Cave lion (*Panthera spelaea*) from the Pleistocene of Chuvashiya, European Russia

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ABSTRACT. Two mandibles of the cave lion referred to the nominotypical subspecies *Panthera spelaea* spelaea are recorded for the first time in the Pleistocene of Chuvashiya. The distribution map of this subspecies in the Eastern Europe is given.

KEY WORDS: Panthera spelaea, Pleistocene, Eastern Europe.

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Пещерный лев (*Panthera spelaea*) из плейстоцена Чувашии, Европейская Россия

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РЕЗЮМЕ. Две нижнечелюстные кости пещерного льва, впервые найденные в плейстоцене Чувашии, отнесены к номинативному подвиду *Panthera spelaea spelaea*. Приведена карта распространения этого подвида в Восточной Европе.

КЛЮЧЕВЫЕ СЛОВА: Panthera spelaea, плейстоцен, Восточная Европа.

Introduction

The cave lion (*Panthera spelaea* (Goldfuss, 1810)) was widely distributed in the Pleistocene of Holarctic from British Isles to Alaska and Yukon Territory. This animal occupied an important position in the northern ecosystems, being at the top of the trophic pyramid of the mammoth fauna (Vereshchagin & Baryshnikov, 1992).

The taxonomic position of cave lion is variously interpreted. Some authors regard it as a northern subspecies of the recent species *P. leo* (L., 1758) (Kurtén, 1968; Kurtén & Andersen, 1980; Yamaguchi *et al.*, 2004), which is testified by molecular evidence (Burger *et al.*, 2004). Other researchers, mainly Russian ones, consider the cave lion to be a distinct species (Vereshchagin, 1971; Baryshnikov & Boeskorov, 2001; Sotnikova & Nikolskiy, 2006).

Bones and teeth of *P. spelaea* are found in many localities of the Middle and Late Pleistocene of the Northern Eurasia, being there, as a rule, very scant. Vereshchagin (1971) provided a survey of findings from the territory of the former USSR. These data are supplemented here by the information on two mandibles of the cave lion from European Russia, recorded in the territory of Chuvashiya, in the basin of the Volga River. One is kept at the Chuvashiyan National Museum, Cheboksary (CHNM), another is stored in the private collection of the same city. This communication deals with their description.

For the comparison, collections of Zoological Institute, Russian Academy of Sciences in Saint Petersburg (ZIN), Geological-Mineralogical Museum of Kazan University in Kazan (GMMK), Nature History Museum in London (NHM), Muséum National d'Histoire Naturelle in Paris (MNHN), and Institute of Systematics and Evolution of Animals in Krakow (ISEA) were used.

Description

The right mandible (CHNM 9105) originates from the territory of Chuvashiya, the exact place of its discovery being, however, unknown. The canine, cheek teeth p4 and m1, and alveoli of p3 are present (Fig. 1). The anterior mental foramen is doubled; posterior one is situated below the p3. Mental prominence is well developed. Ventral mandibular margin is straight. The ratio between the m1 length and the length of c1–m1 row is 38.0%.

The second finding is represented by the fragment of right mandible (Fig. 2), which was recovered on the bank of Bol'shaya Shatma River in Krasnoarmeisk District of Chuvashiya in the July of 2005. Its mandibular ramus with coronoid, condylar, and angular processes are broken off. The dentition is represented by the incisor i3, canine, cheek teeth p4 and m1, and alveoli of p3. The length and width of the i3 are 8.6 mm and 8.1 mm correspondingly. Postcanine diastema is moderate, mental prominence is well developed. The ventral mar-



Figure 1. Mandible of *Panthera spelaea spelaea* from Chuvashiya (unknown locality), CHNM 9105, in labial (A) and lingual (B) view.

gin of the mandible below the lower carnassial tooth m1 is weakly convex, which is characteristic of the cave lion (Vereshchagin, 1971). The ratio between the m1 length and the length of c1–m1 row is 38.7%.

Other examined mandibles of the cave lion from the various localities in Western and Eastern Europe markedly differ in dimensions, which presumably reflects sexual variation (Tabs 1 and 2). The presence of the sexual dimorphism in the cave lion has been established by Turner (1984) on the basis of difference in size of the upper canine (C1), the lower canine (c1), and the lower carnassial tooth (m1) between males and females. As in the recent *P. leo*, males of *P. spelaea* exceeded females in the size.

