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The distribution of the cave lion *Panthera spelaea* and the cave hyena *Crocuta spelaea* in the Late Pleistocene of Baikal-Yenisei Siberia

Dmitriy G. Malikov*, Valeria V. Burova, Alexey M. Klementiev & Ekaterina L. Malikova

ABSTRACT. An analysis of the geographical distribution of the cave lion (*Panthera spelaea)* and the cave hyena (*Crocuta spelaea*) finds in Baikal-Yenisei Siberia has shown that these species were predominantly confined to different landscapes. The cave lion tended to inhabit plains and river valleys, whereas the cave hyena inhabited foothill areas. The cave hyenas were especially abundant at the beginning of Karginian interstadial (MIS 3) and persisted up to Karginian–Sartanian boundary (MIS 3–MIS 2). The cave lion had a broader chronological distribution during the second half of the Late Pleistocene. *Panthera spelaea* persisted in the region almost until the terminal Pleistocene, and its demise was apparently associated with extinction of the largest representatives of the mammoth fauna.

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KEY WORDS: cave lion, cave hyena, palaeozoogeography, Late Pleistocene, ^{14}C-dating, extinction.

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Распространение пещерного льва *Panthera spelaea* и пещерной гиены *Crocuta spelaea* в позднем плейстоцене Байкало-Енисейской Сибири

Д.Г. Маликов*, В.В. Бурова, А.М. Клементьев, Е.Л. Маликова

РЕЗЮМЕ. Анализ географического распространения находок пещерного льва (*Panthera spelaea*) и пещерной гиены (*Crocuta spelaea*) в Байкало-Енисейской Сибири показал, что эти виды были преимущественно приурочены к различным ландшафтам. Пещерный лев, как правило, населял равнины и речные долины, тогда как пещерная гиена обитала в предгорьях. Пещерные гиены были особенно многочисленны в начале каргинского интерстадиала (MIS 3) и сохранялись до каргинско-сартанской границы (MIS 3–MIS 2). Пещерные львы имели более широкое хронологическое распространение во второй половине позднего плейстоцена. *Panthera spelaea* сохранялся в регионе почти до конца плейстоцена, и его вымирание, по-видимому, было связано с вымиранием крупнейших представителей мамонтовой фауны.

КЛЮЧЕВЫЕ СЛОВА: пещерный лев, пещерная гиена, палеозоогеография, поздний плейстоцен, ^{14}C-датирование, вымирание.

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Introduction

The cave lion *Panthera spelaea* (Goldfuss, 1810) and cave hyena *Crocuta spelaea* (Goldfuss, 1823) were the apex mammalian predators of the Middle and Late Pleistocene in Siberia. As the predominant prey of these species were large gregarious ungulates (reindeer, horses and bison), these extinct carnivorans directly competed for food with Paleolithic people, who also mostly hunted the aforementioned herbivores. As such, the distribution of the cave lion and cave hyena is interesting not only from strictly paleontological point of view, but is also important for understanding the relationship between humans and animal populations.

The cave lion and cave hyena are widely represented in the Pleistocene fossil assemblages of Eurasia, and are especially common in the Southern Siberia. Whereas the cave lion remains are widespread and were even found beyond the Polar Circle (Boeskorov & Baryshnikov, 2013; Stuart & Lister, 2011), the finds of cave hyena are confined only to the southern regions, and in Siberia are not known north of 57 parallel (Baryshnikov & Vereshchagin, 1996; Shpansky & Kuzmin, 2021; Stuart & Lister, 2014). In the south of Siberia, remains of *C. spelaea* occur sporadically and for a long time were restricted to cave sites in Altai and alluvial deposits of Western Siberia (Baryshnikov & Vereshchagin, 1996; Alekseeva, 1980). For the territory of the Baikal-Yenisei Siberia (a vast area in Eastern Eurasia) data on the distribution of both species remained scarce until recently (Ovodov, 2009a). An array of new finds, many of which were ^{14}C-dated, may shed new light on the geographical distribution and extinction of *P. spelaea* and *C. spelaea* in this poorly studied region. In this paper *C. spelaea* is considered as a separate species following Lewis & Werdelin (2022).

Materials and methods

This paper summarizes the previously published and original data on the cave lion and cave hyena bone remains, including those collected by the authors over the years in localities of various types (cave and alluvial sites, slope deposits, Paleolithic sites) and further those stored at the Institute of Geology and Mineralogy of the Siberian Branch of the Russian Academy of Sciences (IGM SB RAS), the Institute of the Earth's Crust SB RAS (IEC SB RAS), Irkutsk State University, and Khakass National Regional Museum. To display the spatial distribution of the finds, a map was made using remote sensing methods. It is based on a digital terrain model taken from the US Geological Survey website (https://earthexplorer.usgs.gov/). The processing of remote sensing materials and the design of the map were performed in the ArcGIS Pro software package. All materials are included in the attachment (Table 1).

AMS-radiocarbon dates were obtained from the following laboratories: 14CHRONO Centre Queens University Belfast (UK) — coded UBA; Accelerating mass-spectrometer of the Institute of Nuclear Physics SB RAS (Novosibirsk, Russia) — coded NSKA and GV; Korea Institute of Geoscience and mineral resources (South Korea) — coded KGM. All dates were 2-sigma calibrated using OxCal 4.4 software (https://c14.arch.ox.ac.uk/oxcal/OxCal.html) and IntCal20 calibration set (Reimer et al., 2020). Both non-calibrated (^{14}C a BP) and calibrated (cal a BP) dates are provided.

The reliability of the isotopic signatures of the collagen extracts was addressed using their chemical composition. These values must be similar to those of collagen extracted from fresh bone to be considered reliable for isotopic measurements and radiocarbon dating. The collagen with atomic C/N ratios lower than 2.9 or higher than 3.6 is altered or contaminated, and should be discarded (DeNiro, 1985; Ambrose, 1990).

Results and discussion

Distribution of cave lions and cave hyenas

The analysis of the geographical distribution of the finds of *C. spelaea* and *P. spelaea* revealed an interesting pattern, characteristic of the entire region of the Baikal-Yenisei Siberia (Fig. 1). Virtually all finds of *P. spelaea* are confined to the plain areas of the region, predominately river valleys. Remains are largely known from alluvial or archaeological sites (Abramova *et al*., 1991; Klement'ev *et al*., 2011). Even in the Selenga Highlands (Western Transbaikalia) remains of this predator have also been found in the valley deposits of large rivers.

