explained by their habitat in mountain landscapes (except for musk ox), reducing their chances of burial.

5.2. Landscape-biotopic features of large mammals in North-Minusinsk basin in the LGP

The mammals of open steppe landscapes dominated in the region in landscape-biotopic features in Sartanian time. The species biodiversity of mammals of open steppe landscapes is three times higher than the biodiversity of animals of closed and semi-closed forest biotopes (Fig. 2). This indicates that the open steppe landscapes dominated in the region in the Late Glacial Period. The palynological data does not contradict this. The pollen of herbaceous plants (50–59%) dominated in Kashtanka 1 site (24 800–20 800 BP) and the percentages of tree pollen and spores are 30–34% and 6–20% respectively (Drozdov et al., 2005). Grass pollen reaches 97% (Abramova, 1979a) in the cultural layer of Kokorevo 2 site (13 300–12 100 BP).

Species of closed and semi-closed forested landscapes are dominant in the modern fauna of the North-Minusinsk basin (Fig. 2). A large part of the depression is still occupied by steppe and steppe-forest landscapes (Polozhij et al., 2002). These landscapes are caused by the peculiarities of the atmospheric circulation in the region. The meridially-aligned Kuznetsk Alatau is a barrier to the transfer of air masses. Therefore, the western part of Minusinsk depression receives less rainfall as compared with the eastern part of the region.

Unfortunately the palynological data from the Pleistocene-Holocene boundary is extremely limited. Therefore, it is difficult to assess the climate at that time. The palynological data are known from several incisions to the Pleistocene-Holocene boundary. Grass pollen is predominant (about 65%), in the layer 4–5 deposits (under 13 000 years) in Listvenka site (East Sayans), and tree pollen is about 30%, with spores about 5% (Akimova et al., 1992). Tree pollen (65%), grasses (20%), and spores (15%) occur in the deposits of the overlying layer 3 (end of Sartanian time; Akimova et al., 1992). Tree pollen (80%) prevails (Yamskikh, 2006) over grass pollen (20%) in Eleneva cave (East Sayans) in the deposits of layer 18 (12 040 ± 150; Kuzmin et al., 2011). The tree and grass pollen is present in approximately equal amounts (Yamskikh, 2006) in the Holocene layers 16–17 (10 485 ± 310 BP; Kuzmin et al., 2011).

Thus there was some moistening of climate at the Pleistocene-Holocene boundary in the North-Minusinsk basin and adjacent areas, following the previous period of desiccation. According to Yamskikh (2006), the annual rainfall could reach ~2100 mm near Eleneva cave. About 600 mm of precipitation falls in the cold season. At the Pleistocene-Holocene boundary the annual rainfall decreased to ~600 mm, only ~150 mm of which fell during the cold season (Yamskikh, 2006). Because there is a “rain shadow” from Kuznetsk Alatau, in the west part of North-Minusinsk basin the atmospheric deposition was even less.

The available information indicates that open landscapes continuously existed in the North-Minusinsk basin from LGP to the present. The findings of steppe animals in Holocene deposits from some caves confirms the existence of steppe landscapes in the Holocene (Ovodov, 2009): Proskurjakova Grotto (*Lepus timidus*, *Marmota* sp., *Ovis* or *Capra*), Archaeological Cave (home horses(?), *Lepus timidus*, *Lepus tolai*, *Marmota* sp., *Equus* small form), Kashkulak Cave (home horses, home sheep, *Lepus timidus*, *Marmota* sp.).

Despite the existence of an enabling environment in the region, the biodiversity of large mammal species considerably decreased. Of the 20 species of mammals that lived in the LGP in the open landscapes, only 5 survived to the present. In addition, there was a reduction of areas and population of *Rangifer tarandus* and *Ovis ammon*. There was a change of their biotopes (Table 3). Although previously, these species were abundant in the plain part of the basin, currently these species are preserved only in the mountain landscapes (Red data book…, 2014). *Ovis nivicola* is an extinct

Table 3
Landscape-biotopic structure of large mammals in LGP and currently in Minusinsk depression.

