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# Quaternary large mammals from the Imanay Cave

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ABSTRACT

The composition of large mammal fauna from the Imanay Cave in the Southern Urals (53°02' N, 56°26' E) is described in the present study. The paper aims to provide an preliminary description of the large mammal remains from the Imanay Cave in order to establish their taxonomic status, geological age and to detect the factors that led to accumulation of the bone remains in the cave. An analysis of species composition of vertebrate fauna, archaeological finds and radiocarbon dates has shown that accumulation of fossils in the Imanay Cave spanned the whole period of the Late Pleistocene and Holocene. Remains of the small cave bear (*Ursus* "*savini*") and cave lion (*Panthera* ex gr. *fossilis-spelaea*) are prevalent in the Pleistocene groups: 9414 (93%) and 536 (5%) bone specimens, respectively. The cave is the only site in the world where mass bone assemblages of two large terrestrial Carnivora species - small cave bear and cave lion – were found simultaneously. The composition of the skeletal samples for both species was described and the age and sex distributions were determined. Though Mousterian stone tools were found in the cave, no trace of the hunt of the bears and lions by humans was detected. The period during which the accumulation of the fossils took place can be broadly determined as the first half of the Late Pleistocene (MIS5–3).

## 1. Introduction

The Imanay Cave is located in the Southern Urals (Bashkortostan Republic, Meleuz Region, coordinates 53°02' N, 56°26' E), 7 km northeast of Nugush village (Fig. 1, A), at 420 m above the sea level. The cave has been excavated by the authors and their colleagues (see Acknowledgements) from 2010 to 2016. The Imanay Cave is a locality of the mammoth faunal complex (MIS5-2). Cave and lake-alluvial localities of the mammoth faunistic complex (MIS5-2) are particularly abundant in North Asia and Europe. The former are prevalent in mountainous areas (Pyrenees, Alps, Carpathians, Crimea, Caucasus, Urals, Altai etc.) while the latter in flat areas. Despite the composition of the type of locality, large mammals are typically represented by several species among that remains of large herbivores are prevalent. Localities, containing mass accumulation bones of a single species not accumulated by human activity are commonly referred to as "graveyards". Large graveyards of the cave bear are known in Europe (Nopdman, 1858; Pidoplychko, 1956; Musil, 1980; Döppes and Rabeder, 1997,; Nagel et al., 2005) and in the Urals (Kuzmina, 1971; Smirnov et al., 1990; Kosintsev and Vorob'ev, 2001). There are some rare evidences of mass graveyards of the brown bear (Kosintsev and Bachura, 2015) and cave lion (Vereshchagin, 1971; Diedrich, 2011b). Nevertheless, no cave site with such abundant accumulation of more than one species are known in literature. The Imanay Cave from the South Urals is unique since numerous bone remains of both cave bears and cave lions were excavated there. Thus, the cave represents a mass bone assemblage of two species of large carnivorous mammals not directly related to each other in the trophic chain. In this paper, an initial description of the large mammal remains from the Imanay Cave is provided. Further goals of this study were to establish the taxonomic status of the remains, to determine geological age of the assemblages, and to explore factors of accumulation of bone remains in the cave. Importantly, we set out to demonstrate on the basis of taphonomic analysis that the Imanay Cave was a "cemetery" of two species of large predatory mammals simultaneously. Therefore, a taxonomic analysis of the fossils will be carried out as well as an analysis of the prevalence of different elements of the skeleton and, finally, sex and age distribution of the cave lion and cave bear remains.

## 2. Regional settings

The Imanay Cave is located in the Southern Urals in a mountainous region. The oorographic province Southern Urals are located between 51° and 56° N and between 56° and 62° E. The Southern Urals consist of two large geomorphologic regions: the Transuralian peneplain and the mountain region. The climate of the Southern Urals is continental and

