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Mammalian fauna of the Late Pleistocene from the Barsuchiy Dol Cave (Southern Urals)

Pavel A. Kosintsev*, Anatoly G. Yakovlev, Natalya A. Plasteeva & Dmitriy O. Gimranov

ABSTRACT. The study describes mammalian fauna from Barsuchiy Dol cave in the Southern Urals, Russia. The accumulation of faunal remains in the cave deposits occurred due to natural processes. The remains from layers 1–4 were disturbed by fossorial activities of badgers. The faunal assemblage from these layers contain mixed remains of Pleistocene and Holocene age. The faunal assemblage from the layer 5 was excavated from *in situ* deposits. The of taxonomic composition and representation of skeletal element indicate that bone remains were accumulated in the layer 5 as digging activities of a badger (*Meles meles*), and natural death of larger (*Ursus kanivets*) and smaller (*Ursus rossicus*) cave bears during hibernation. The mammalian fauna from Barsuchiy Dol included typical species of the mammoth complex, as well as the mole (*Talpa europaea*), desman (*Desmana moschata*), red squirrel (*Sciurus vulgaris*), Malayan porcupine (*Hystrix brachyura*), forest dormouse (*Dryomys nitedula*), European mink (*Mustela lutreola*), European badger (*M. meles*), lynx (*Lynx lynx*), and Merck's rhinoceros (*Stephanorhinus kirchbergensis*). The remains of steppe (*Ochotona, Spermophilus, Lagurus, Allocricetulus, Cricetulus* and *Eolagurus*) and "tundra-steppe" (*Lasiopodomys gregalis*) species comprise about 50% of the small mammal fauna. The remains of relatively thermophilic (*Dryomys, Hystrix*), mesophilic (*Cricetus*) and "forest" (*Sciurus, Apodemus, Clethrionomys, Microtus agrestis*) species account for about 40% of the assemblage. The taxonomic composition and ecological structure of the fauna evidence interglacial conditions. The chronological position of the fauna was determined based on the analysis of the enamel differentiation quotient (SDQ) and the size of the m1 of the water vole (*Arvicola* spp.). The SDQ values in voles from layer 5 are close to the values observed in voles from Eastern European and Ural localities dated to the end of OIS6 and OIS5-2. The length of the tooth in voles from Barsuchiy Dol cave is similar to that in the voles from the OIS5-2 sites. Based on the data on evolutionary morphology of *Arvicola* and taxonomic composition of fossil assemblage, the fauna from layer 5 was dated to the OIS 5e (Mikulino, Tabulda, Streletsk, Kazantsevo, and Eemian) interglacial.

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Фауна млекопитающих позднего плейстоцена из пещеры Барсучий Дол (Южный Урал)

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РЕЗЮМЕ. В статье приводится описание фауны млекопитающих из отложений пещеры Барсучий Дол на Южном Урале. Накопление костного материала в отложениях пещеры происходило в результате естественных процессов. Фаунистические комплексы из слоев 1–4 представляют собой смешение костей плейстоценового и голоценового возраста в результате роющей деятельности барсуков. Фаунистический комплекс из слоя 5 происходит из отложений *in situ*. Анализ таксономического состава

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и соотношения элементов скелета свидетельствует, что накопление костей в слое 5 происходило в результате обитания барсуков, гибели большого (*Ursus kanivets*) и малого (*Ursus rossicus*) пещерных медведей во время зимней спячки. В состав фауны млекопитающих местонахождения Барсучий Дол наряду с типичными видами мамонтового комплекса входили крот (*Talpa europaea*), выхухоль (*Desmana moschata*), обыкновенная белка (*Sciurus vulgaris*), малайский дикобраз (*Hystrix brachyura*), лесная соня (*Dryomys nitedula*), европейская норка (*Mustela lutreola*), европейский барсук (*Meles meles*), рысь (*Lynx lynx*), носорог Мерка (*Stephanorhinus kirchbergensis*). В составе фауны мелких млекопитающих остатки «степных» (*Ochotona, Spermophilus, Lagurus, Allocricetulus, Cricetulus* и *Eolagurus*) и «тундро-степных» (*Lasiopodomys gregalis*) видов составляют около 50%. Остатки относительно теплолюбивых (*Dryomys, Hystrix*), мезофильных (*Cricetus*) и «лесных» (*Sciurus, Apodemus, Clethrionomys, Microtus agrestis*) видов составляют около 40% ассоциации. Видовой состав и экологическая структура указывают на межледниковые условия существования фауны. Хронологическое положение фауны определено на основе анализа коэффициент дифференциации эмали (SDQ) и размеров зуба m1 водяной полевки (*Arvicola* spp.). Значения SDQ у полевок из слоя 5 пещеры Барсучий Дол близки таковым у полевок из местонахождений Восточной Европы и Урала, датируемых концом OIS 6 и периодами OIS 5-2. Длина зуба у полевок из этого слоя соответствует размерам зубов полевок из местонахождений, датируемых OIS 5-2. На основании полученных данных фауна млекопитающих из слоя 5 пещеры Барсучий Дол датирована периодом OIS 5e (микулинское межледниковье, табулдинское, стрелецкое, казанцевское, эем).

КЛЮЧЕВЫЕ СЛОВА: млекопитающие, фауна, плейстоцен, Микулинское межледниковье, Эем, OIS 5e, Урал.

Introduction

The mammalian faunas of the last interglacial (Mikulino, Tabulda, Streletsk, Kazantsevo, Eemian, OIS 5e) are known from only a few Eastern European and Ural regions (Markova & Puzachenko, 2018). Almost all of them were found in alluvial deposits, which often contain remains from mixed assemblages. The known interglacial faunas from sites of this type originate from three locations in the Urals: the Makhnevskaya Ledyanaya cave (Fadeeva *et al*., 2020) and the Bobylyok grotto (Smirnov, 1993; Danukalova *et al*., 2020) in the Middle Urals and the Ignatievskaya cave (Fadeeva *et al*., 2019) in the Southern Urals. All three faunas are indirectly dated to the Mikulino interglacial (OIS 5e).