Species	LGP	Currently
Lepus sp.	Open landscapes	Open and semi-open landscapes
Marmota sp.	Open landscapes	–
Canis lupus	Eurytopic landscapes	Eurytopic landscapes
Alopex lagopus	Open landscapes	–
Vulpes vulpes	Open and semi-open landscapes	Open and semi-open landscapes
Cuon alpinus	Mountain landscapes	Mountain landscapes
Ursus arctos	Closed and semi-closed landscapes	Closed and semi-closed landscapes
Ursus savini rossicus	Open landscapes	–
Gulo gulo	Closed and semi-closed landscapes	Closed and semi-closed landscapes
Mels leucurus	Open and semi-open landscapes	Open and semi-open landscapes
Mustela sp.	Closed and semi-closed landscapes	Closed and semi-closed landscapes
Crocuta spelea	Open landscapes	–
Panthera spelaea	Open landscapes	–
Uncia uncial	Mountain landscapes	Mountain landscapes
Felis manul	Mountain landscapes	Mountain landscapes
Panthera spelaea	Open landscapes	–
Mammuthus primigenius	Open landscapes	–
Equus large form	Open and semi-open landscapes	–
Equus small form	Open landscapes	–
Coelodonta antiquitatis	Open landscapes	–
Sus scrofa	Closed and semi-closed landscapes	Closed and semi-closed landscapes
Moschus moschiferus	Closed and semi-closed landscapes	Closed and semi-closed landscapes
Cervus elaphus	Closed and semi-closed landscapes	Closed and semi-closed landscapes
Capreolus pygargus	Closed and semi-closed landscapes	Closed and semi-closed landscapes
Megaloceros giganteus	Open landscapes	–
Alces alces	Closed and semi-closed landscapes	Closed and semi-closed landscapes
Rangifer tarandus	Open landscapes	mountain landscapes
Bison priscus	Open landscapes	–
Bos sp.	Open landscapes	–
Saiga borealis	Open landscapes	–
Ovibos moschatus	Open landscapes	–
Capra sibirica	Mountain landscapes	Mountain landscapes
Ovis ammon	Open landscapes	Mountain landscapes
Ovis nivicola	Mountain landscapes	–

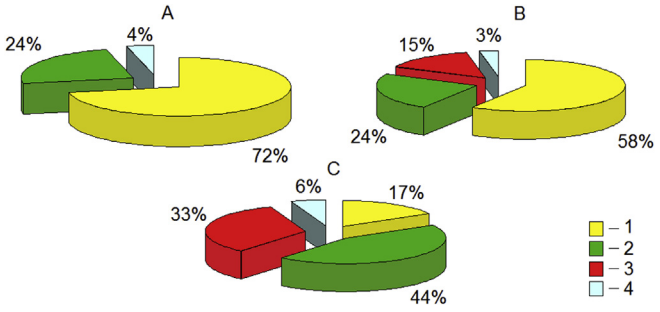

Fig. 2. The ecological structure of the large mammal fauna of North-Minusinsk basin: A – in LGP are reliable present species; B – in LGP with disputed species; C – modern; 1 – open landscapes species; 2 – closed and semi-closed landscapes species; 3 – mountain landscapes species; 4 – eurytopic species.

species that lived in mountain landscapes in the LGP. The modern biodiversity of mountainous animals is greater than in the LGP, due to reindeer and argali (Fig. 2). The extinction of mammals of closed and semi-closed forest landscapes is not detected, in contrast to open and mountain landscapes species.

5.3. Time and causes of large mammal extinction in the North-Minusinsk basin at the Pleistocene-Holocene boundary

At the turn of the Pleistocene-Holocene in most parts of the boreal zone, there was a crisis in the mammoth steppe ecosystem. As a result, drastic restructuring happened in the mammalian fauna. Most large herbivores either became extinct, or their distribution and abundance decreased to a minimum (Vereshchagin and Baryshnikov, 1980, 1985). The North-Minusinsk Basin is not an exception. Of the 14 species of order Artiodactyla that inhabited this area in the Last Glacial period, up to the present only 8 species survived (though occasionally there are 3 species), and of 13 species of Carnivora only 9 remained (4 species are scarce, and 3 are casual visitors). Representatives of the two orders, Proboscidea and Perissodactyla, are totally extinct. All extant species dwell in forest and mountain taiga landscapes (Sokolov, 1979; Vasilchenko and Smirnov, 2010). In the steppe landscapes, hare is the largest, wild herbivorous animal.