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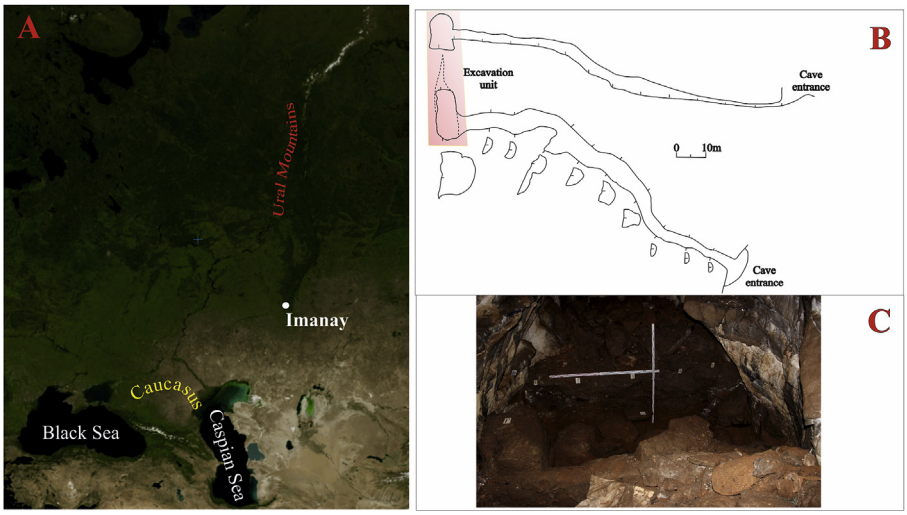


**Fig. 1.** Location of the Imanay Cave. A: map of Eastern Europe showing the position of the Imanay Cave; B: vertical and planar views of the Imanay Cave; C: views of the site.

moderately warm in the present days. Summers a long and middle warm, there is cold winters. (Rumyantseva, 1964). The two areas have different climates: is cooler in mountainous and more humid in the plain. This is reflected in a different vegetation. The Transuralian peneplain is characterized of the forest-steppe and steppe zones. The mountainous area there is different landscape: mountain-steppe, mountain-forest, mountain-subalpine and mountain-tundra altitudinal belts (Gorchakovskiy, 1975). On the tops of large mountains such as Iremel and Yaman-Tau, a mountain-tundra altitudinal belt is located. In the central part of the mountains of the South Ural grows by coniferous taiga, where the dominant species are by spruce and fir. In the south-eastern part of the Southern Urals distributed only the mountain-steppe altitudinal belt. On the eastern slope, there are light coniferous pine and larch forests. The broadleaf forests consisting of linden and oak dominate the western slope of the South Ural (Igoshina, 1964).

## 3. Materials and methods

### 3.1. Methods

According to a conventional protocol, sediments were rinsed in water and then sieves with mesh sizes of 0.5 and 1.0 mm were used in order to separate vertebrate remains from the sediment. Large-mammalian bones were collected previously during the excavation. The age distribution of the cave lion and bear specimens was assessed based on three indicators: number of bones of newborn individuals (clearly different from other bones in size); number of tubular bone with fused or non-fused epiphyses; number of deciduous teeth. Three age cohorts were employed: under 1 year (newborn); from 1 to 5 years (bones with non-fused epiphyses); over 5 years (bones with fused epiphyses). The age of fusion of the epiphyses was determined based on the standards created for modern brown bears (Weinstock, 2009). Deciduous teeth were considered separately and were not included in any of the cohorts. The sex composition of the samples was determined based on the size of teeth and the metapodia. The greatest length and greatest width of the lower canine (in areas crown and root contact) was measured in the cave bears while the greatest length and greatest width of the lower carnassial (m1) was measured in the cave lions. The maximum length (L) and width (W) of the distal epiphysis of the metacarpus 4 were measured in the cave bears as well. Measurements were taken using a digital caliper, to the nearest 0.1 mm. The minimum number of individuals of the *U.* "*savini*" species was estimated based on the number of permanent m1. The degree of bone fragmentation was determined based on the methods proposed earlier (Erokhin and Bachura, 2011).