This study presents new data on small and large mammal fauna recovered from the Barsuchiy Dol cave deposits which correspond to the Mikulino interglacial. Here we describe the taxonomic composition and ecological structure of the fauna, and examine the dental morphology of the water vole (*Arvicola* spp.).

Material and methods

The Barsuchiy Dol cave is located on the western slope of the Southern Urals (Fig. 1) in Asha District of Chelyabinskaya Oblast (55.183° N, 57.417° E) in the zone of small coniferous and mixed forests. The cave entrance is 1.2 m in width and 1.4 m in height (Fig. 1C). The karst cavity of the cave is a corridor approximately 100 m in length and 2–8 m in width. A 2 m^2 excavation pit was placed 11 m from the cave entrance.

The deposits were divided into six layers:

Layer 1 — humus-rich soil with several plant remains; the contact with the next layer was distinct; thickness = 0.25 m

Layer 2 — light brown loam with limestone fragments; thickness = 0.7 m

Layer 3 — dark brown loam with limestone fragments; thickness = 0.4 m

Layer 4 — brown sandy loam with limestone fragments; thickness = 0.4 m

Layer 5 — dark brown loam with limestone fragments; thickness = 1.05 m

Layer 6 — limestone rocks

Layer 1 included plant remains with a small amount of soil. It was divided into three horizons: two 10 cm thick and one 5 cm thick. Its contact with layer 2 was distinct as the latter comprised dense loam. At the top of layer 2, holes (20–25 cm in diameter) filled with loose humus loam were clearly visible. The sediments of layer 2 were mixed owing to badger activity. The sediments were removed by 10 cm horizons and screened using a 5 mm sieve. This technique of excavation was applied until the depth of 2.15 m. No holes were observed from 1.75 to 2.15 m; in other words, sediments deeper than 1.75 can be considered *in situ*. As such, starting from the depth of 2.15 m, the excavation was performed by 5 cm horizons, and the sediments were screened using a 0.9 mm sieve. At 2.8 m, a layer of limestone was detected, which was difficult to dig through.

The contents of the holes were separated as much as possible and screened separately. The animal remains obtained from these sediments are referred to as “Holes” in Tab. 1. Also, some bones were collected from the floor of the cave (“Surface” in Tab. 1). The remains from layer 5 were divided into two samples. The first sample was obtained from depths of 1.75 to 2.15 m using the 5 mm sieve. The second sample was collected from depths of 2.15 to 2.8 m using wet screening. These samples are referred to in Tab. 1 as layers 5A and 5B, respectively.

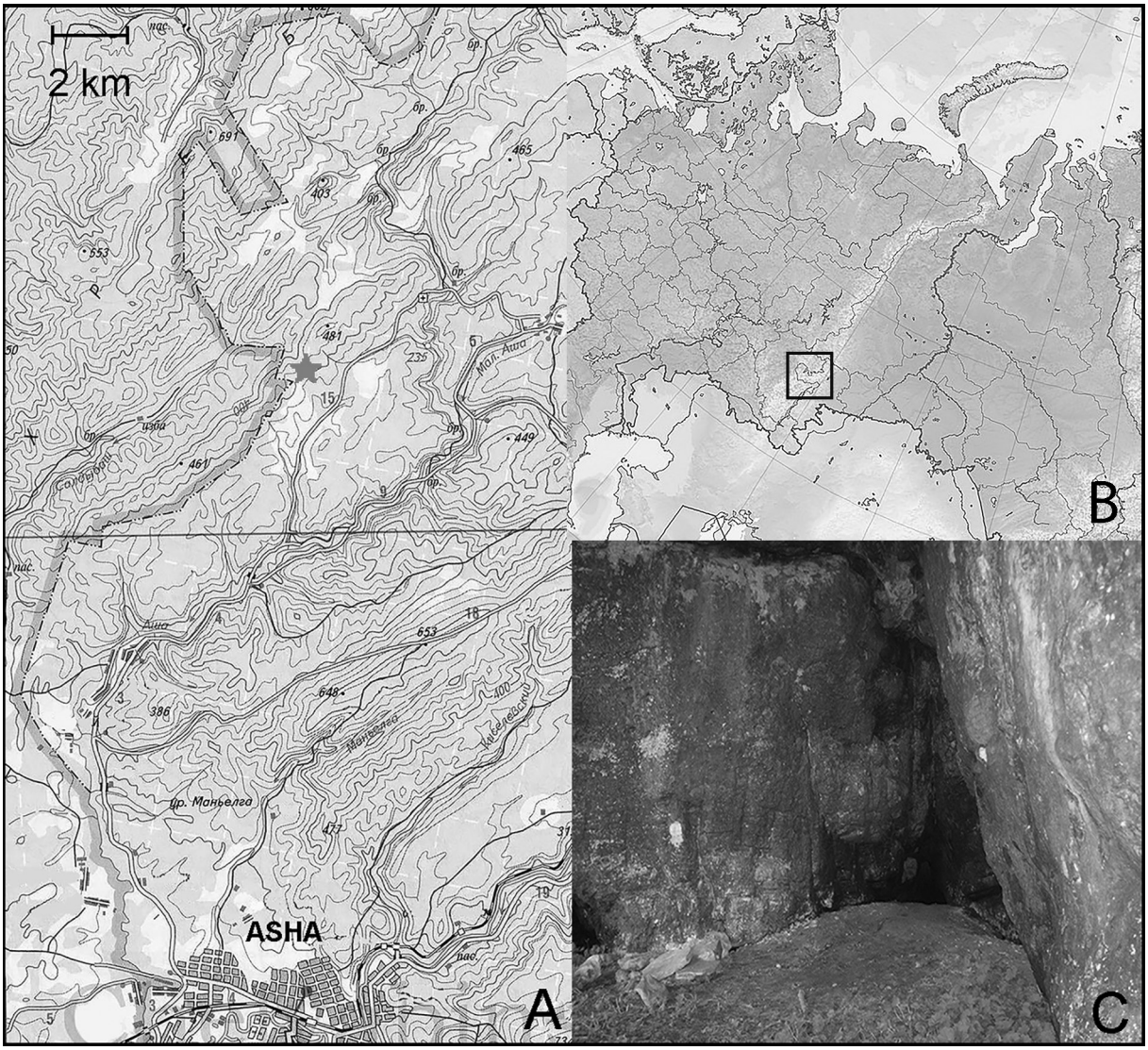

Fig. 1. Geographic location (A, B) and entrance (C) of the Barsuchiy Dol Cave.