In contrast to the above observed distribution of *P. spelaea* finds, that of *C. spelaea* displays a different pattern. In the Baikal-Yenisei Siberia, remains of the cave hyena mainly come from cave taphocoenoses, including such sites as Proskuryakov and Dvuglazka grottoes, Archaeologicheskaya, Zapovednay, Kurtun-1, and Gorome-1 caves, among many others (Ovodov, 2009a; Klement'ev *et al*., 2011; Malikov & Mitchenko, 2022). Exclusions are isolated Late Pleistocene finds of the cave hyena, which were found in several Palaeolithic sites and few unstratified beach localities (Klement'ev *et al*., 2011; Ovodov, 2009b; Motuzko *et al*., 2010).

These data show that in the region of the Baikal-Yenisei Siberia, cave lions preferred plain areas whereas cave hyenas mostly inhabited low and middle altitude highlands, where they used caves as dens. In those cave sites where remains of hyenas cooccur with bones of cave lions, the former always significantly prevail over the latter. So, in Kurtun-1 cave, 21 bones of *C. spelaea* and just three bones of *P. spelaea* were found (Filippov *et al*., 2012); in Proskuryakov grotto, the cave hyena is represented by 94 bones, while the cave lion is only known from one bone (Ovodov, 2009a); the prevalence of the cave hyena was also observed at Gorome-1 cave and Dvuglazka grotto (Abramova *et al*., 1991; Tashak & Kobylkin, 2015). We assume that bones or carcasses of the cave lions might have been brought to these caves by hyenas. In the absolute majority of cave sites of the region, the remains of the cave lion are absent.

Table 1. The sites of *Crocuta spelaea* and *Panthera spelaea* remains in the Baikal-Yenisei Siberia region

				General site age		Number of bones					
Site name	**Latitude**	**Longitude**	**Site type**	**MIS***	**14C age BP based on non-lion/hyena material**	**Lion**	**Hyena**	**Lion/hyena skeletal element**	**14C age BP based on lion/hyena bone**	**Reference for lion/hyena**	**General reference**
Novoselovo log	55.0295	90.9845	open	MIS 5-4			1		>48428 (UBA-39703)	this paper	
Arheologicheskaya cave	54.4071	89.4138	cave	MIS 5-4			+		>45785 (UBA-46351)	this paper	Ovodov, 2009a
Zapovednaya cave	53.90	90.60	cave	MIS 5-4			3	maxilla, mandibula, dente	>45853 (UBA-46352)	this paper	
Berezhekovo (Kurtak)	55.1456	91.5551	open	MIS 5-4		+				this paper	
Krasnoturansk	54.3322	91.6015	open	MIS 5-4	>48747	1		femur		this paper	Malikov, 2021
Zaktui	51.7030	102.6602	open	MIS 5-4 + MIS 3	>50100 basal layer		2	R metacarpal III (MIS3) and ulna (MIS5-4)	35560±300 (OxA-19719)	Shchetnikov *et al.*, 2015a	
Kurtun-1 cave	52.5967	105.9466	cave	MIS 3	>40000–33500	3	21			Filippov *et al.*, 2012	
Ineyskaya cave	53.8481	89.6932	cave	MIS 3			29			this paper	
Fanatikov cave	53.31	90.35	cave	MIS 3			315		42140±330 (GV-02630); 37350±448 (GV-02629)	Vasiliev *et al.*, 2020	Ovodov, 2009a
Proskuryakov grotto	54.4515	89.4557	cave	MIS 3	45770–40595	1	94			Ovodov, 2009a	
Dvuglazka grotto	54.0726	91.0695	cave	MIS 3	28600–26580	+	102			Ovodov, 2009a	Abramova, 1985
Tamir	50.2666	107.4	open	MIS 3		1		ulna	40210±350 (OxA -18712)	Stuart & Lister, 2011	
Shchapova 2	52.2987	104.3049	open	MIS 3		1		tibia		Malikov *et al.*, 2020	
Hotyk	52.2280	109.8322	open	MIS 3			1	cranium		Klement'ev *et al.*, 2011	Khubanova *et al.*, 2016
Arta-2	51.2333	112.3833	open	MIS 3	37360±2000	+				Kirillov & Kasparov, 1990	Khenzykhenova *et al.*, 2011
Derbina IV	55.3192	92.4976	open	MIS 3		+		mandibula	35750±400 (OxA -20252); 35390±280 (OxA-20257)	Stuart & Lister, 2011	

Table 1 (*continued*).

Ust-Odinsk	52.4638	103.7592	open	MIS 3		1		femur	34600±600 (OxA -25677)	Klement'ev *et al.*, 2011	Shchetnikov *et al.*, 2015b
Tuyana	51.70	102.6833	open	MIS 3	47800–26350	1	2			this paper	Kozyrev *et al.*, 2012
Yasnoe 1	56.0647	92.8805	open	MIS 3	33610–26660	2		cranium, atlas		Klement'ev, 2021	
Derbina V	55.3328	92.443	open	MIS 3	32430–29230		1			Motuzko *et al.*, 2010	
Nepa	59.2472	108.2347	open	MIS 3	33100–26065	1		metacarpal II		Klement'ev, 2013	
Novoselovo alluvial	55.0406	91.0253	open	MIS 3		1		humerus	26248±199 (UBA-41723); 26190±215 (NSKA-02214)	this paper	
Ust'-Maltat-2, Pokrovka-1,2	55.3214	92.4842	open	MIS 3	27740±150		3			Motuzko *et al.*, 2010	Kuzmin *et al.*, 2011
Gorome-1 cave	52.1125	99.7352	cave	MIS 3		+	+	sceletum	26180±810 (LU-7588)	Tashak & Kobylkin, 2015	
Kurtak 4	55.1372	91.5199	open	MIS 3		1		cranium	25700±130 (OxA -17373)	Stuart & Lister, 2011	
Kamenka A	51.7475	108.2911	open	MIS 3	40500–22675	1		ulna		Germonpre & Lbova, 1996	
Shergol'dzhin	50.15	108.3166	open	MIS 3		1		radius		Konstantinov & Nemerov, 1978	
Buret'	52.9868	103.5081	open	MIS 2	27695–21190	+				this paper	Kuzmin *et al.*, 2011
Sedova	52.2697	104.2991	open	MIS 2	25520–23900	1		phalanx I		Klement'ev *et al.*, 2011	Rogovskoy *et al.*, 2013
Kurtak, Kashtankovsky beach	55.1366	91.5144	open	MIS 2	24800–20800	1		mandibula		this paper	Drozdov *et al.*, 2005
Mal'ta	52.8452	103.5220	open	MIS 2		1		metatarsale II	21500±100 (OxA-17033)	Stuart & Lister, 2011	
Malye Goly	53.9351	106.0823	open	MIS 2		1		mandibula	20540±80 (KGM-IBn170035)	this paper; Erbajeva *et al.*, 2017	
Volchika II	55.3047	92.298	open	MIS 2		1		humerus	20085±80 (OxA-20251)	Stuart & Lister, 2011	

Table 1 (*continued*).