### 3.2. Osteological material

The number of identifiable Pleistocene remains exceeds 100 000 specimens. The number of Holocene specimens was more than 10 000. All the mammal remains from the excavation unit were classified into two groups based on their colour and state of fossilization: non-fossilized bones of creamy-white and light-yellow colour and fossilized bones of darker colour, from light-brown to black. Light-coloured remains from the first group are dated to the Holocene (Table 2), while those from the second group are thought to be older and dated to the Pleistocene (Table 1). Only bones of large mammals including, besides the bears and lions, small mustelids, hares and marmots are described and discussed below. In our previous publication on the Imanay Cave (Gimranov et al., 2018) we reported findings of amphibians, reptiles, birds and small mammals from a small part of the excavation unit. The study of those bird and small vertebrate remains is yet in progress. We did not include the number of unidentified specimens in the tables as it was difficult to determine their number precisely. It can only be concluded that the number of such specimens is roughly equal across all the horizons. As most of the bone specimens excavated belong to the cave bear and cave lion, we find it useful to separately describe these taxa from the stratigraphic and taphonomic points of view.

## 4. Results

### 4.1. Lithology and age of the studied deposits

The Imanay Cave was formed in grey dolomite limestone of the Kungurian stage of the Lower Permian. The cave begins by a low and narrow entrance (height is 0.7 m; width is 1.0 m) and continues as an 80-m corridor (Fig. 1, B). At the end of the corridor, there is a grotto of 5 m in height and 8 m in width. A 6 $m^2$ excavation unit was placed in the grotto in the inner part of the cave. More than 10000 animal bone specimens were excavated from 12 $m^3$ deposits composed of light-brown gravel sands. The faunal remains were unequally distributed within the sediments: 99% of the bones were obtained from the upper horizon of 0.6 m thick. The deposits were being excavated by 10 cm horizons. In total, four lithological layers were detected during the excavation (Fig. 1, C; Fig. 2):

Layer 1 (depth 0–0.1 m)

Limestone fragments with an admixture of silt–pelite fraction of 5 wt (weight) %, light brown, corresponding to marl in composition,

**Table 1**
Stratigraphical distribution of remains of large mammals in the Imanay Cave (Late Pleistocene).

| Taxa | Layer 1 | Layer 2 | Layer 3 | | Layer 4 | | NISP |
|---|---|---|---|---|---|---|---|
| | depth* 0–0.1 | depth 0.1-0.2 | depth 0.2-0.3 | depth 0.3-0.4 | depth 0.4-0.5 | depth 0.5-0.6 | |
| *Lepus* sp. | 3** | 2 | | | | | 5 |
| *Marmota* sp. | 12 | | 1 | | | | 13 |
| *Castor fiber* (Linnaeus, 1758) | | | | | 1 | 1 | 2 |
| *Panthera* ex gr. *fossilis-spelaea* | 135 | 236 | 65 | 43 | 31 | 26 | 536 |
| *Cuon* sp. | | | | | 2 | | 2 |
| *Canis lupus* (Linnaeus, 1758) | 7 | 10 | 9 | 5 | 5 | 6 | 42 |
| *Canis* sp. | | | | | 1 | | 1 |
| *Vulpes lagopus* (Linnaeus, 1758) | | 1 | 1 | | | | 2 |
| *V. vulpes* (Linnaeus, 1758) | | 1 | | 1 | | 1 | 3 |
| *Vulpes* sp. | 2 | | | 1 | 1 | 13 | 17 |
| *Meles* sp. | | | | | 1 | 1 | 2 |
| *Gulo gulo* (Linnaeus, 1758) | 8 | 13 | | 1 | | 2 | 24 |
| *Mustela erminea* (Linnaeus, 1758) | | | | | | 1 | 1 |
| *M.* ex gr. *putorius-eversmanii* | 1 | 4 | | | 1 | | 6 |
| Mustelidae gen. indet. | | | | 1 | | | 1 |
| *Ursus "savini"* (Andrews, 1922) | 1165 | 2143 | 975 | 1388 | 1790 | 1953 | 9414 |
| *U. arctos* (Linnaeus, 1758) | 2 | 4 | 1 | | 5 | 4 | 16 |
| *U. thibetanus* (Cuvier, 1823) | | 1 | | | 1 | 1 | 3 |
| *Mammuthus primigenius* (Blumenbach, 1799) | 1 | | | | 1 | | 2 |
| *Equus ferus* (Boddaert, 1785) | 1 | 2 | | | | 1 | 4 |
| Rhinocerotidae gen. indet. | 2 | | | | | | 2 |
| *Saiga tatarica* (Linnaeus, 1766) | 2 | 3 | | 4 | 7 | 6 | 22 |
| *Ovis ammon* (Linnaeus, 1758) | 1 | | | 5 | 7 | 4 | 17 |
| Total NISP | 1342 | 2420 | 1052 | 1449 | 1854 | 2020 | 10137 |

Legend: * Depth in meters. ** NISP.

with fragments of bones of large and small mammals. At the base of the layer there was a broken calcite crust, 3–4 mm thick with bone debris. Palaeolithic stone tools were found in the layer.