The bone remains were separated into three distinct groups based on their color and degree of fossilization. The first group includes light yellow, non-fossilized bones and teeth with white enamel. The second group comprises yellow, weakly fossilized bones with dark spots and teeth with light enamel. The third group includes dark brown, fossilized bones and teeth with light brown enamel. These differences, in our opinion, reflect different geological ages of the bones: the remains in the first group are modern, whereas the remains in the second group can be dated to the Holocene, and the bones in the third group represent the Late Pleistocene. The total number of bones and fragments in the first and second groups is presented in Tab. 1 by layers. In this table, numerators indicate the number of bones in the first and second groups, whereas denominators indicate the number of bones in the third group. All bones found in layer 5 belong to the third group (Tab. 1).

A taxonomic determination of the remains was performed using the reference collection of the zoological museum of the Institute of Plant and Animal Ecology UB RAS and standard protocols. Fossil remains of badgers (*Meles* spp.) were determined based on cranial and mandibular morphology (Gasilin & Kosintsev, 2012; Crégut-Bonnoure *et al*., 2018) as well as dentition (Baryshnikov & Potapova, 1990; Baryshnikov *et al*., 2003). The remains of genus *Martes* and genus *Mustela* were assigned to species based on features of the cranium, mandible (Gasilin & Kosintsev, 2013), and dentition (Gimranov, 2013; Gimranov & Kosintsev, 2015). Similarly, the remains of Merck's rhinoceros were examined using the structure of the enamel surface of the tooth (Kosintsev *et al*., 2020). The porcupine remains were assigned to the extinct *Hystrix brachyura vinogradovi* (Argyropulo, 1941) species. Later Lopatin (2019) argued that this subspecies should be considered a

Table 1. Taxonomic composition of mammal remains from the Barsuchiy Dol Cave.

Species	Layers							
	Surface	1	2	3	4	5A	5B	Holes
Erinaceus sp.	–	–	1/0[1]	–	–	–	–	–
Talpa europaea	13/0	7/0	–	–	–	0/1	0/13	37/2
Chiroptera gen. indet.	25/0	37/0	2/0	0/1	–	–	–	3/0
Ochotona pusilla	–	–	–	0/3	0/1	0/1	–	–
Lepus timidus	11/0	36/0	9/0	0/3	0/1	0/1	0/24	2/0
Spermophillus sp.	–	–	–	–	0/1	–	0/3	–
Marmota bobak	–	–	–	–	0/2	0/2	0/6	1/1
Castor fiber	–	–	–	–	–	0/1	0/1	–
Hystrix brachyura	–	–	–	–	–	–	0/4	–
Cricetus cricetus	5/0	21/0	2/0	–	–	–	–	22/0
Canis lupus	–	1/2	–	–	–	0/1	–	0/3
Vulpes vulpes	3/0	3/0	–	–	–	0/1	0/10	–
Ursus arctos	2/0	3/0	3/0	–	–	–	–	–
Ursus kanivets	–	–	0/11	0/17	0/48	0/61	0/638	0/26
Ursus rossicus	–	–	–	–	0/2	0/9	0/12	0/2
Spelaearctos sp.	0/3	0/2	0/7	0/11	0/9	0/27	0/94	0/27
Martes martes	2/0	2/0	0/1	–	–	–	–	1/0
Martes sp.	4/0	0	1/0	–	–	–	0/7	–
Mustela lutreola	–	–	–	–	–	–	0/1	–
Mustela nivalis	–	–	1/0	0/2	0	0	0/1	–
Mustela erminea	–	–	1/0	0/1	0/1	0	0/1	–
Mustela eversmanii	–	–	1/0	–	–	–	–	–
Mustela sp.	–	1/0	1/0	–	–	–	–	–
Meles meles	–	–	–	0/1	–	–	0/1	1/1
Meles leucurus	1/0	15/0	2/0	2/0	–	–	–	–
Meles sp.	39/0	97/0	50/1	2/1	–	–	–	29/5
Lynx lynx	–	–	–	–	–	–	0/1	–
Equus ferus	–	–	0/1	–	0/1	–	–	–
Coelodonta antiquitatis	–	–	–	0/1			0/2	–
Stephanorhinus kirchbergensis	–	–	–	–	–	–	0/1	–
Sus scrofa	–	–	1/0	–	–	–	–	–
Rangifer tarandus	–	–	–	–	–	–	0/1	–
Cervus elaphus	–	–	–	–	–	0/1	0/2	–
Megaloceros giganteus	–	–	–	–	–	0/1	0/1	–
Alces alces	3/0	16/0	3/0	–	–	–	–	6/0
Capreolus pygargus	1/0	4/0	1/0	–	–	–	–	1/0
Bison priscus	–	–	0/2	–	0/1	–	–	–
Saiga tatarica	–	–	–	–	–	–	0/1	–
Equus caballus	2/0	–	1/0	1/0	–	–	–	–
Sus scrofa domestica	–	–	2/0	–	1/0	–	–	2/0
Bos taurus	2/0	–	1/0	–	–	–	–	–
Ovis aries	3/0	1/0	–	1/0	1/0	–	–	–
Mammalia indet.	7/3	20/9	3/31	11/123	0/417	0/491	0/4509	17/45
Aves indet.	10/0	26/0	11/1	0/1	0/1	0/2	0/3	43/1
Reptilia indet.	–	–	–	–	–	–	0/36	–
Amphibia indet.	24/0	6/0	26/0	–	0/1	0/81	0/1322	13/2
Pisces indet.	1/0	–	–	–	–	–	–	2/0

[1] The numerator shows the number of modern and Holocene bones; the denominator shows the number of Pleistocene bones.

separate species (*H. vinogradovi* Argyropulo, 1941). The taxonomic status of the Pleistocene porcupine requires confirmation using ancient DNA.