Elovka	51.789	102.66	open	MIS 2		1		radius	18350±75 (OxA-20672)	Stuart & Lister, 2011; Shchetnikov *et al*., 2015b	
Kubekovo	56.149	93.113	open	MIS 2		1		metatarsale	17915±70 (OxA-17054)	Stuart & Lister, 2011	
Onon River	50.58	115.4	open	MIS 2		1		radius	17910±75 (OxA-16982)	Stuart & Lister, 2011	
Kokorevo 2	54.9437	90.9619	open	MIS 2	13300–11550	24				Abramova, 1979	Kuzmin *et al*., 2011
Afontova Gora II	55.9938	92.8069	open	MIS 2		9				Akimova *et al*., 2021	Akimova *et al*., 2021
Tashtyk 1	54.6961	90.8492	open	MIS 2	14020–12180	1				Abramova, 1979	Kuzmin *et al*., 2011
Tarachiha	55.0576	91.0797	open	MIS 2	19850–18930	2				this paper	Kuzmin *et al*., 2011
Sannyy mys	52.15	109.45	open	MIS 2	20000–18000	1		ulna		this paper	
Roshcha Zvezdochka	52.2733	104.2604	open	MIS 2		1		radius		Klement'ev *et al*., 2011	Rogovskoy *et al*., 2013
Baday-II	52.8693	103.6051	open	Late Pleistocene		1		metacarpal		Ermolova, 1978	
Pshenichnaya	52.3001	104.3012	open	Late Pleistocene		+				Klement'ev *et al*., 2011	
Ozernaya Balya	55.8354	102.9704	open	Late Pleistocene		1		radius		this paper	
Pervomayskiy, Bratsk Reservoir beach	53.7475	103.2471	open	Late Pleistocene		+				this paper	
Sagan-zaba	52.6827	106.4776	open	Late Pleistocene		1		metacarpal		Klement'ev *et al*., 2011	
Ilganskaya	53.6	102.4833	open	Late Pleistocene		1		mandibula		Klement'ev *et al*., 2011	
Malyshevka	53.6124	103.5336	open	Late Pleistocene		1		mandibula		Klement'ev *et al*., 2011	
Tayturka	52.8751	103.4840	open	Late Pleistocene		1		calcaneus		Klement'ev *et al*., 2011	
Markova	53.9295	102.0777	open	Late Pleistocene		1		radius		Klement'ev *et al*., 2011	
Bain-zurhe	51.1166	106.4	open	Late Pleistocene		+				this paper	

Table 1 (*ended*).

Kyahta	50.3333	106.4666	open	Late Pleistocene	+				Arembovskii, 1958	
Shimbilik	50.6	109.5666	open	Late Pleistocene	1		mandibula		this paper	
Yugolok	54.1833	103.2833	open	Late Pleistocene	1		mandibula		this paper	
Gorohovo	52.2613	104.3002	open	Late Pleistocene	1		humerus		this paper	
Novogrudinino	52.1516	104.4202	open	Late Pleistocene	1		axis		this paper	
Verhnemarkovo	57.3166	107	open	Late Pleistocene	1		calcaneus		this paper	
Ul'kan	57.2408	107.3125	open	Late Pleistocene	1		scapula		this paper	
Kondabaevo	50.9656	108.7108	open	Late Pleistocene	1		scapula		Klement'ev *et al.*, 2011	
Ulazy	54.9945	91.0890	open	Late Pleistocene	1		mandibula		this paper	
Svirsk	53.0833	103.3333	open	Late Pleistocene	1		metatarsale		this paper	
Koma	52.15	107.45	open	Late Pleistocene		1	tibia		Klement'ev *et al.*, 2011	
Zaigraevo	51.8166	108	open	Late Pleistocene		1	cranium		Baryshnikov & Vereshchagin, 1996; Klement'ev *et al.*, 2011	
Bol'shoy Kunaley	51.4166	107.6	open	Late Pleistocene		1	mandibula		this paper	
Titovo	52.2546	104.2735	open	Late Pleistocene	1		metatarsale		Klement'ev *et al.*, 2011	
Beliy gorod cave	55.6013	93.5027	cave	Late Pleistocene	+				Privalikhin *et al.*, 2013	
Unylkskaya cave	54.4371	98.9871	cave	Late Pleistocene		+			Baryshnikov & Vereshchagin, 1996	
Torgashinskoe	55.9581	92.9524		Late Pleistocene		+			Baryshnikov & Vereshchagin, 1996	
Tohzasskiy grotto	54.4452	89.4681	cave	Late Pleistocene		4			Ovodov, 2009a	
Petuhovskaya cave	54.4199	89.4588	cave	Late Pleistocene	12				this paper	
Uzhur	55.3209	89.8724	open	Late Pleistocene	1		cranium		Ovodov & Zaika, 2008	
Primorsk	55.1833	91.85	open	Late Pleistocene	1		mandibula		this paper	

* — MIS: Marine Isotope Stages

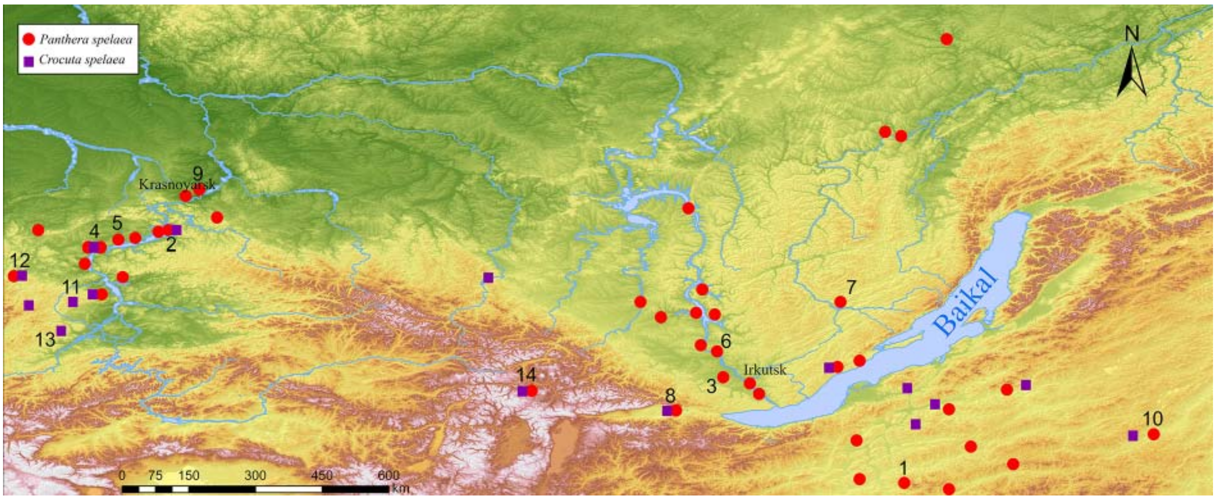

Fig. 1. The geographical distribution of the Late Pleistocene remains of cave lion *P. spelaea* and cave hyena *C. spelaea* in the region of Baikal-Yenisei Siberia. The numbers correspond to the numbers in Table 2.