Layer 2 (depth 0.1–0.2 m)

Dolomite-calcareous limestone fragments with an admixture of silt–pelite material of 5.8 wt %. There were areas of carbonate tufa. Bones of large and small mammals were found.

Layer 3 (depth 0.2–0.4 m)

Dolomite-calcareous dark brown limestone fragments with an admixture of silt–pelite material in 9.2 wt % and abundant angular cobbles of 10–20 cm in size. There were carbonate tufa formations and complete bones of large mammals found in this layer. Carbonate sand saturated with fine gravel formed the base of the layer.

Layer 4 (depth 0.4–0.6 m).

Brown calcareous-dolomite limestone fragments, with an admixture of aleurite–pelite material of 7.7 wt %. Less dense than in layer 3. Limestone rubbles were not numerous, but single angular blocks of 10–25 cm in size were present. The layer contained bones of large mammals.

Two radiocarbon dates for the cave bear and one date for the cave lion remains were obtained: 26320 ± 1790 BP (GIN-14244), 34940 ± 140 BP (IGAN-5652) and 42410 ± 260 BP (IGAN-5652), respectively. Collagen was extracted from the tubular bones found in the layer 1.

### 4.2. Notes on taxonomy

The taxonomic diversity of Ursidae in North Eurasia during the Pleistocene was substantially higher than at present. In different periods of the Pleistocene, a number of bear species inhabited the Urals: *U.*

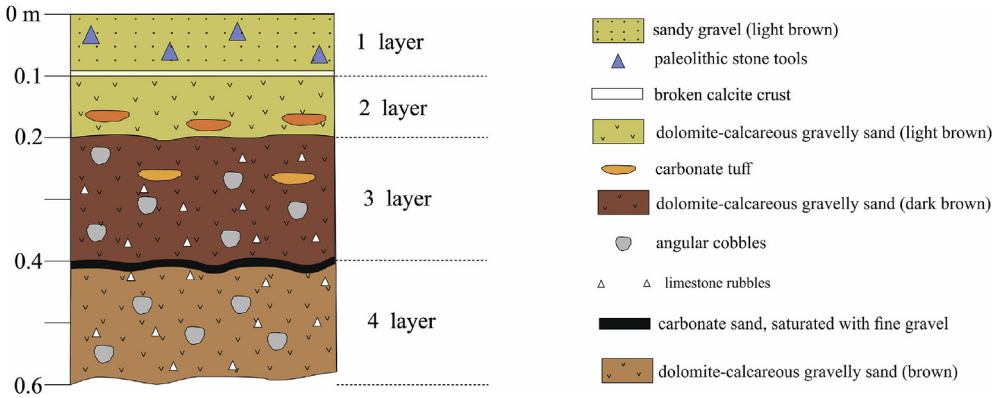


**Fig. 2.** General scheme of section composition of the Imanay Cave excavation pit.

*thibetanus* (G. Cuvier, 1823), *U. arctos* (Linnaeus, 1758), *U. savini* (Andrews, 1922) and *U. kanivetzi* (Vereshchagin, 1973) (Baryshnikov, 2007). The taxonomic position of *U. savini* has been hotly debated and revised many times (Borissiak, 1932; Vereschagin, 1982; Vereschagin and Baryshnikov, 2000; Baryshnikov, 2007; Rabeder et al., 2010; Baryshnikov and Puzachenko, 2017; Spassov et al., 2017). The largest number of U. *savini* bone specimens so far was found in the Kizel Cave in the Urals – the cave was probably a trap for the animals (Vereschagin, 1982). But there is still no consensus regarding the taxonomic position of this species (Vereschagin, 1982; Vereschagin and Baryshnikov, 2000; Baryshnikov, 2007; Baryshnikov and Puzachenko, 2017) thus for a precise determination of the taxonomic status of the cave bear remains from the Imanay Cave a separate publication dedicated to a revision of the small cave bear taxa is needed. In this study, we employ the species name suggested by G. Rabeder et al. (2010) and define the cave bears from the Imanay Cave as *U. "savini"*. In order to morphologically distinguish *U. savini* from the other bear species we followed the method based on teeth patterns described by Borissiak (1932) and Baryshnikov (2007).