The question of the time and cause of the extinction of large mammals at the turn of the Pleistocene-Holocene is under discussion. To answer this question it is necessary to use radiocarbon dating methods. However, such data from the Minusinsk depression are not sufficient at present. Most of the radiocarbon dating of localities in the region was made on charcoal and wood. The direct dating of fossil mammal remains is limited, and much involves a mixture of bone remains without exact species identification (Graf, 2009; Kuzmin et al., 2011). From the material identified to species, the main array of radiocarbon dates are on mammoth and reindeer bones (Table 4).

The available data is not sufficient to discuss the time of the extinction of certain species of mammoth fauna in the region. The maximum population of woolly mammoth in the region occurred in the first half of the Sartanian time. The abundance and distribution of this species was considerably reduced by the beginning of the Holocene (Tables 1, 2, 4). Reindeer lived in the region during the whole LGP in contrast to mammoth, with a large number of *Rangifer tarandus* remains in Paleolithic sites with numerical dating (Table 4). Estimates of the time and the reasons for the extinction of other representatives of the mammoth fauna are not currently possible.

Probably, the largest (*Mammuthus primigenius, Coelodonta antiquitatis, Panthera spelaea, Crocuta spelaea*) and highly specialized (*Vulpes lagopus, Vulpes corsac, Saiga tatarica, Procapra gutturosa, Ovibos pallantis*) species of mammoth fauna did not survive after the Pleistocene and Holocene boundary. Their remains are not found in Holocene locations (Ovodov, 2009; Zubkov et al., 2012).

Table 4
The some radiocarbon dates of mammals bones from North-Minusinsk basin.

№	Species	Bone	14C date	Error	Lab code	Site	Source
1	*Panthera spelaea*	Cranium	25 700	130	OxA-17373	Kurtak 4	Stuart and Lister, 2011
2	*Panthera spelaea*	Mandibula	35 750	400	OxA-20252	Derbina 4	Stuart and Lister, 2011
3	*Panthera spelaea*	Mandibula	35 390	280	OxA-20257	Derbina 4	Stuart and Lister, 2011
4	*Panthera spelaea*	Humerus	20 085	80	OxA-20251	Volchika 2	Stuart and Lister, 2011
5	*Coelodonta antiquitatis*	?	~46 000		SOAN-848	Proskurjakova Grotto	Ovodov, 1992
6	*Bison priscus*	?	40 770	1075	SOAN-1519	Proskurjakova Grotto	Ovodov et al., 1992
7	*Bison priscus*	?	40 690	1150	SOAN-1517	Proskurjakova Grotto	Ovodov, 1992
8	*Bison priscus*	?	40 595	875	SOAN-1518	Proskurjakova Grotto	Ovodov, 1992
9	*Equus* or *Bison priscus*	?	17 660	700	GIN-2862	Shelenka	Graf, 2009
10	*Equus* or *Bison priscus*	?	18 600	2000	GIN-2862	Shelenka	Graf, 2009
11	*Mammuthus primigenius*						Kuzmin et al., 2001
12	*Mammuthus primigenius*	Tusk	20 100	100	GIN-2863	Shelenka	Graf, 2009
13	*Mammuthus primigenius*	?	19 700	200	GIN-2861	Shelenka	Graf, 2009
14	*Mammuthus primigenius*	?	20 200	100	GIN-2860	Chulym river	Kuzmin et al., 2001
15	*Mammuthus primigenius*	?	19 960	80	GIN-3016	Chulym river	Kuzmin et al., 2001
16	*Mammuthus primigenius*	?	20 100	300	GIN-3017	Middle Yenisey	Kuzmin et al., 2001
17	*Mammuthus primigenius*	?	19 500	200	GIN-2859	Middle Yenisey	Kuzmin et al., 2001
18	*Mammuthus primigenius*	?	12 160	175	SOAN-4954	Konzhul	Akimova, 2010
19	*Mammuthus primigenius*	?	11 980	155	SOAN-4953	Konzhul	Akimova, 2010
20	*Mammuthus primigenius*	?	18 930	320	LE-3834	Tarachiha	Kuzmin et al., 2001
21	*Rangifer tarandus*	?	19 850	180	LE-3821	Tarachiha	Graf, 2009
22	*Rangifer tarandus*	?	25 250	1200	LE-4918	Malaya Syia	Ovodov, 2009
23	*Rangifer tarandus*	?	18 090	940	LE-4807	Novoselovo 6	Graf, 2009
24	*Rangifer tarandus*	?	15 950	120	LE-4802	Novoselovo 7	Graf, 2009
25	*Rangifer tarandus*	?	14 220	170	LE-4803	Novoselovo 7	Graf, 2009
26	*Rangifer tarandus*	?	15 030	620	LE-4896	Novoselovo 13	Graf, 2009
27	*Rangifer tarandus*	?	13 630	200	LE-4805	Novoselovo 13	Graf, 2009
28	*Ovis ammon*	Cranium	17 888[a]	110	UBA-28341	Kozhuchovo 1	This paper
29	*Equus ovodovi*	Metatarsale	>45 178		UBA-28340	Kozhuchovo 1	This paper