The mole (*Talpa europaea*), steppe pika (*Ochotona pusilla*), mountain hare (*Lepus timidus*), steppe marmot (*Marmota bobak*), ground squirrel (*Spermophilus* spp.), beaver (*Castor fiber*), carnivore (Carnivora) and ungulate (Ungulata) remains were determined on the basis of all available skeletal elements. The hamster (*Cricetus cricetus*) remains were determined based on cranial and mandibular morphology. The mole and ground squirrel from layer 5B (Tab. 1) were only represented by postcranial skeletal elements. Table 2 presents the results of the determination of small mammal remains based on dental features. Almost all unidentifiable bone fragments (Mammalia indet.) belong to large animals about the size of a roe deer or larger. The remains of smaller animals are few.

The absolute age of the fauna from the Barsuchiy Dol cave could not be determined using the radiocarbon method because of the poor collagen preservation in the mammalian bones. Thus, indirect dating for the fauna from layer 5 were obtained using the enamel differentiation quotient (Schmelzband-Differenzierung-Quotient; SDQ), and the size of the first lower molar (m1) of water vole. It is known that the ratio of enamel thickness of the anterior and posterior walls of the conids of molars in water voles (*Arvicola* spp.) has changed over time (Heinrich, 1978, 1982; Kolfschoten, 1990; Kalthoff *et al*., 2007; Agadzhanyan, 2012), and the size of m1 has increased gradually (Agadzhanyan, 2009, 2012; Markova, 1982, 2000; Yakovlev, 1988). Although the chronological position of the fauna cannot be determined solely on the basis of these indicators (Markova, 2006; Escude *et al*., 2008), in our opinion, they make it possible to correlate faunal assemblage from the layer 5 of the Barsuchiy Dol cave with other interglacial faunas in Europe and the Urals. To do this, the enamel thickness was measured (Kolfschoten, 1990; Heinrich, 1990) on whole water vole teeth M1 (n=7), M2 (n=11), M3 (n=9), m1 (n=6), m2 (n=11), and m3 (n=4) from the layer 5B. The teeth of young individuals were not measured.

The scientific names of the large and small cave bears (*Ursus kanivetz* and *U. rossicus*) are given according to the modern views on the taxonomy of cave bears (Baryshnikov & Puzachenko, 2017, 2019; Baryshnikov *et al*., 2018; Barlow *et al*., 2020).

The collection of fossil remains from the Barsuchiy Dol cave is stored at the Zoological Museum of the Institute of Plant and Animal Ecology in Yekaterinburg (collection number 1774).

Results

Taphonomy

No cut marks were observed on the bones, and no signs of human activity (e.g., artifacts, traces of fires) were found at the excavation site, suggesting that the bone remains were accumulated in the cave as a result of natural processes and not due to human activity. A small number of specimens displayed corrosion owing to the action of digestive enzymes. A few bones of elk (*Alces alces*), Siberian roe deer (*Capreolus pygargus*), wild horse (*Equus ferus*), red deer (*Cervus elaphus*), reindeer (*Rangifer tarandus*), steppe bison (*Bison priscus*) and saiga antelope (*Saiga tatarica*) exhibited traces of gnawing by carnivores.

As mentioned above, the holes made by badgers penetrated the sediments reaching a depth of 1.75 m. These holes were filled with loose humus loam and contained Pleistocene and Holocene bones, including those of domestic pig (Tab. 1; layers 1–5). Domestic pigs were present in the mountain–forest zone of the Southern Urals since the arrival of settlers from Central Russia in the sixteenth century (Preobrazhenskii, 1972). According to the information provided by locals, the Barsuchiy Dol cave was previously inhabited by badgers that were hunted until the end of the twentieth century. As such, the badger's holes in the cave are not older than 300 years.

Almost all Holocene remains were collected from the floor of the cave and from layers 1 and 2 (Tab. 1). Single bones of this age, including those of domestic animals, were also found in layers 3 and 4, which suggest that the sediments were disturbed by the badgers. The Pleistocene remains were present in all the layers and on the surface. Only *in situ* sediments from layer 5 did not contain bones of the Holocene age. The remains of Holocene age were excluded from the present study.

The most representative and complete sample was collected from layer 5B. The taphonomic analysis of the assemblage can help to determine the process of bone accumulation in this layer. Among large mammals, the cave bear (*Spelaearctos* spp.) prevails (Tab. 1). The cave bear remains from layer 5B are represented mostly by deciduous teeth (Tab. 3). Other skeletal elements belonged to individuals with different age, including embryos and newborns. Thus, the cave was used by cave bears as a winter den. A similar observation was made in layers 3 and 4: cave bear bones were prevalent among mammalian remains (Tab. 1), and deciduous teeth were abundant. This suggests that the cave was used for hibernation during the period of formation of these two layers as well. The cave bear bones were accumulated in the Barsuchiy Dol cave sediments as a result of the death of animals during hibernation. Such cave bear winter dens with a similar composition of faunal complexes have been found in other caves in the Southern Urals (Smirnov *et al*., 1990; Kosintsev & Vorob'ev, 2001).

A peculiarity of the cave bear bone sample from layer 5B was the prevalence of isolated teeth (Tab. 3). Another feature of this layer was the abundance of unidentifiable remains of large mammals (Tab. 4), which were also prevalent in layers 3, 4, and 5A (Tab. 1). All these fragments were 3–4 cm in diameter. Some indirect evidence (thickness and texture of the bone surface) suggests that almost all the fragments belonged to cave bears. Thus, for an unknown reason, all cave bear bones found in the cave were strongly fragmented.