The *Panthera fossilis* and *P. spelaea* species are widely present in Middle and Late Pleistocene localities in Europe (Sabol, 2011). As well as for the cave bear, there is no firm consensus about the taxonomic status and evolutionary relationships of this group of Felidae (Marciszak et al., 2014). All cave lion fossils from the Asiatic part of Russia so far have been identified as *P. spelaea*. But recently obtained data suggest a more complicated taxonomic composition of this carnivore group (Baryshnikov, 2001; Baryshnikov and Boeskorov, 2001; Ovodov and Tarasov, 2009; Boeskorov and Baryshnikov, 2013). For instance, *P. fossilis* from Pleistocene deposits from the Kuznetsk Basin in Siberia was described, and this fossil is considered to be the oldest in Eurasia (Sotnikova and Foronova, 2014). As such, we cannot perform a taxonomic revision of the cave lion fossils found in the Imanay Cave at the moment. Based on the large size of the animals, we determine them as *Panthera* ex gr. *fossilis-spelaea* (Sotnikova and Gimranov, 2017). A more detailed taxonomic analysis of the fossils will be published separately.

### 4.3. Faunal composition

#### 4.3.1. Pleistocene fauna

Most of bone specimens excavated at the Imanay Cave displayed the Pleistocene state of preservation: these were fossilized bones of darker color, from light-brown to black (Table 1). Fragmentation of these bones was high, the number of unidentifiable fragments was very large. These were found in all horizons at almost equal proportion.

The bulk of the Pleistocene specimens belong to the small cave bear (*U. "savini"*) (NISP = 9414) and cave lion (*P.* ex gr. *fossilis-spelaea*) (NISP = 536). Other large mammal species only comprise 2% of identified bones. Of these, five bones belonged to the hare, 15 – to the marmot and beaver, 67 – to Canidae, 34 – to Mustelidae, 19 – to other ursine species, 2 – to mammoth, 45 – to different ungulate species (Table 1). The Pleistocene fossils are quite evenly distributed across the whole excavation unit. Only in the third layer their number decreases due to the presence of limestone blocks that take up a large part of the volume of that third layer (see description of the layers above).

#### 4.3.2. Holocene fauna

Some of bone specimens excavated at the Imanay Cave displayed a Holocene state of preservation: non-fossilized and light-coloured (Table 2). The bones are highly fragmented which results in a large number of unidentifiable fragments. Most of the Holocene bones belong to the marmot (NISP = 624) and hare (NISP = 418). The genus *Vulpes* is represented by 92 bone specimens while 61 fragments belong to Mustelidae (Table 2). Most of the Holocene remains were concentrated in the first and second horizons (76%). Hare and marmot bones were found in all the horizons. Some of these specimens – 14% of the marmot and 11% of the hare remains - display signs of digestive corrosion. Some bones of *Vulpes* and *Mustela* demonstrate similar signs as well.

High fragmentation of the bones and the observed signs of digestive corrosion suggest that the accumulation of the bones in the cave during the Holocene was a result of activity of carnivorous mammals. The presence of badger (*Meles* sp.) bones is related to their continuous inhabitation in the cave until present.

### 4.4. Cave bear

#### 4.4.1. Distribution of the skeletal elements

An inventory of skeletal elements of *U. "savini"* is given in Table 3. The minimal number of individuals based on the quantity of the most frequently found tooth (right m1) was determined as 110. All parts of the skeleton are present in the sample (see Table 3). Teeth are the prevalent element (3912 specimens) followed by the phalanges 1–3 (1578 specimens) and *os sesamoideus* (1274 specimens). A large number of costal fragments (704 specimens) and metapodia (742 specimens) are present as well. The bones are highly fragmented and the number of complete long bones (*costa, femur, fibula, humerus, pelvis, radius, scapula, tibia, ulna*) is negligible: from one to three of each. The bones are quite evenly distributed across all layers except the third layer – accordingly to the prevalence of bones of other species (see the previous section).