[a] ^{14}C data, the calibrated data is 20 015–19 382 BC.

The time of extinction of wild horses (*E. ferus* and *E. ovodovi*), large Bovidae, giant deer and marmot in the region is still discussed. In the Holocene sediments of some caves, the remains of a marmot (Grotto Proskuryakova, Archaeological Cave, Kashkulak Cave) tolai (archaeological cave) and "hemione-like" horses (Archaeological Cave) was found (Ovodov, 2009). A bone of a "hemione-like" horse was discovered in the upper layers (about 10 000 BP) of Ui 2 (Vasiliev, 1996). As in the Maina and Ui 2 sites, there are single finds of bison in the layers attributed to the Pleistocene-Holocene boundary. Many images of wild horses and large bulls (bison or wild ox) are known from Holocene rock-art (Kyzlasov, Leontiev, 1980; McNeil, 2005).

Of special note is the *Megaloceros giganteus* extinction. At the present time, the region is extremely poor in giant deer remains, with remains from 5 locations. In the literature, giant deer remains are mentioned in the fauna lists for 3 locations (Drozdov et al., 2005; Motuzko et al., 2010; Polyakov et al., 2014). Other information about *M. giganteus* in the Minusinsk depression is absent. The age of the finds from the Irba-2 site (11 300 ± 190 (LE-0006) 12 550 ± 120 (LE-9927), Polyakov et al., 2014) and the Derbina Gulf (~10 000 (Motuzko et al., 2010)) indicate that the giant deer survived in the Minusinsk depression until the Holocene-Pleistocene boundary. It is quite possible that the giant deer continued to live in the region and in the early Holocene. Dates confirm finds as Holocene (Van der Plicht et al., 2015): in the Baraba Steppe (7865 ± 40 (GrA-56935), and others.) and in the Angara (9235 ± 40 (GrA-56936), and others.). It is possible that these findings are part of a common area, which includes the Minusinsk depression (Van der Plicht et al., 2015, Fig. 6).

Thus, the extinction of the mammoth fauna in Minusinsk depression is not even, and some taxa continued to exist in the Holocene. The possible cause of the mammoth fauna extinction in Minusinsk depression includes the changes in the landscape in the neighboring regions (Malikov, 2014). Reduction of the steep landscapes outside of the basin caused disruption of migration routes of the major representatives of the mammoth fauna. Steppe plant communities that have survived in the basin at present (Kuminova et al., 1976; Polozhij et al., 2002), were not able to maintain the stability of the mammoth fauna, which could have led to the extinction. At the same time, the stability of steppe ecosystems in the region contributed to the preservation of the micro-mammals (Vinogradov, 2010; Dupal et al., 2013), as well as the later extinction of some large mammals (marmot, tolai-hare, wild horse).

However, data for definite conclusions about the reasons for the extinction of the mammoth fauna in the region is currently insufficient. Therefore, further detailed studies using modern methods of dating are necessary.

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