The mandibles, whose width of lower canine measured at the level of the lower margin of enamel exceeds 19.5 mm, are ascribed by us to males. In these mandibles,

lower carnassial tooth m1 exceeds 31 mm in the length. Therefore, the minimum value of the m1 length in examined specimens coincides with the mean of this length (30.73 mm, n=77) calculated by Kurtén (1985) for the European males of *P. spelaea*. Judging from rather small size of the lower canine and small length of m1, both mandibles from Chuvashiya belong to females.

Stratigraphical position of the Chuvashiyan samples is indefinite. These mandibles are morphometrically very close to the specimen found near Mansurovo village at the mouth of the Kama River (Averianov *et al.*, 1992). Similar dimensions are established for the cave lion mandibles from other localities of Western and Eastern Europe, including Zoolithen Cave, which is the type locality for *P. spelaea* (Tabs 1 and 2).

The right mandible with broken m1 from the early Middle Pleistocene of Forest Bed (NHM M6165) in

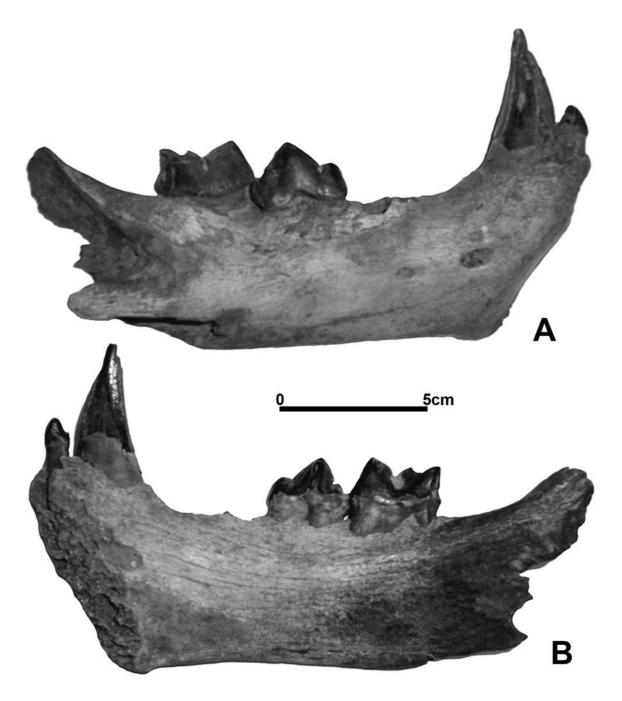


Figure 2. Mandibular fragment of *Panthera spelaea spelaea* from Bolshaya Shat'ma River, Chuvashiya, private collection, in labial (A) and lingual (B) view.

England possesses the lower canine (length 26.5 mm, width 19.1 mm) corresponding to a female. In the length of the c1-m1 row (132.7 mm) and length of the p3-m1 row (81.5 mm), this specimen is only inconspicuously larger than female specimens of *P. spelaea* from the European Late Pleistocene. Thus, the mandibular size does not seem to be a reliable criterion in determining the geological age of the cave lion remains. Meantime, the index of correlation between the width of the lower carnassial tooth m1 and its length is treated to be

considerably more important for the geological attribution of cave lion findings. For the examined mandibles it is varied from 46.4% to 54.7%, 49.8% in average (n=20). In the specimens from the early Middle Pleistocene localities of Europe, the value of this index is considerably higher, varying from 53.5% to 56.5% and constituting in average 55.5% (n=7) (Schütt & Hemmer, 1978). Similar index has been obtained by us for the isolated lower carnassial tooth m1 (NHM F66, length 30.5 mm, width 17.0 mm) from early Middle

Table 1. Measurements of mandible of Panthera spelaea spelaea from Eastern Europe.