The taxonomic analysis of the fauna from layer 5B pointed to the sources of the accumulation of bones of other species in the cave. A large number of amphibian

Table 2. Taxonomic composition of small mammal assemblages from the Barsuchiy Dol Cave (layer 5B).

Species	Horizons, cm												
	215–220	220–225	225–230	230–235	235–240	240–245	245–250	250–255	255–260	260–265	265–270	270–275	275–280
Chiroptera gen. indet.	–	–	–	1	–	–	1	1	–	–	–	–	–
Desmana moschata	–	–	–	–	–	–	–	–	2/1[1]	2/1	2	1	4/1
Talpa europaea	1	–	–	2/1	1	–	2/1	1	1	–	6/4	2	2/1
Sorex sp.	3/1	2/1	1	–	1	4	2/1	2/1	–	1	2/1	1	3/2
Neomys fodiens	–	–	–	–	–	–	–	–	1	–	–	–	–
Ochotona pusilla	5/2	14/1	9/2	10/2	6/2	4/2	10/1	18/1	14/2	13/4	15/2	24/6	24/4
Spermophilus sp.	–	–	1	–	1	–	–	1	–	1	1	1	2/1
Dryomys nitedula	–	–	–	–	–	–	–	1	–	–	–	–	–
Apodemus ex gr. *uralensis-agrarius*	–	–	–	1	–	–	–	–	–	–	2	1	–
Cricetus cricetus	2/1	–	–	–	1	2/1	1	1	1	–	4/2	1	2
Clethrionomys rufocanus	–	4/2	–	–	–	–	–	5/1	2/1	–	–	2/1	–
Cl. ex gr. *glareolus-rutilus*	4/2	–	3/1	14/3	3/2	5/2	12/5	7/3	17/3	9/4	6/4	14/1	6/1
Lagurus lagurus	–	1	–	4/1	1	–	–	–	1	–	–	–	3/1
Dicrostonyx sp.	–	–	1	–	–	–	–	1	–	–	1	–	–
Lemmini gen.	–	1	2/1	2	1	2/1	2/1	1	3/2	1	2/1	1	2/1
A. amphibius	7/3	6/2	8/2	11/3	17/1	20/5	16/2	22/3	17/6	15/3	11/2	14/2	20/5
Lasiopodomys gregalis	4	1	3	6	4	4	2	5	3	4	5	7	7
Microtus oeconomus	4	4	4	9	12	6	5	8	6	9	3	7	2
M. agrestis	–	1	–	1	1	4/2	–	4	2/1	4/3	–	5/2	4/2
M. ex gr.*arvalis-agrestis*	–	–	–	–	1	1	–	4	–	–	–	–	–
M. arvalis	1	–	–	1	–	3	1	2	4	2	–	5	2
Microtus sp.	26/9	36/14	27/11	63/15	68/17	45/11	40/15	57/21	61/20	34/10	26/9	58/19	46/11
Total	58	70	59	125	118	110	94	142	136	92	86	144	142

[1] The number of identified specimens (NISP) / minimum number of individuals (MNI).

Table 3. The number of identified specimens (NISP) of *Spelaearctos* spp.

Horizons, cm	Deciduous teeth	Permanent teeth	Skeletal remains
215–220	15	8	3
220–225	10	5	3
225–230	9	8	1
230–235	15	6	4
235–240	7	12	0
240–245	14	8	2
245–250	25	17	0
250–255	48	28	1
255–260	60	13	9
260–265	92	104	2
265–270	77	19	5
270–275	10	3	6
275–280	13	3	7
Total	395	234	43

Table 4. Number (NISP) and percentage (%) of animal remains in the layer 5B of the Barsuchiy Dol Cave.

Horizons, cm	Large mammals				Small mammals		Amphibians	
	Identifiable		Unidentifiable					
	NISP	%	NISP	%	NISP	%	NISP	%
215–220	24	16	125	84	57	21	220	89
220–225	16	9	170	91	70	33	143	67
225–230	14	9	135	91	59	53	53	47
230–235	25	22	91	78	125	36	219	64
235–240	19	35	35	65	119	49	125	51
240–245	22	29	55	71	90	40	141	60
245–250	43	38	71	62	94	50	94	50
250–255	92	27	251	73	141	37	241	63
255–260	92	11	761	89	135	59	95	41
260–265	231	22	791	78	95	91	10	9
265–270	100	8	1151	92	88	91	10	9
270–275	30	7	421	93	144	99	3	1
275–280	32	7	452	93	120	99	4	1

bones were found in layer 5 (Tab. 1); they comprised 12% and 16% of the vertebrate specimens from layer 5A and 5B, respectively. Amphibian bones were prevalent among the small vertebrate remains in layer 5B (Tab. 4). There are two possible reasons for the mass accumulation of amphibian bones: death of large groups of these animals during hibernation or activity of carnivores such as birds and mammals. Since mass hibernation of amphibians is unknown for North Eurasia, the second explanation seems more plausible. Birds do not occupy the deep parts of these caves; thus, the amphibian remains were brought to the cave by predators, such as badgers and otters, that inhabit caves and feed on amphibians (Heptner *et al*., 1967). However, the diet of otters also includes a significant amount of fish (Heptner *et al*., 1967), the remains of which are almost absent in the cave deposits (Tab. 1). Therefore, the sediments of layer 5 were formed when the cave was inhabited by badgers. The remains of amphibians and most other small mammals were accumulated in this layer as a result of badger activity.

Remains of large mammals were brought into the cave by large carnivores. The latter do not inhabit deep parts of caves but make their dens near the entrance of a cave. The remains of the prey and the predators themselves may have occasionally fallen into the internal part of the caves. Thus, bones accumulated in layer 5 due to the following reasons:

— cave bear bones: death of cave bears during hibernation;

— amphibian and most small mammal bones: accumulation by badgers;

— other remains: occasional displacement from the cave entrance.