The distribution of skeletal elements of *U. "savini"* across the horizons of the excavation unit is presented in Table 4. Isolated teeth (41.6%) and bones of the distal limbs (38.8%) – *os sesamoideus, calcaneus, talus, metapodium, phalanx 1, phalanx 2, phalanx 3* – are prevalent. The skeletal elements are evenly distributed across the horizons except the almost complete absence of deciduous teeth in the horizons 5 and 6.

#### 4.4.2. Age

The age composition of the *U. "savini"* sample is presented in Table 5. The table includes data on 2862 tubular bones suitable for analysis, deciduous teeth not included. Individuals of the cohort over 5 years old are prevalent (83.6%). The distribution of remains of all three age cohorts between the horizons is even, it is of note that the proportion of the cohort from 1 to 5 years is increased in horizon 5 and 6. The number of deciduous teeth is given in Table 4. These teeth comprise only a small portion of the dental sample (4%). They are evenly distributed across the horizons except a substantially reduced number of the teeth in horizons 5 and 6 (Table 4).

#### 4.4.3. Sex

The sex distribution of the *U. "savini"* sample was determined based on the size of the lower canine (Fig. 3). The greatest length (L) and width (W) of 31 specimens were measured. Of these specimens, 21 were assigned to males, 7 – to females and three displayed an intermediate position and could be hardly reliably determined. Based on this result, it can be hypothesized that most *U. "savini"* fossils from the Imanay Cave belonged to males.

### 4.5. Cave lion

#### 4.5.1. Distribution of skeletal elements

An inventory of the skeletal elements of *P.* ex gr. *fossilis-spelaea* is given in Table 6. The minimum number of individuals based on the quantity of the most frequently found teeth (P4, p4 and m1) was determined as 11. All bones of the skeleton except the sternum and *os penis* are present in the sample. The phalanges (128 specimens) and *os sesamoideus* (120 specimens) are prevalent, followed by teeth (90 specimens) and costal fragments (66 specimens). The bones are highly fragmented: no complete long bones – *costa, femur, fibula, humerus, pelvis, radius, scapula, tibia, ulna* – were found. The bones are unevenly distributed across the horizons: most bones (69%) were concentrated in the horizons 1 and 2.

The distribution of skeleton elements of *P.* ex gr. *fossilis-spelaea*

**Table 2**
Stratigraphical distribution of remains of large mammals in the Imanay Cave (Holocene).

| Taxa | Layer 1 | Layer 2 | Layer 3 | | Layer 4 | | NISP |
|---|---|---|---|---|---|---|---|
| | depth* 0–0.1 | depth 0.1-0.2 | depth 0.2-0.3 | depth 0.3-0.4 | depth 0.4-0.5 | depth 0.5-0.6 | |
| *Lepus* sp. | 154** | 179 | 11 | 14 | 22 | 38 | 418 |
| *Marmota* sp. | 253 | 251 | 40 | 22 | 24 | 34 | 624 |
| *Vulpes lagopus* (Linnaeus, 1758) | | | | | 1 | | 1 |
| *V. vulpes* (Linnaeus, 1758) | 2 | 2 | | | 1 | 1 | 6 |
| *V. corsac* (Linnaeus, 1768) | | | | 2 | | 1 | 3 |
| *Vulpes* sp. | 14 | 8 | 10 | 6 | 16 | 28 | 82 |
| *Meles* sp. | 17 | 1 | 1 | | | 1 | 20 |
| *Mustela erminea* (Linnaeus, 1758) | | | | | | 1 | 1 |
| *M. nivalis* (Linnaeus, 1766) | 16 | 5 | 1 | 1 | | | 23 |
| *M.* ex gr. *putorius-eversmanii* | 5 | 5 | 1 | 1 | 1 | | 13 |
| Mustelidae indet. | | 2 | 1 | 1 | | | 4 |
| Total NISP | 461 | 453 | 65 | 47 | 65 | 104 | 1195 |

Legend: * Depth in meters. ** NISP.