Measurements,		East European Plain	ean Plain				Urals	
Mm	Unknown locality,	Bolshaya	Mansurovo,	Shubnoe, Don River,				Medvezhiya
	Chuvashiya, CHNM 9105	Shat'ma River, Private collection	Kama River, GMMKU 378	ZIN 29417 (Vere-shchagin, 1971)	Secrets Ca	Secrets Cave, Private collection	collection	Cave, ZIN 29397-2, cast
Total length	225.3	1	237.0	247	260.0	260.0	283.5	221.1
Length of c1-m1 row	1	121.2	122.3	123	140.0	135.0	163.0	114.7
Length of p3-m1 row	76.4	75.7	0.97	I	78.2	76.3	85.3	73.6
Height of the mandible behind m1	49.31	I	50.0	-	58.0	56.7	64.0	44.1
Height of the mandible behind p3	48.30	I	47.5	-	55.0	52.4	61.8	47.0
Teeth:								
c1, length	27.7	26.6		28		23.8	2.62	
width	18.1	17.5		61		17.5	21.2	
p3, length					18.8	18.6		
width					10.0	10.1		
p4, length	25.2	27.2		26	28.6	27.1	30.5	27.6
width	12.5	12.2		13	13.5	13.2	15.7	13.0
m1, length	29.0	28.2	30.4	28	30.1	29.4	33.0	26.7
width	14.1	13.6	13.7	13	14.8	14.8	17.5	13.4
Index for ml width/length, %	48.6	48.2	45.1	46.4	49.2	50.3	53.0	50.1

Table 2. Measurements of mandible of Panthera spelaea spelaea from Western Europe.

Measurements,	Germany				Poland					France	
mm	Zoolithen			Wier	Wierzchowska Górna	órna			l'Herm	Unknown locality	locality
	MHN 272M	ISEA 6602	ISEA 6710	ISEA 6799	ISEA 6803	ISEA 6804	ISEA 6806	ISEA 6809	NMNM 1903-20	MNMN 1868-68, cast	1868-68,
Total length		245.5	246		1		1	218.5		251.1	256.1
Length of c1-m1 row	135.3	127.5	120.2	1	ı	128.0	118.0	117.4	135.7	133.2	134.3
Length of p3-m1 row	75.4	ı	69.1	ı	ı	75.1	68.4	70.1	81.0	81.2	79.4
Height of the mandible behind m1	I	50.1	51	57.8	61.0	52.9	46.1	51.3	8.09	52.8	53.2
Height of the mandible behind p3	49.3	44.7	46	52.8	57.4	52.3	42.9	44.4	56.0	47.3	49.1
Teeth:											
cl, length					29.2	27.0		22.7		28.2	26.0
width					21.6	19.5		16.6		21.5	20.3
p3, length	18.2		18.3			19.3	17.3	17.8	21.1	20.8	20.8
width	11.0		9.4			11.1	9.6	9.0	11.6	11.7	11.7
p4, length	27.7		26.3		30.3	28.1	27.5	24.5	28.6	29.4	29.2
width	14.5		12.3		17.0	14.4	11.8	13.0	14.8	15.9	16.0
m1, length	28.1		26.4	30.6	31.1	30.9	26.4	27.1	31.3	32.5	31.9
width	14.4		13.0	15.7	17.0	16.2	12.7	12.8	15.3	16.1	16.4
Index for ml width/length, %	51.2		49.2	51.3	54.7	52.4	48.1	47.2	48.9	49.5	51.4