Faunal analysis

The mammalian fauna from the Barsuchiy Dol cave includes species — extant and extinct — that are typical for the Late Pleistocene (OIS 5-2) and Holocene (OIS 1). The cave bear became extinct during OIS 3, while woolly rhinoceros (*Coelodonta antiquitatis*) persisted until the end of OIS 2 (Stuart, 2015), giant deer (*Megaloceros giganteus*) went extinct in the middle of OIS 1 (Stuart *et al*., 2004). Merck's rhinoceros (*S. kirchbergensis*) lived in Europe, the Urals, and Russian Primorye until the beginning of the Late Pleistocene (OIS 5). The Malayan porcupine (*H. brachyura*) is an extant species whose range decreased at the beginning of the Late Pleistocene. This species inhabited Europe and the Urals during the last interglacial, whereas it survived in the Altai until OIS 3 (Kuzmin *et al*., 2017).

The diverse insectivore fauna collected from the layer 5 (Tab. 1, 2) includes species that do not inhabit permafrost areas, such as the desman (*Desmana moschata*) and mole (*T. europaea*). The fauna of this layer also includes a forest species such as lynx (*Lynx lynx*) and thermophilic species such as the porcupine and dormouse, which were found only in interglacial faunas of Eastern Europe and the Urals (Yakhemovich *et al*., 1988; Markova, 2000; Agadzhanyan, 2009; Kuzmin *et al*., 2017; Fadeeva *et al*., 2018, 2019, 2020). Certain species represented in layer 5 are extremely rare in the Late Pleistocene faunas of Eastern Europe and the Urals (Markova *et al.,* 1995; Kosintsev, 2007): beaver (*Castor fiber*), forest mice (*Sylvaemus* spp.), common hamster (*Cricetus cricetus*), European mink (*Mustela lutreola*), and European badger (*M. meles*). In contrast, remains of the most typical species of stadial and interstadial faunas of the Late Pleistocene (OIS 4-2) in these regions (according to Markova *et al*., 1995), steppe vole (*Lagurus lagurus*), lemming (*Dicrostonyx* sp., Lemmini gen.), and narrow-headed vole (*Lasiopodomys gregalis*), were present in small numbers in the faunal assemblage. All these observations taken together suggest that the mammalian fauna existed in interglacial conditions.

Species inhabiting different types of landscape were present in the faunal assemblage. Some of them represent forest landscapes (e.g., *Clethrionomys* spp., *Microtus agrestis*, *L. lynx*). A large group of species is associated with half-open (e.g., *Hystrix* spp., *Dryomys nitedula*, *C. cricetus, M. meles*, *S. kirchbergensis*, *C. elaphus*, and *M. giganteus*) and open landscapes (e.g., *O. pusilla*, *Spermophillus* spp., *M. bobak*, *L. lagurus*, *Dicrostonyx* spp., *L. gregalis*, *Microtus arvalis*, *U. kanivetz*, *U. rossicus*, *C. antiquitatis*, *S. tatarica*). Some of the species are intrazonal and dependent on water reservoirs (*D. moschata*, *Neomys fodiens*, *C. fiber*, *Arvicola amphibius*, *Microtus oeconomus*, *M. lutreola*). Finally, the fauna included ubiquitous animals inhabiting various types of landscapes. Thus, the composition of the fauna was very diverse, which suggests that the landscape was diverse as well. The open steppe landscapes were likely present in the upper parts of the mountains, whereas the middle zone of the mountains was likely covered with tree and shrub vegetation. Forests, vast enough to support the lynx population, grew upon the foot of the mountains and along river valleys. The area, in general, was not a permafrost region.

Discussion

We compared the faunal data obtained from layer 5 of the Barsuchiy Dol cave with those from a cave complex near the Ignatievskaya cave, which is situated 50 km from the Barsuchiy Dol cave (Smirnov *et al*., 1990). Faunal assemblages from these caves are dated to the late Middle Pleistocene (OIS 6) and Late Pleistocene (OIS 5e, OIS 3, and early and late OIS 2; Smirnov *et al*., 1990; Fadeeva *et al*., 2018; 2019). The fauna from these assemblages includes species from different taxonomic and ecological groups: insectivore (Lipotyphla), relatively thermophilic (e.g., *Dryomys* and *Hystrix* spp.), mesophilic (e.g., *Cricetus* spp.), "forest" (e.g., *Sciurus*, *Apodemus*, and *Clethrionomys* spp. and *M. agrestis*), cold-tolerant (e.g., *Dicrostonyx* spp.), "steppe" (e.g., *Ochotona*, *Spermophilus*, *Lagurus*, *Allocricetulus*, *Cricetulus*, and *Eolagurus* spp.), and "tundra-steppe" (e.g., *L. gregalis;* Tab. 5).

Three types of fauna are identified based on the prevalence of the above-mentioned groups. The first type is OIS 2 fauna, in which remains of the cold-tolerant, steppe, and tundra-steppe species constitutes

Table 5. The composition and structure of the small mammal fauna from the localities in the Southern Urals, %.

Mammal groups	Localities[1]					
	1	2	3	4	5	6
Lipotyphla	11	10	14	3	9	2
Dryomys, *Hystrix*	1	0	0,1	0	0	0
Cricetus	3	0.1	0.6	0.6	0	0
Sciurus, Pteromys, Apodemus, Clethrionomys, *M. agrestis*	33	19	24	30	4	6
Dicrostonyx sp.	1	7	3	11	12	8
L. gregalis	12	29	21	40	28	44
Ochotona, Spermophilus, Lagurus, *Allocricetulus, Cricetulus, Eolagurus*	39	35	36	15	47	40
NISP	471	1259	4223	664	1381	633