Other finds that should be discussed here are cave hyena remain from Yakutia mentioned by Diedrich (2022). It is not clear from the latter article from where exactly the material comes from and its current place of storage. According to section "3.1 Institutional abbreviations": "One mandible is from the 545 km long Vilyuy River terraces near Tynda in Amur Oblast, Middle-East Siberia, Far East Russia, similar to other cranial material figured herein from other former collections" (Diedrich, 2022). Also, the article says: "Several specimens were used from the recent e-bay portal and by photographs send by https://ninijian.com/, and www.henskensfossils.nl/) which 'Siberian sites' were not mentioned there in some cases" (ibid.).

Based on this information the material comes from the Vilyui River near Tynda (the Amur region) (Diedrich, 2022). The Vilyui River, being one of the largest tributaries of the Lena River, originates in Krasnoyarsk region and is mostly located in Yakutia, where it flows through the Central Siberian Plateau (Gavrilov, 1971). There are no Tynda town or Tynda River there. Yet there is the Gilyui River (545 km long, a right tributary of the Zeya River, Amur basin) in the Amur Region, with Mogot and Tynda being its main tributaries (Prohorov, 1971). The Tynda town in the Amur region is located at the same latitude (N 55.1496°, E 124.7364°) as the northernmost hyaenas finds from Baikal-Yenisei Siberia (Table 1). Thus, there is probably an error in Diedrich's article and it is the Gilyui River in the Amur region where the material comes from. Hence there is still no evidence on the occurrence of the cave hyena north of 56°N in Eastern Siberia.

It is currently impossible to determine the boundary between the ranges of the Siberian *C. spelaea* and Far Eastern *C. ultima ussurica* Baryshnikov et Vereshchagin, 1996 (Baryshnikov & Vereshchagin, 1996; Baryshnikov, 2014). Far eastern *C. u. ussurica* is characterized by larger cheek teeth with a relatively smaller postcranial skeleton (Lewis & Werdelin, 2022). Most publications lack morphological descriptions of hyena remains from Baikal-Yenisei Siberia. The hyena remains analyzed in this article do not differ morphologically from typical Siberian *C. spelaea* bones. On this basis, we assume that all these finds belong to *C. spelaea*. Further detailed morphological and paleo-DNA studies are necessary to clarify the distribution boundary between these two fossil hyena species.

Radiocarbon dating and temporal distribution of the cave lion and cave hyena

The history of cave lions in Baikal-Yenisei Siberia can be reconstructed quite confidently. Remains of Pantherinae are known in Southern Siberia starting as early as the Early Pleistocene; their bones are present in such sites as Bachatsky quarry, Kurtak and Zasukhino (Vangengejm *et al*., 1990; Sotnikova & Foronova, 2014). Undisputed *P. spelaea* is recorded no later than the early Late Pleistocene; at this time, their remains are numerous in localities of the Kurtak archaeological area. The Late Pleistocene history of the latter species can be reconstructed using numerous ^{14}C dates of its bones and associated fauna remains (Table 2). These dates come from both Minusinsk depression and Baikal part of the discussed region and cover the time interval of 40.2–17.9 ka without significant interruptions. They attest the regular presence of cave lions throughout the studied territory during the whole span of the Karginian interstadial (MIS 3) and the LGM (Fig. 2).

Remains of the cave lion with radiocarbon dates are not known in the region after 17915±70 or 17910±75 ^{14}C a BP (Stuart & Lister, 2011), which corresponds to the end of the LGM (Fig. 2). They are however present in some sites of the Late Paleolithic (Abramova *et al*., 1991), some of which may be younger than these dates.