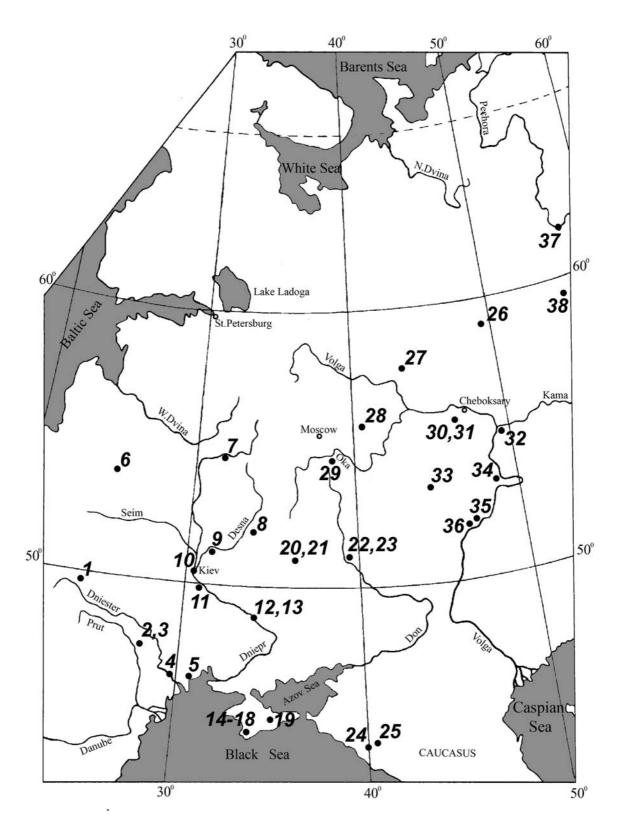


Figure 3. Map of localities of *Panthera spelaea* in the late Middle Pleistocene and Late Pleistocene of Eastern Europe (according to Sukachev *et al.*, 1966; Vereshchagin, 1971; Soffer, 1985; Kalinovski & Kuzmina, 1993; Baryshnikov *et al.*, 1996; Averianov *et al.*, 1999; Enloe *et al.*, 2000; Chubur, 2001; Burova, 2002; Sotnikova & Nikolskiy, 2006; and original data).

Pleistocene locality of Westbury Quarry Cave in England (55.7%).

There are two currently recognized subspecies of *P. spelaea* in Europe (Schütt & Hemmer, 1978): the early Middle Pleistocene *P. s. fossilis* (von Reichenau, 1906) and later *P. s. spelaea* (Goldfuss, 1810) occurring in the Europe from the late Middle Pleistocene to the end of Pleistocene. The cave lion from Chuvashiya seems to belong to the nominotypical subspecies. It should be mentioned that these subspecies are occasionally considered as distinct species (Sotnikova & Nikolskiy, 2006).

Discussion

The examined first findings of the cave lion (*P. spelaea*) in Chuvashiya appear to be among the northernmost ones for the East European Plain.

The mapping of localities with presence of the cave lion remains shows that this animal was widespread in the Eastern Europe, with exception of the area covered by the ice sheet (Fig. 3). In the western part of Eastern Europe, the localities do not occur northwards to 54°N, being spread in the central part as far as 58°N and approaching 62°N in the North Ural (Medvezhiya Cave).

Unlike the cave bear (*Ursus spelaeus* Rosenmüller, 1794) and cave hyena (*Crocuta spelaea* (Goldfuss, 1823)), who were absent in the northern and central regions of the East European Plain, the cave lion occurred throughout all this territory. *P. spelaea* inhabited river valleys occupied by flood-plain forests and thickets bordering with steppe and tundra-steppe on watersheds.

The existence in the severe conditions of the periglacial landscape was provided by a dense fur coat as well as by the capability to hunting herbivores of various sizes, up to bison and young mammoths, which gave a possibility for predators to consume fresh meet by summer as well as by winter. Judging from the presence of canine dimorphism similar to that in the modern lion, the cave lion lived and hunted in groups (Yamaguchi *et al.*, 2004), which was a part of its survival strategy.

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References

Averianov A.O., Baryshnikov G.F., Garutt V.E., Garutt N.V. & Fomicheva N.L. 1992. [Volga River Fauna of Pleistocene Mammals in Geological-Mineralogical Museum

- of Kazan University]. Kazan: Izdatelstvo Kazanskogo Universiteta. 164 p. [in Russian].
- Baryshnikov G. & Boeskorov G. 2001. The Pleistocene cave lion, *Panthera spelaea* (Carnivora, Felidae) from Yakutia, Russia // Cranium. Vol.18. No.1. P.7–24.
- Baryshnikov G., Hoffecker J. & Burgess R. 1996. Paleontology and zooarchaeology of Mezmaiskaya Cave (northwestern Caucasus, Russia) // Journal of Archaeological Science. Vol.23, No.3, P.313–335.
- Burger J., Rosendahl W., Loreille O., Hemmer H., Eriksson T., Götherström A., Hiller J., Collins M.J., Wess T. & Alt K.W. 2004. Molecular phylogeny of the extinct cave lion *Panthera leo spelaea* // Molecular Phylogenetics and Evolution. Vol.30. No.3. P.841–849.
- Burova N.D. 2002. [Peculiarities of accumulation of mammal bone remains in the Upper Paleolithic site of Yudinovo] // Sinitsyn A.A., Sergin V.Y. & Hoffecker J.F. (eds.). [Peculiarity of Development of the Upper Palaeolithic in Eastern Europe. Kostenki in the Context of the Palaeolithic of Eurasia. Research. Vol.1] Sankt-Peterburg. P.196–205 [in Russian].
- Chubur A.A. 2001. [Byki. New Paleolithic Microregion and its Position in the Upper Paleolithic of Russian Plain]. Bryansk: Bryansk segodnya. 132 p. [in Russian].
- Enloe J., David F. & Baryshnikov G. 2000. Hyenas and hunters: Zooarchaeological investigations at Prolom II Cave, Crimea // International Journal of Osteoarchaeology. Vol.10. No.5. P.310–324.
- Kalinovski P.F. & Kuzmina I.E. 1993. [First find of remains of cave lion in Belarus] // Doklady Academii Nauk Belarusi. T.37. No.6. P.108–110 [in Russian].
- Khromov A.A., Arkhangelsky M.S. & Ivanov A.B. 2001. [Large Quaternary Mammals of Middle and Lower Volga River Basin]. Dubna. 256 p. [in Russian]
- Kurtén B. 1968. Pleistocene Mammals of Europe. London: Weidenfeld and Nicolson. 317 p.
- Kurtén B. 1985. The Pleistocene lion of Beringia // Annales Zoologici Fennici. Vol.22. No.1. P.117–121.
- Kurtén B. & Anderson E. 1980. Pleistocene mammals of North America. New York: Columbia Universty Press. 443 p.
- Schütt G. & Hemmer H. 1978. Zur Evolution des Löwen (*Panthera leo* L.) im europäischen Pleistozän // Neues Jahrbuch für Geologie und Paläontologie. Hf.4. S.228–255
- Soffer O. 1985. The Upper Paleolithic of the Central Russian Plain. San Diego, New York, London et al.: Academic Press. 539 p.
- Sotnikova M. & Nikolskiy P. 2006. Systematic position of the cave lion *Panthera spelaea* (Goldfuss) based on cranial and dental characters // Quaternary International. Vol.142/143. P.218–228.
- Sukachev V.N., Gromov V.I. & Bader O.N. 1966. [Upper Paleolithic site Sungir'] // Trudy Geologicheskogo Insti-

^{1 —} Malaya Ilovitsa; 2 — Starye Duruitory; 3 — Vykhvatintsy; 4 — Tiraspol'; 5 — Odessa; 6 — Smorgon'; 7 — Smolensk; 8 — Yudinovo; 9 — Chernigov; 10 — Kirillovskaya; 11 — Mezhirichi; 12 — Kremenchug; 13 — Kodak; 14 — Shaitan-Koba; 15 — Adzhi-Koba; 16 — Buran-Kaya; 17 — Syuren'1; 18 — Syuren'2; 19 — Prolom 2; 20 — Avdeevo; 21 — Byki 1; 22 — Kostenki 1, 2, 4, 8; 23 — Shubnoye; 24 — Mezmaiskaya Cave; 25 — Gubs River; 26 — Sobolevo; 27 — Rossolovo; 28 — Sungir'; 29 — Tula; 30 — Bolshaya Shat'ma River; 31 — Chuvashiya (no exact locality); 32 — Mansurovo; 33 — Pustyn' 2; 34 — Tunguz; 35 — Devichi Gorki; 36 — Khoroshevkiy; 37 — Medvezhiya Cave; 38 — Secrets Cave.

tuta AN SSSR. T.162. P.1-140 [in Russian].

Turner A. 1984. Dental sex dimorphism in European lions (*Panthera leo* L.) of the Upper Pleistocene: Palaeoecological and palaeoethological implications // Annales Zoologici Fennici. Vol. 21. No.1. P.1–8.

Vereshchagin N.K. 1971. [The cave lion and its history in the Holarctic and on the territory of the USSR] // Trudy Zoologicheskogo Instituta AN SSSR. T.49. P.123–199

[in Russian].

Vereshchagin N.K. & Baryshnikov G.F. 1992. The ecological structure of the "Mammoth Fauna" in Eurasia // Annales Zoologici Fennici. Vol.28. No.3–4. P.253–259.

Yamaguchi N., Cooper A., Werdelin L. & Macdonald D.W. 2004. Evolution of the mane and group-living in the lion (*Panthera leo*): A review // Journal of Zoology. Vol.263. No.4. P.329–342.