[1] Localities: 1 — Barsuchiy Dol cave; 2 — Ignatievskaya cave (pit V, layer 10, 1985 year of excavation), OIS 6 (Smirnov *et al*., 1990); 3 — Ignatievskaya cave (pit V, layer 10, 2014 year of excavation), OIS 5e (Fadeeva *et al*., 2019); 4 — Ignatievskaya cave (pit V, layer 8–9), OIS 3 (Smirnov *et al*., 1990); 5 — Prizhim II, beginning of the OIS 2 (Smirnov *et al*., 1990); 6 — Ignatievskaya cave (pit II, layer 2a), end of OIS 2 (Smirnov *et al*., 1990).

approximately 90% of samples (Tab. 5). The second type includes OIS 3 fauna, approximately 30% and 15% of which are forest and steppe species, respectively (Tab. 5). Finally, the third type includes OIS 6 and OIS 5e faunas containing cold-tolerant, steppe, and tundra-steppe species (approximately 60%); forest species (approximately 20%); and specimens of relatively thermophilic species (Tab. 5). The share of The steppe and tundra-steppe species and forest species constituted approximately 50% and more than 30%, respectively, of the faunal sample from layer 5 of the Barsuchiy Dol cave; this sample also contained bones of relatively thermophilic species (Tab. 5). As such, the faunal composition of the small mammal sample from layer 5 is similar to faunas of the third type, particularly to the fauna from layer 10 of excavation pit V (2014) of the Ignatievskaya cave, which is dated to OIS 5e (Fadeeva *et al*., 2018; 2019). Notably, in the Urals, remains of the dormouse (*Dryomys* and *Eliomys* spp.) and red squirrel (*Sciurus* spp.) have been found only in faunal assemblages dated to interglacial periods (OIS 5e and OIS 1; Smirnov, 1993; Smirnov *et al*., 1990; Bachura & Kosintsev, 2007; Kosintsev & Bachura, 2013; Danukalova *et al*., 2020; Fadeeva *et al*., 2018, 2019, 2020). Thus, the fauna from layer 5 should be considered interglacial.

Relative age of the fauna

The relative age of the faunal assemblage from layer 5B of the Barsuchiy Dol cave can be determined on the basis of the analyses of the taxonomic composition and ecological structure of the fauna, SDQ and absolute size of m1 of water vole. The validity of using SDQ for relative dating of faunal complexes has been previously questioned (Escude *et al*., 2008; Markova, 2006). Though, in our opinion, this indicator analyzed together with the size of m1 can be successfully used for assigning faunas to major chronological periods, for example, the Late Pleistocene.

The average, minimum and maximum SDQ values for 48 water vole teeth from layer 5B of the Barsuchiy Dol cave are shown in Table 6. Table 6 shows separately the SDQ values for m1 only. These values are typical for *A. amphibius* and are close to the values obtained for water voles from localities dated to the Middle Pleistocene (Dnieprovian, Saalian, OIS 6) and Late Pleistocene (Mikulino, Valdai, Eemian, Weichselien, OIS 5–2) of Europe (Kolfschoten, 1990; Markova, 2000; Kalthoff *et al*., 2007; Agadzhanyan, 2012; Tab. 6). However, these values are higher than those of the Holocene and recent vole samples (Tab. 6). Thus, on the basis of SDQ values, the fauna from layer 5 can be assigned to the late Middle Pleistocene – Late Pleistocene.

Table 6. The enamel differentiation quotient (SDQ) in water vole (*Arvicola* spp.) from the Pleistocene and Holocene localities of Eastern Europe and the Urals.

Localities	Region	Age	n	SDQ Min–M–Max
Chigirin [1] *A. cantianus*	Eastern Europe	Middle Pleistocene (Likhvin Interglacial, MIS 11)	62	101.6–129.0–166.67
Krasnyi Yar *A.* cf. *chosaricus*	Eastern Europe	Middle Pleistocene (MIS 8)	1	85.5
Novonekrasovka[1] (upper layer) *A. amphibius*	Eastern Europe	OIS 5e	18	60.0–87.0–140.0
Novonekrasovka[1] (lower layer) *A. amphibius*	Eastern Europe	OIS 5e	14	60.0–92.0–110.0
Malyutino[1] *A. amphibius*	Eastern Europe	OIS 5e	4	42.0–61.0–100.0
Krasnyi Bor[2] *A. amphibius*	Eastern Europe	OIS 5e	15	64.00–74.28–88.33
Makhnevskaya Ledyanaya[3] *A. amphibius*	Middle Urals	OIS 5e	18	86.3–91.9–97.6
Ignatievskaya (pit V, layer 10, 2014)[4] *A. amphibius*	Southern Urals	OIS 5e	14	83.0–96.7–111.3
Barsuchiy Dol *A. amphibius*	Southern Urals	OIS 5e	48	77.3–85.9–97.7
Barsuchiy Dol *A. amphibius* (m1)	Southern Urals	OIS 5e	6	77.3–83.3–85.7
Ziganskii[5] *A. amphibius*	Southern Urals	end of OIS 1	14	57.1–69.98–74.91
Nugush[5] *A. amphibius*	Southern Urals	Recent	40	54.52–73.88–97.27

[1] Markova, 2000; [2] Yakovlev, 1992; [3] Fadeeva *et al*., 2020; [4] Fadeeva *et al*., 2019; [5] Yakovlev, 1988.

The absolute size of m1 in water vole gradually increased during the Pleistocene (Yakovlev, 1988; Markova, 1982, 2000; Maul *et al*., 2000; Agadzhanyan, 2009, 2012). The size of m1 in voles from layer 5B of the Barsuchiy Dol cave are the following: minimal length = 3.5 mm; maximal length = 4.5 mm; and average = 4.0 mm (Tab. 7). These values are similar to those in voles from the Late Pleistocene localities from Eastern Europe, the Urals, and the Trans-Urals (Tab. 7). Furthermore, these values are lower than those of present-day water voles from the Southern Urals and the Trans-Urals, but greater than those of water voles from the Middle Pleistocene (Tab. 7). Thus, on the basis of absolute size of m1, the water voles from layer 5B can be dated to the Late Pleistocene.

Data on SDQ values and size of m1 in water voles suggest that faunal assemblage from layer 5 of the Barsuchiy Dol cave can be reliably dated to the Late Pleistocene. Based on the presence of the Malayan porcupine and Merck's rhinoceros, the fauna from layer 5 cannot postdate OIS 5e. The ecological structure of the fauna also indicates that it is related to interglacial climate conditions. Taken together, these results suggest that mammalian fauna from layer 5 of the Barsuchiy Dol cave is dated to the Mikulino interglacial (Eemian, Tabulda, Streletsk, Kazantsevo, OIS 5e).

Conclusion

The accumulation of faunal remains in the Barsuchiy Dol cave deposits occurred due to natural processes. The faunal assemblages from layers 1–4 were mixed as a result of digging activity of badgers. The faunal sample from layer 5 recovered from undisturbed deposits. The skeletal elements of cave bear prevail in the assemblage from this layer. The cave bear remains represent animals that died during winter hibernation. The mammalian fauna from the layer 5 of the Barsuchiy Dol cave consisted of typical species of the "mammoth complex" as well as species such as Merk's rhinoceros, Malayan porcupine, desman, vole, red squirrel, forest dormouse, European mink, European badger, and lynx. The steppe

Table 7. The size of m1 in water vole (*Arvicola* spp.) from the Pleistocene and Holocene localities of Eastern Europe and the Urals, mm.

Sites	Region	Age	*n*	Length Min–M–Max
Chigirin[1] *A. cantianus*	Eastern Europe	Middle Pleistocene	48	3.2–3.5–3.9
Krasnyi Yar[2] *A.* cf. *chosaricus*	Eastern Europe	Middle Pleistocene	1	3.77
Vladimirovka 1[3] *A. chosaricus*	Eastern Europe	Middle Pleistocene	4	3.4–3.6–3.8
Vladimirovka 2[3] *A. chosaricus*	Eastern Europe	Middle Pleistocene	49	2.90–3.44–3.70
Strelitsa[3] *A. chosaricus*	Eastern Europe	Middle Pleistocene	20	2.90–3.45–3.70
Chornyi Yar[2] *A. chosaricus*	Eastern Europe	Middle Pleistocene	6	3.55–3.72–3.90
Malkovo[4] *A. chosaricus*	Middle Trans-Urals	Middle Pleistocene	17	3.50–3.74–4.00
Nitsa[4] *A. chosaricus*	Middle Trans-Urals	Middle Pleistocene	7	3.40–3.69–3.85
Komintern[3] *A. amphibius*	Eastern Europe	end of OIS 6	26	3.00–3.64–4.15
Serpievskaya (layer 3), Ignatievskaya (pit V, layer 10, 1985)[5] *A. amphibius*	Southern Urals	end of OIS 6	?	? –3.89–?
Mikhailovka 5[3] *A. amphibius*	Eastern Europe	OIS 5e	11	3.45–3.82–4.40
Novonekrasovka[1] (upper layer) *A. amphibius*	Eastern Europe	OIS 5e	18	3.5–3.8–4.1
Novonekrasovka[1] (lower layer) *A. amphibius*	Eastern Europe	OIS 5e	14	3.6–3.8–4.0
Shkurlat[1] *A. amphibius*	Eastern Europe	OIS 5e	3	3.8–3.9–4.2
Krasnyi Bor[2] *A. amphibius*	Eastern Europe	OIS 5e	16	4.0–4.2–4.7
Makhnevskaya Ledyanaya[6] *A. amphibius*	Middle Urals	OIS 5e	22	3.75–4.10–4.70
Ignatievskaya (pit V, layer 10, 2014)[7] *A. amphibius*	Southern Urals	OIS 5e	4	3.65–3.80–3.95
Barsuchiy Dol *A. amphibius*	Southern Urals	OIS 5e	11	3.5–4.0–4.5
Ignatievskaya (pit V, layer 10, 1985)[5] *A. amphibius*	Southern Urals	OIS 3	?	? –3.85–?
Ignatievskaya (pit II), Prizhim II[5] *A. amphibius*	Southern Urals	OIS 2	?	? –4.02–?
Troitsa II[1] *A. amphibius*	Eastern Europe	OIS 3	3	3.67–3.91–4.10
Malkovo[4] *A. amphibius*	Middle Trans-Urals	Late Pleistocene	9	4.05–4.18–4.35
Verkhnyaya Alabuga[4] *A. amphibius*	Southern Trans-Urals	Late Pleistocene	6	4.25–4.33–4.55
Sim III[5] *A. amphibius*	Southern Urals	OIS 1	?	?–4.13–?
Ziganskii[8] *A. amphibius*	Southern Urals	end of OIS 1	16	3.55–4.25–4.62
Nugush[2] *A. amphibius*	Southern Urals	Recent	43	4.0–4.3–4.9
Kurgan[4] *A. amphibius*	Southern Trans-Urals	Recent	36	3.75–4.38–4.75

[1] Markova, 2000; [2] Yakovlev, 1992; [3] Agadzhanyan, 2009; [4] Maleeva & El'kin, 1986; [5] Smirnov *et al*., 1990; [6] Fadeeva *et al*., 2020; [7] Fadeeva *et al*., 2019; [8] Yakovlev, 1988.

and tundra-steppe species comprised approximately 50% of the small mammal remains, whereas the forest species comprised more than 30% of remains. Such taxonomic composition and ecological structure of the fauna indicate interglacial conditions. The chronological position of the fauna was estimated on the basis of SDQ values and the size of m1 in water voles. The SDQ values in water voles from layer 5 are similar to those in voles from sites in Eastern Europe and the Urals dated to the end of OIS 6 and OIS 5-2. The size of m1 falls into the range of the size of water vole teeth dated to OIS 5-2. Based on these data, we can conclude that mammalian fauna from the layer 5 of the Barsuchiy Dol cave can be dated as Mikulino (Tabulda, Streletsk, Kazantsevo, Eemian, OIS 5e) interglacial.

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