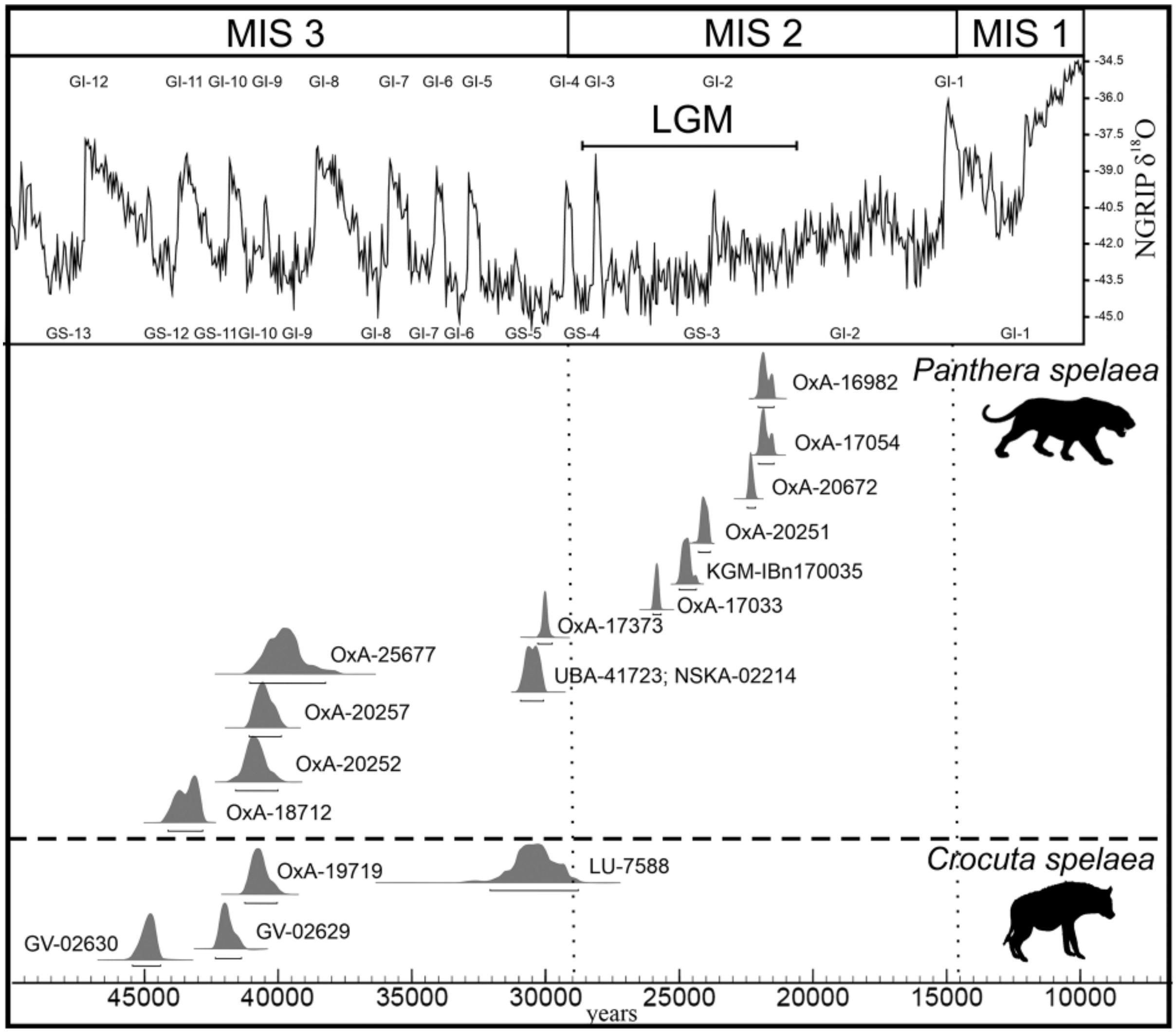

Fig. 2. Calibrated age distributions of the Late Pleistocene remains of *Panthera spelaea* and *Crocuta spelaea* in the region of Baikal-Yenisei Siberia along the $\delta^{18}O$ curve of ice core NGRIP GICC05 (Rasmussen *et al*., 2014). The graphs express the distribution of age in calibrated years at two standard deviations (95.4%).

The youngest finds of the cave lion are known from Tashtyk 1, Afontova Gora II and Kokorevo 2 sites in Yenisei Siberia, which are dated to the terminal Pleistocene (~14–11.5 ka). It is thus possible that *P. spelaea* persisted in the Southern Siberia until the final of Pleistocene.

In the south of Western Siberia, the distribution of lions follows the same pattern. The youngest lion remains are known in the upper reaches of the Ob River and its tributaries. These remains date to 15.9 ka (Vasiliev *et al*., 2018). In the Tomsk Ob region, the youngest lion remains are aged 39.3 ka (Shpanskiy & Svyatko, 2018).

Reconstruction of the history of *C. spelaea* in Baikal-Yenisei Siberia is difficult due to the small number of available dates for this species. To date, only seven dated finds of the cave hyena are known for the region (Table 1). Of these, five were obtained from the bones of hyenas from the Minusinsk depression, one from the Tunka Valley and one from the Eastern Sayan. We consider the remains of a hyena from the Novosyolovo log locality to be the most ancient find. Radiocarbon dating of a jaw from this locality showed an extra-limit age of more than 48428 ^{14}C a BP (UBA-39703). It is most likely that the jaw comes from the deposits of the first half of the Late Pleistocene (one of the warm intervals within MIS 5), which are found in this area. Two other dates, which also showed an extralimital age, were obtained from the remains of hyenas from the Archeologicheskaya (>45785 ^{14}C a BP) and Zapovednaya (>45853 ^{14}C a BP) caves. In our opinion, these remains date back to the very beginning of the Karginian interstadial (MIS 3) and, for this reason, were beyond the scope of the ^{14}C-dating method. For the remains of *C. spelaea* from the Fanatikov cave, dates have been obtained indicating their early Karginian age (Vasiliev *et al*., 2020).

Table 2. ^{14}C dates of the bone remains of *Crocuta spelaea* and *Panthera spelaea* in the region of Baikal-Yenisei Siberia. The numbers correspond to the numbers in Fig. 1.

№	Bone	Lab. code	^{14}C age BP	C/Nat	Site	Reference
			Panthera spelaea			
1	ulna	OxA-18712	40210±350	3.1	Tamir	Stuart & Lister, 2011
2	mandibula	OxA-20252	35750±400	3.2	Derbina IV	Stuart & Lister, 2011
2	mandibula	OxA-20257	35390±280	3.2	Derbina IV	Stuart & Lister, 2011
3	femur	OxA-25677	34600±600		Ust-Odinsk	Shchetnikov *et al*., 2015c
4	humerus	UBA-41723	26248±199	3.17	Novoselovo alluvial	this paper
		NSKA-02214	26190±215	3.12		
5	cranium	OxA-17373	25700±130	3.3	Kurtak 4	Stuart & Lister, 2011
6	metatarsale II	OxA-17033	21500±100	3.3	Mal'ta	Stuart & Lister, 2011
7	mandibula	KGM-IBn170035	20540±80		Malye Goly	this paper
2	humerus	OxA-20251	20085±80	3.2	Volchika II	Stuart & Lister, 2011
8	radius	OxA-20672	18350±75	3.4	Elovka	Stuart & Lister, 2011
9	metatarsale	OxA-17054	17915±70	3.1	Kubekovo	Stuart & Lister, 2011
10	radius	OxA-16982	17910±75	3.1	Onon River	Stuart & Lister, 2011
			Crocuta spelaea			
4	mandibula	UBA-39703	>48428	3.06	Novoselovo log	this paper
11	dente	UBA-46352	>45853	3.14	Zapovednaya cave	this paper
12	costa	UBA-46351	>45785	3.18	Arheologicheskaya cave	this paper
13	sacrum	GV-02630	42140±330		Fanatikov cave	Vasiliev *et al*., 2020
13	sacrum	GV-02629	37350±448		Fanatikov cave	Vasiliev *et al*., 2020
8	metacarpal	OxA-19719	35560±300		Zaktui	Shchetnikov *et al*., 2015a
14	—	LU-7588	26180±810		Gorome-1 cave	Tashak & Kobylkin, 2015

The remains of cave hyena from Zaktui site are of special interest (Shchetnikov *et al*., 2015a). Previously, the date 35560±300 ^{14}C a BP was obtained from a hyena metacarpal found in the middle part of the geological section (Table 1). Later a radius of *C. spelaea* (stored at IEC SB RAS) was excavated from the base of the section. These deposits are older than 50 ka (Shchetnikov *et al*., 2015a). Hence, Zaktui is the only locality in Southern Siberia where *in situ* remains of *C. spelaea* are known from differently aged parts of the section.