**Table 3**
Stratigraphical distribution of skeletal elements of *U. "savini"* in the Imanay Cave.

| Bones | Layer 1 | Layer 2 | Layer 3 | | Layer 4 | | Total |
|---|---|---|---|---|---|---|---|
| | depth* 0–0.1 | depth 0.1-0.2 | depth 0.2-0.3 | depth 0.3-0.4 | depth 0.4-0.5 | depth 0.5-0.6 | |
| *Atlas* | 3** | 4 | 1 | 0 | 4 | 4 | 16 |
| *Calcaneus* | 7 | 6 | 7 | 6 | 6 | 16 | 48 |
| *Costa* | 105 | 157 | 73 | 81 | 136 | 152 | 704 |
| *Cranium* | 22 | 31 | 36 | 35 | 21 | 55 | 200 |
| *Dentes* | 514 | 943 | 447 | 585 | 718 | 705 | 3912 |
| *Femur* | 9 | 8 | 4 | 6 | 20 | 24 | 71 |
| *Fibula* | 9 | 17 | 10 | 8 | 12 | 13 | 69 |
| *Humerus* | 6 | 14 | 3 | 8 | 30 | 22 | 83 |
| *Mandibula* | 23 | 22 | 11 | 18 | 14 | 21 | 109 |
| *Metapodium* | 97 | 169 | 61 | 109 | 150 | 156 | 742 |
| *Os hyoideuin* | 1 | 4 | 0 | 1 | 2 | 4 | 12 |
| *Os penis* | 1 | 2 | 1 | 1 | 4 | 2 | 11 |
| *Os petrosus* | 0 | 0 | 1 | 0 | 0 | 0 | 1 |
| *Os sesamoideus* | 122 | 282 | 120 | 188 | 253 | 309 | 1274 |
| *Pelvis* | 8 | 2 | 2 | 5 | 6 | 7 | 30 |
| *Phalanx 1* | 99 | 146 | 57 | 114 | 119 | 142 | 677 |
| *Phalanx 2* | 59 | 134 | 58 | 76 | 115 | 102 | 544 |
| *Phalanx 3* | 35 | 86 | 41 | 71 | 56 | 68 | 357 |
| *Radius* | 9 | 13 | 3 | 14 | 19 | 24 | 82 |
| *Scapula* | 1 | 4 | 3 | 3 | 5 | 4 | 20 |
| *Sternum* | 0 | 1 | 0 | 1 | 2 | 2 | 6 |
| *Talus* | 1 | 7 | 2 | 0 | 1 | 2 | 13 |
| *Tibia* | 11 | 8 | 3 | 7 | 13 | 19 | 61 |
| *Ulna* | 4 | 12 | 3 | 7 | 21 | 16 | 63 |
| *Vertebra* | 19 | 71 | 28 | 44 | 63 | 84 | 309 |
| Total | 1165 | 2143 | 975 | 1388 | 1790 | 1953 | 9414 |

Legend: * Depth in meters. ** number of specimens.

across the horizons of the excavation unit is outlined in Table 7. Bones of the distal parts of the limbs – *os sesamoideus, calcaneus, talus, metapodium, phalanx 1, phalanx 2, phalanx 3* – are prevalent (55.6%). These are followed by the vertebrae and ribs (17.4%), and teeth (16.8%). The bones are unevenly distributed across the horizons: most bones were concentrated in the horizons 1 and 2. Deciduous teeth were completely absent.

#### 4.5.2. Age

Bones with non-fused epiphyses and mandibles with emerging permanent teeth were not observed in the sample, as well as isolated deciduous teeth or strongly worn permanent teeth. As such, we suppose that all the remains of *P.* ex gr. *fossilis-spelaea* belonged to mature adult individuals in full vigor.

#### 4.5.3. Sex

The sexual composition of the *P.* ex gr. *fossilis-spelaea* sample was determined based on the size of the lower carnassial (m1) (Fig. 4). The greatest length (L) and width (W) of 11 specimens were measured. Of these specimens, 6 were assigned to males, 5 – to females. Thus, the sex ratio is equal in the cave lion sample from the Imanay Cave. The published materials on the cave lion from Weirzchowska Gorna Cave and published data on modern lions are used for comparison (Turner, 1984) (Fig. 4).

## 5. Discussion

### 5.1. