ISSN 0012-4966, Doklady Biological Sciences, 2018, Vol. 482, pp. 191–193. © Pleiades Publishing, Ltd., 2018.
Original Russian Text © D.O. Gimranov, V.G. Kotov, M.M. Rumyantsev, V.I. Silaev, A.G. Yakovlev, T.I. Yakovleva, N.V. Zelenkov, M.V. Sotnikova, M.M. Devyashin, N.A. Plasteeva, N.E. Zaretskaya, I.M. Nurmukhametov, N.G. Smirnov, P.A. Kosintsev, 2018, published in Doklady Akademii Nauk, 2018, Vol. 482, No. 2.

GENERAL BIOLOGY

A Mass Burial of Fossil Lions (Carnivora, Felidae, *Panthera* (*Leo*) *ex gr. fossilis-spelaea*) from Eurasia

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Received April 11, 2018

Abstract—The vertebrate fauna from the cave deposits in Imanai Cave in the Southern Urals (53°02′ N, 56°26′ E) has been studied. It contains 715 bones that belonged to at least 11 individuals of fossil lion (*Panthera* (Leo) ex gr. *fossilis-spelaea*). It has been established that this is one of the largest Eurasian burial sites of fossil lions. The bones were accumulated due to the natural death of animals inside the cave. The age and sex estimations have shown that at least six adult males and five adult females died there. According to the accompanying fauna, radiocarbon, geochemical, and mineralogical analyses and archaeological finds, the interval of the lion bone accumulation is determined as the first half to middle of Late Pleistocene (OIS 5–3).

DOI: 10.1134/S0012496618050046

Mass burials of large predatory mammals unconnected with human activities are quite rare in the Late Pleistocene. The most common localities of this type are burials of cave bears (*Ursus spelaeus* Rosenmuller, 1794) [1, 2]. Sporadic "graveyards" are known of the small cave bear (*U. savini* Andrews, 1922) and brown bear (*U. arctos* L., 1758) [3, 4]. These species used caves for hibernation during the cold season. Natural deaths of animals resulted in the accumulation of their bones in the cave deposits. Lions, unlike bears, did not use caves as dens, except for the part of the cave near the entrance. The largest known locality of fossil felids is Rancho La Brea in California. This locality contained bones of more than 80 individuals of *P. (Leo) atrox* Leidy, 1853 [5, 6] which died in tar pits that formed a natural trap. The bones of cave lions (*P. spelaea* Goldfuss, 1810) also accumulated in the Binagadi locality in the Caucasus [7], which contained 64 bones from 11 individuals. A single mass burial of cave lions is known in Eurasia, Zoolithen Cave in Germany [8]. It contained 229 bones of at least eight animals. The remains of lions were found in the inner part of the cave, and accumulated due to predatory activity of cave hyenas (*Crocuta spelaea* Goldfuss, 1823) [8].

In 2009, we studied the Imanai Cave (Southern Urals, Republic of Bashkortostan, Meleuz raion, 53°02′ N, 56°26′ E). This paper describes remains from this cave.

In the inner part of the cave, we found 715 bone remains of at least 11 individuals of cave lion. The remains included 381 distal limb bones (carpals, tarsals, metapodials, phalanges, and sesamoids), 37 teeth, 120 vertebrae and ribs, 39 bones of proximal limb bones (humerus, radius, ulna, femur, and tibia), 19 fragments of shoulder blade, and pelvis, and 18 skull fragments. The bones did not show any evidence of human or predator activity. The collection is housed in the Museum of the Institute of Plant and Animal Ecology, Ural Branch of the Russian Academy of Sciences, Yekaterinburg (collection no. 2284).

Age estimation. The estimation of the individual age of the lions was based on the following characters: stage of eruption, fusion of the skull sutures and postcranial epiphyses. We found only permanent teeth. The sutures in all skulls are obliterated; the epiphyses are fused in all bones. No heavily worn teeth, i.e.,

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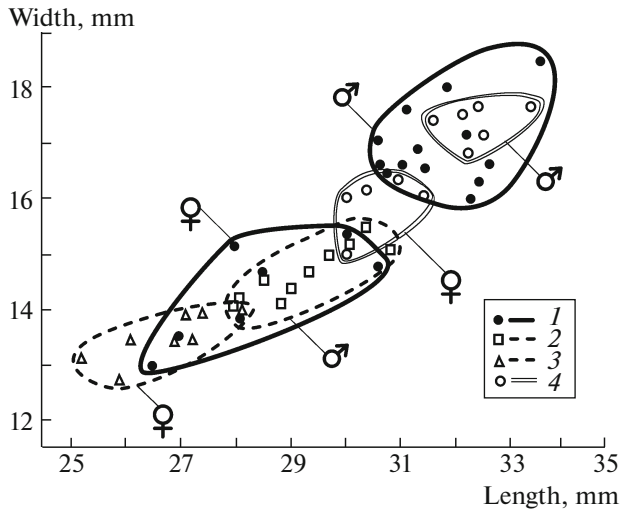