In addition to dated remains, several sites in the Minusinsk depression contain undated remains of hyenas. These are mainly cave taphocenoses of the Karginian (MIS 3) interstadial (Ovodov, 2009a): grottoes of Proskuryakov (40595–45770 ^{14}C a BP), Tokhzasky and Dvuglazka (26580–28600 ^{14}C a BP). Hyena remains come from Sartanian (MIS 2) sites, including Derbinsky Bay (Motuzko *et al*., 2010) and layer 4 (17420±330 ^{14}C a BP) of Dvuglazka Grotto (Ovodov & Martynovich, 1992). These finds, originating from relatively young (MIS 2) deposits, require to be assessed in light of the cave hyena demise (see below), as we believe that they were indeed redeposited. The youngest remains of a cave hyena in the south of Western Siberia indicate the extinction of this species no earlier than 38.2 ka (Vasiliev *et al*., 2018).

The dynamics of the species extinction in the Northern Eurasia indicates that the cave hyena died out no later than 31 ka, and in Siberia its extinction is thought to happen earlier than in Europe, at about 43 ka (Shpansky & Kuzmin, 2021; Stuart & Lister, 2014). Nevertheless, there is one date for Southern Siberia that implies a later extinction of *C. spelaea*. The date 26180±810 ^{14}C a BP (LU-7588), recovered from the cave hyena bone from Gorome-1 cave, is the youngest for *C. spelaea* remains in the discussed region (Tashak & Kobylkin, 2015). This ^{14}C date is however problematic as no information was provided regarding the material used, methods applied (liquid scintillation method or AMS), and the C/N ratio of the studied sample. Even if the date from Gorome-1 is valid, it would imply that the extinction of the cave hyena in the Southern Siberia occurred about 31 ka (a calibrated value for the above date), i.e., near the boundary between the Karginian interstadial (MIS 3) and Sartanian stadial (MIS 2). There is however a gap of 10 ka (Fig. 2) between the aforementioned date and other dates for the cave hyena obtained from the territory of Southern Siberia (e.g., Fanatikov cave and Zaktui site). New dates are thus necessary to confirm the presence of the cave hyena in the region during this time interval.

Conclusion

The accumulation of an array of ^{14}C dates for the cave lion *P. spelaea* and the cave hyena *C. spelaea* made it possible to clarify their distribution and extinction history in Baikal-Yenisei Siberia. It is shown that in the region the cave lion tended to inhabit lowland environments, and the cave hyena mostly inhabited mountainous regions. In large numbers, the remains of hyenas are found only in cave taphocenoses; in open-type localities, they are scarce.

The cave hyena lived in the region in the Middle–early Late Pleistocene. The species was especially abundant at the beginning of the Karginian time (MIS 3) — at that time hyenas inhabited many caves of the region, which they obviously used as dens. It is possible that hyenas survived here up to the Karginian-Sartanian (MIS 3–MIS 2) boundary, but no reliable finds of this animal are known in younger deposits. In Eastern Siberia hyaenas did not disperse beyond the Altai-Sayan mountain region and their bones were not found north of 56°N.

Unlike hyenas, cave lions were ubiquitous in Baikal-Yenisei Siberia almost until the end of the Late Pleistocene. This is confirmed both by the ^{14}C dating of their remains and by the regular finds of the cave lion bones at Paleolithic sites. This species apparently became extinct near the terminal Pleistocene along with other representatives of the mammoth fauna.

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References

Abramova Z.A. 1979. [Palaeolithic of Yenisei River: Afontovskaya Culture]. Novosibirsk: Nauka. 157 p. [in Russian].

Abramova Z.A. 1985. [Mousterian grotto in Khakasii] // Kratkie Soobshcheniya Instituta Arkheologii Akademii Nauk SSSR. Vol.181. P.92–98 [in Russian].

Abramova Z.A., Astahov S.N., Vasiliev S.A., Ermolova N.M. & Lisitsyn N.F. 1991. [Palaeolithic of Yenisei River]. Leningrad: Nauka. 158 p. [in Russian].

Akimova E.V., Anoikin A.A., Vasiliev S.K., Galukhin L.L., Drozdov N.I., Dudko A.A., Zolnikov I.D., Klementiev A.M., Lysenko D.N., Razgildeeva I.I., Slavinsky V.S., Stasyuk I.V., Tomilova E.A., Harevich V.M. & Tsybankov A.A. 2021. [Afontova Gora II Late Paleolithic site: Results of multidisciplinary research in 2014]. Novosibirsk: IAET SB RAS Publishing. 260 p. [in Russian].

Alekseeva E.V. 1980. [Mammals from the Southeast of Western Siberia (Carnivores, Proboscides, Ungulates)]. Moscow: Nauka. 188 p. [in Russian].

Ambrose S.H. 1990. Preparation and characterization of bone and tooth collagen for isotopic analysis // Journal of Archaeological Science. Vol.17. P.431–451.

Arembovskii I.V. 1958. [Stratigraphy of Quaternary deposits of the South of Eastern Siberia] // Proceedings of Irkutsk University. Geological series. Vol.14. No.2. P.9–55 [in Russian].

Baryshnikov G.F. 2014. Late Pleistocene hyena *Crocuta ultima ussurica* (Mammalia: Carnivora: Hyaenidae) from the paleolithic site in Geographical Society cave in the Russian Far East // Proceedings of the Zoological Institute RAS. Vol.318. No.3. P.197–225.

Baryshnikov G.F. & Vereshchagin N.K. 1996. [A brief review of Quaternary hyenas (Hyaenidae) of Russia and adjoining regions] // Proceedings of the Zoological Institute. Vol.270. P.7–65 [in Russian, with English summary].

Boeskorov G.G. & Baryshnikov G.F. 2013. [Late Quaternary of Yakutia]. Saint-Petersburg: Nauka. 197 p. [in Russian].

Diedrich C. 2022. Thick skin cutters of Siberian frozen mummies — the coevolutionary adaptation of Eurasian Ice Age spotted hyenas // Acta Zoologica. Vol.103. No.2. P.220–241.

DeNiro M.J. 1985. Postmortem preservation and alteration of in-vivo bone collagen isotope ratios in relation to palaeodietary reconstruction // Nature. Vol.317. P.806–809.

Drozdov N.I., Chekha V.P. & Haesaerts P. 2005. [Geomorphology and Quaternary Deposits of Kurtak Geoarchaeological District (North-Minusinsk Depression)]. Krasnoyarsk: RIO KSPU, V.P. Astaf’eva. 112 p. [in Russian].

Erbajeva M.A., Shchetnikov A.A., Filinov I.A., Krainov M.A., Malikov D.G. & Nechaev I.O. 2017. [New data on geology and paleontological characteristics of Pleistocene site Malye Goly (Prebaikalia)] // Bulletin of Moscow Society of Naturalists. Geological Series. Vol.92. No.4. P.27–33 [in Russian, with English summary].

Ermolova N.M. 1978. [Late Anthropogene Theriofauna of the Angara River Valley]. Novosibirsk: Nauka. 220 p. [in Russian].

Filippov A.G., Grebnev I.E., Henzyhenova F.I., Erbaeva M.A., Martynovitch N.V. & Popova SM. 2012. [The stratigraphy and faunal remains in sediments Kurtun-1 cave on Baikal. Eurasia in the Cenozoic] // The Stratigraphy, Paleoecology, and Culture. Vol.1. P.226–238 [in Russian, with English summary].

Gavrilov A.M. 1971. [The Great Soviet Encyclopedia]. Vol.5. Veshin-Gazeli. Moscow: Soviet Encyclopedia. P.69 [in Russian].

Germonpre M. & Lbova L. 1996. Mammalian remains from the Upper Paleolithic site of Kamenka, Buryatia (Siberia) // Journal of Archaeological Science. Vol.23. P.35–57.

Kirillov I.I. & Kasparov A.K. 1990. [Archeology of Transbaikalia. Problems and prospects: the Paleolithic Age] // Khronostratigrafiya Paleolita Severnoi, Tsentralnoi i Vostochnoi Azii i Ameriki. Doklady Mezhdunarodnogo Simpoziuma. Novosibirsk. P.194–198 [in Russian].

Khenzykhenova F., Sato T., Lipnina E., Medvedev G., Kato H., Kogai S., Maximenko K. & Novosel’zeva V. 2011. Upper paleolithic mammal fauna of the Baikal region, east Siberia (new data) // Quaternary International. Vol.231. P.50–54.

Khubanova A.M., Klement’ev A.M., Khubanov V.B., Posokhov V.F. & Murzintseva A.E. 2016. Diet and environment reconstruction of *Coelodonta antiquitatis* in the Late Pleistocene by C-N isotope analyses of paleontological material (archeological complex Khotyk and Kamenka, West Transbaikalia) // Environmental Dynamics and Global Climate Change. Vol.7 (13). P.163–169.

Klementiev A.M. 2011. [The steppes of the Selengin Dauria in the prehistoric era (paleontological excursion)] // Steppes of Northern Eurasia. Orenburg. P.385–388 [in Russian].

Klement'ev A.M. 2013. [Fauna of the Late Karga Period of the Irkutsk Amphitheater] // Bulletin of the Irkutsk State University. Geoarchaeology, Ethnology, and Anthropology Series. Vol.1. No.2. P.30–43 [in Russian, with English summary].

Klementiev A.M. 2021. [Paleogeography of the Krasnoyarsk depression in the paleolithic era based on paleotheriological data] // Routes of Evolutionary Geography. Issue 2: Proceedings of the 2nd Scientific Conference in Memory of Professor A.A. Velichko. Moscow: Institute of Geography, RAS. P.611–616 [in Russian].

Klement'ev A.M., Shchetnikov A.A., Sizov A.V. & Filinov I.A. 2011. [Rare and problematic species of macroteriofauna in the Pleisocene fossil record of Southern Baikal region] // Baikal Zoological Journal. Vol.3. No.8. P.5–9 [in Russian, with English summary].

Konstantinov M.V. & Nemerov V.F. 1978. [Antiquities of the Chikoi River (on the northern borders of Mongolia)] // Archeology and Ethnography of Mongolia. Novosibirsk. P.205–217 [in Russian].

Kozyrev A.S., Shchetnikov A.A., Klementyev A.M., Filinov I.A., Fedorenko A.B. & Henzyhenova F.I. 2012. [The Geoagraphy and Age of Upper Neopleistocene Fossil Artefacts of the Tunka Rift Valley] // Bulletin of the Irkutsk State University. Geoarchaeology, Ethnology, and Anthropology Series. Vol.1. No.1. P.106–125 [in Russian, with English summary].

Kuzmin Y.V., Orlova L.A., Zenin V.N., Lbova L.V. & Dementiev V.N. 2011. [Radiocarbon dating of the Palaeolithic of Siberia and the Russian Far East: materials for 14C data catalogue (as of the end of 2010)] // Stratum Plus. Vol.1. P.171–200 [in Russian, with English summary].

Lewis M.E. & Werdelin L. 2022. A revision of the genus *Crocuta* (Mammalia, Hyaenidae) // Palaeontographica, Abteilung A: Palaeozoology — Stratigraphy. Vol.322. No.1–4. P.1–115.

Malikov D.G. 2021. [Krasnoturansk — new location of mammot fauna of the first half of Late Pleistocene in Minusinsk depression] // Scientific Notes of the Minusinsk Museum of Local Lore named after N.M. Martyanova. Vol.3. P.3–25 [in Russian, with English summary].

Malikov D.G. & Mitchenko A.M. 2022. [Zapovednaya Cave — the new location of Pleistocene and Holocene mammals fauna in Minusinsk depression (Southern Siberia)] // Geosfernye issledovaniya. Vol.1. P.87–97 [in Russian, with English summary].

Malikov D.G., Sizova V.V., Berdnikova N.E., Berdnikov I.M. & Lokhov D.N. 2020. [Archeozoological characteristics of the Shchapova 2 Paleolithic site in Irkutsk] // Bulletin of the Irkutsk State University. Geoarchaeology, Ethnology, and Anthropology Series. Vol.33. P.3–22 [in Russian, with English summary].

Motuzko A.N., Vasiliev S.Yu., Vashkov A.A., Elenskiy Yu.N., Kravchenko E.N. & Oreshnikov I.A. 2010. The mammoth and mammoth fauna of late Pleistocene from Northern areas of the Minusinskaya hollow // Proceedings of the VI International Mammoth Conference. Yakutsk. P.139–149.

Ovodov N.D. 2009a. [Ancient beasts of Khakassia] // Astroarheologii — natural science a tool for learning protoscience and astral religions priesthoods of ancient cultures of Khakassia. Krasnoyarsk. P.189–199 [in Russian].

Ovodov N.D. 2009b. [Cave hyena (*Crocuta spelaea* Goldf.) of the Altai-Sayan Mountains] // 200 years of national paleontology. Moscow. P.93 [in Russian].