Fig. 1. Sexual dimorphism in the size of the lower carnassial (m1) of giant cave felines: (*1*) cave lion from Weirzchowska Gorna Cave (Poland), (*2*) male of modern African lion, (*3*) female of modern African lion [9, 10], (*4*) cave lion from Imanai Cave.

belonging to old individuals, have been found. All bones belonged to adult animals.

Sexual dimorphism. Males of modern African lion *P.* (*Leo*) *leo* L., 1758 are usually considerably larger than females [9]. Similar size differences can be observed in the fossil lions from Imanai Cave. The most interesting results come from the analysis of teeth, e.g., from the ratio diagram of the maximum crown length to the width of the lower carnassial (m1) (Fig. 1). The sample from Imanai Cave, as well as a sample from Weirzchowska Gorna in Poland [9, 10], consists of two size groups. Modern African lions in the size of m1 are clearly separated into males and females [9, 10], therefore a group of larger teeth from Imanai belonged to males, and the group of smaller teeth belonged to females (six and five teeth, respectively, Fig. 1); i.e., in Imanai Cave, remains of males and females were represented almost equally.

Accompanying fauna. Along with the bones of fossil lions, we found remains of other large mammals (*Lepus* sp., *Castor fiber*, *Marmota bobak*, *Canis lupus*, *Cuon alpinus*, *Vulpes vulpes*, *V. corsac*, *Meles* sp., *Gulo gulo*, *Martes* sp., *Mustela* sp., *Ursus kanivetz*, *U. savini*, *U. arctos*, *U. thibetanus*, *Mammuthus primigenius*, *Equus ferus*, *Coelodonta antiquitatis*, *Alces alces*, *Bison priscus*, *Saiga tatarica*, *Ovis ammon*), small mammals (*Talpa europaea*, *Sorex* sp., *Crocidura* sp., *Ochotona pusilla*, *Spermophilus* sp., *Eliomys quercinus*, *Sicista* sp., *Allactaga major*, *Apodemus uralensis*, *A.* ex gr. *uralensis-agrarius*, *Ellobius talpinus*, *Cricetulus migratorius*, *Allocricetulus eversmanni*, *Cricetus cricetus*, *Clethrionomys rufocanus*, *Cl.* ex gr. *glareolus-rutilus*, *Cl. rutilus*, *Lagurus lagurus*, *Eolagurus luteus*, *Arvicola terrestris*, *Microtus gregalis*, *M. oeconomus*, *M. agrestis*, *M. arvalis*), birds (*Coturnix coturnix*, *Tetrao tetrix*, *Tadorna tadorna*, *Apus apus*, *Turdus viscivorus*, *Lagopus lagopus*, *Calcarius lapponicus*, *Emberiza* ?*schoeniclus*, *Corvus corax*, *Falco tinnunculus*), reptiles (*Elaphe* cf. *dione*, *Zamenis* cf. *longissimus*, *Vipera berus*, *V. ursinii*, *V.* cf. *berus*, *Serpentes* indet.), amphibians (*Bufo* sp., *Anura* indet.), and fishes (*Esox lucius*, *Perca fluviatilis*). The fossil assemblage is dominated by the small cave bear remains (*U. savini*).

The geological age of the fauna. Most species of this fauna inhabited the Southern Urals during the Late Pleistocene and Holocene [11]. The Aesculapian snake (*Z.* cf. *longissimus*) and Asian black bear (*U. thibetanus*) were part of the fauna of the Mikulino Interglacial (oxygen isotope stage 5e , OIS 5e) [12, 13]. The dhole (*C. alpinus*), small cave bear (*U. savini*), cave bear (*U. kanivetz*) and mountain sheep (*O. ammon*) occurred in the area in the first half of the Late Pleistocene (OIS 5–OIS 3) [11]. The mammoth (*M. primigenius*), woolly rhinoceros (*C. antiquitatis*) and steppe bison (*B. priscus*) were present in the Southern Urals throughout the Late Pleistocene (OIS 5–2) [11]. The garden dormouse (*E. quercinus*) [11] and Lapland longspur (*C. lapponicus*) are unknown from the Pleistocene deposits of Eurasia [14], and belong to the Holocene fauna. The presence of species dated to different geological periods in the same faunal assemblages indicates that the sediment has been disturbed.

Together with the bone remains in the upper "horizons" we found stone tools equivalent to bifacial axes from layer 3 of the Mousterian Site Il'skaya in the Northern Caucasus. The archaeological material of Il'skaya Site is dated to the beginning–first half of the Late Pleistocene [15]. The ^{14}C date obtained from the bone of small cave bear provided an age of 26320 ± 1790 years BP (GIN-14244). This corresponds to the end of OIS 3 or the Bryansk (Denekamp) Interstadial. The total of the analysis of the composition of the vertebrate fauna, archaeological material, and the radiocarbon dating show that the bone remains in Imanai Cave were accumulated throughout the Late Pleistocene and Holocene.

The results of mineralogical and geochemical studies at the Institute of Geology of Komi Research Centre of the Ural Branch of the Russian Academy of Sciences have shown that the bones of the cave lion and the small cave bear differ considerably in most ways. In particular, bones of these species differ in the degree of leaching and collophanization of bioapatite, as well as the degree of calcitization, which in lion bones is 1.5 times that of the bear bones. This is reflected in the values of the Ca/P atomic proportion in bone bioapatite, which is 2.18 ± 0.24 (n = 15) and 2.31 ± 0.24 (n = 14) for the bear and lion, respectively. The bones of the lion and bear have different chemical and reference mineral compositions of the contaminating substance of the host layers. The lion bones typically have argillaceous-quartz composition of

washout material and quartz–argillaceous and argillaceous composition of the siliciclastic material illuviated in the bones, and for the the bones of bears respectively, quartz–clayey and clayey–quartz materials. The composition of microelements in the bones of both species is almost the same. The bones contain 11 strong microelements (Be, Rb, Th, Ag, Zn, Cd, Pb, Mo, As, Bi, and Se), 18 moderately essential microelements (Li, Cs, Sr, Ba, Ga, Ge, Y, Ti, Zr, Hf, V, U, Cu, Sn, Cr, Mn, Co, Ni, and Sb), and 22 antibiont microelements (Sc, Nb, Ta, La, Ce, Pr, Nd, Sm, Eu, Gd, Tb, Dy, Ho, Er, Tm, Yb, Lu, Tl, W, B, and Te). However, the total concentration of these elements in the bear bones was ~1.5 times that in the lion bones. The lion bones, unlike those of bears, retained almost no natural correlation between the content of microelements, which can be explained by their more intense calcitization. The lion bones contained considerably less collagen (0.03–2.90 wt %) than the bear bones (0.5–10.77 wt %), and also C_{org} (1.05 ± 0.94 and 3.45 ± 2.87 wt %). The degree of the collagen degradation, judging from the results of the thermal analysis, was noticeably higher in the lion bones. The lion and bear bones were considerably different in the degree of isotope weight of carbon and oxygen in the bone apatite, determined by the influence of limestones on the fossilizing bones. The lion bones were considerably heavier isotopically both in carbon (–3.5 to –2.2 vs. –8 to –3 ‰), and oxygen (23–28 vs. 19–27 ‰), indicating that the lion bones were more altered. Thus, all mineralogical and geochemical parameters showed that the lion bones were more profoundly fossilized in the cave burial. This can be either because the bear bones were more resistant to secondary changes or because the lion bones were geologically older. Judging from the similar degrees of nanoporosity in the examined bones, different geological ages for these animal burials seems more likely.

The absence of the traces left by humans or other predators on the lion bones suggests that the mass burial of lions was a product of natural causes. Thus, the locality in the Imanai Cave is the first burial of fossil lions discovered in northern Eurasia; it was formed in the period from the first half to the middle of the Late Neo-Pleistocene (OIS 5–3).

ACKNOWLEDGMENTS

We are grateful to V.M. Kuznetsov, Director of the Bashkiria National Park, and to L.A. Sultangareeva for the help during fieldwork.

The material was collected as part of the State Contract of the Institute of the Plant and Animal Ecology, Ural Branch, Russian Academy of Sciences. The mineralogical and geochemical research was supported by the Program of the Ural Branch of the Russian Academy of Sciences (project no. 18-4-4-3).

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Translated by S. Nikolaeva