Ovodov N.D. & Martynovich N.V. 1992. [New data on mammals and birds from Dvuglazka grotto in Khakassia] // Problems of archeology, ethnography, history and local history Yenisei province. Vol.1. Krasnoyarsk. P.78–83 [in Russian].

Privalikhin V.I., Oshchepkov P.V., Podbolotsky A.V. & Ovodov N.D. 2013. [Finds of archaeological artifacts and animal bones in the caves of the upper reaches of the Bazaikha River and its tributaries] // Archaeological research of antiquities of the lower Angara and its tributaries. Krasnoyarsk: Krasnoyarsk Regional Museum of Local Lore. P.29–41 [in Russian].

Prokhorov A.M. (ed.) 1971. [The Great Soviet Encyclopedia]. Vol.6. Gazlift-Gogolevo. M.: Soviet Encyclopedia. P.523 [in Russian].

Rasmussen S.O., Bigler M., Blockley S.P., Blunier T., Buchardt S.L., Clausen H.B., Cvijanovic I., Dahl-Jensen D., Johnsen S.J., Fischer H., Gkinis V., Guillevic M., Hoek W.Z., John Lowe J., Pedro J.B., Popp T., Seierstad I.K., Peder Steffensen J., Svensson A.M., Vallelonga P., Vinther B.M., Walker M.J.C., Wheatley J.J. & Winstrup M. 2014. A stratigraphic framework for abrupt climatic changes during the Last Glacial period based on three synchronized Greenland ice-core records: refining and extending the INTIMATE event stratigraphy // Quaternary Science Reviews. Vol.106. P.14–28.

Reimer P., Austin W., Bard E., Bayliss A., Blackwell P., Bronk Ramsey C., Butzin M., Cheng H., Edwards R.L., Friedrich M., Grootes P.M., Guilderson T.P., Hajdas I., Heaton T.J., Hogg A.G., Hughen K.A., Kromer B., Manning S.W., Muscheler R., Palmer J.G., Pearson C., van der Plicht J., Reimer R.W., Richards D.A., Scott E.M., Southon J.R., Turney C.S.M., Wacker L., Adolphi F., Büntgen U., Capano M., Fahrni S.M., Fogtmann-Schulz A., Friedrich R., Köhler P., Kudsk S., Miyake F., Olsen J., Reinig F., Sakamoto M., Sookdeo A. & Talamo S. 2020. The IntCal20 Northern Hemisphere Radiocarbon Age Calibration Curve (0–55 cal kBP) // Radiocarbon. Vol.62. No.4. P.725–757.

Rogovskoy E.O., Kogai S.A., Kozyrev A.S. & Popov A.A. 2013. [Paleolithic sites of Middle and Upper Neopleistocene in Irkutsk: problems and perspectives of researches] // Vestnik NSU. Series: History and Philology, Archaeology and Ethnography. Vol.12. No.5. P.97–107 [in Russian, with English summary].

Shchetnikov A.A., Khenzykhenova F.I., Klement'ev A.M., Simakova A.N., Semenei E.Y. & Filinov I.A. 2015a. Changes of environments and climate during the Late Pleistocene and Holocene reconstructed from aeolian and colluvial deposits of the Zaktui site (Tunka rift valley, Baikal region) // Quaternary International. Vol.355. P.80–89.

Shchetnikov A.A., Klementiev A.M., Filinov I.A. & Semeney E.Yu. 2015b. Large mammals from the Upper Neopleistocene reference sections in the Tunka rift valley, southwestern Baikal Region // Stratigraphy and Geological Correlation. Vol.23. No.2. P.214–236.

Shchetnikov A.A., Semeney E.Yu., Filinov I.A. & Khenzykhenova F.I. 2015c. New data on the Late Pleistocene stratigraphy and paleoenvironment of the southwestern Baikal area (Siberia) // Quaternary International. Vol.355. P.65–79.

Shpansky A.V. & Svyatko S.V. 2018. Felids (Felidae, Mammalia) in Pleistocene faunas of West Siberian Plain // Podobina V.M. (ed.). Evolution of Life on the Earth: Proceedings of the V International Symposium (November 12–16, 2018). Tomsk: Publishing House of TSU. P.227–229 [in Russian, with English summary].

Shpansky A. & Kuzmin Y. 2021. Chronology of the MIS 3 megafauna in southeastern West Siberia and the possibility of late survival of the Khozarian steppe mammoth (*Mammuthus trogontherii chosaricus*) // Radiocarbon. Vol.63. No.2. P.575–584.

Sotnikova M.V. & Foronova I.V. 2014. First Asian record of *Panthera* (*Leo*) *fossilis* (Mammalia, Carnivora, Felidae) in the Early Pleistocene of Western Siberia, Russia // Integrative Zoology. Vol.9. P.517–530.

Stuart A.J. & Lister A.M. 2011. Extinction chronology of the cave lion *Panthera spelaea* // Quaternary Science Reviews. Vol.30. P.2329–2340.

Stuart A.J. & Lister A.M. 2014. New radiocarbon evidence on the extirpation of the spotted hyaena (*Crocuta crocuta* (Erxl.)) in northern Eurasia // Quaternary Science Reviews. Vol.96. P.108–116.

Tashak V.I. & Kobylkin D.V. 2015. [The exploration of the Gorome cave on the Oka plateau] // Bulletin of the Buryat scientific center of SB RAS. Vol.4. P.11–19 [in Russian, with English summary].

Vangengejm E.A., Erbaeva M.A. & Sotnikova M.V. 1990. Pleistocene Mammals from Zasuhino, Western Transbaikalia // Quartarpalaontologie. Vol.8. P.257–264.

Vasiliev S.K., Parkhomchuk E.V., Serednyov M.A., Milutin K.I., Kuzmin Ya.V., Kalinkin P.N. & Rastigeev S.A. 2018. [Radiocarbon dating of the remains of rare Pleistocene megafauna species in Southern Siberia] // Problems of Archaeology, Ethnography, Anthropology of Siberia and Neighboring Territories. Novosibirsk: IAET SB RAS Publ. Vol.24. P.42–46 [in Russian, with English summary].

Vasiliev S.K., Parkhomchuk E.V., Serednyov M.A., Milutin K.I., Rastigeev S.A. & Parkhomchuk V.V. 2020. [Late Pleistocene megafauna from the south of Western and Central Siberia: new data on radiocarbon dating and new finds from alluvial sites in 2020] // Problems of Archaeology, Ethnography, Anthropology of Siberia and Neighboring Territories. Novosibirsk: IAET SB RAS Publ. Vol.26. P.43–50 [in Russian, with English summary].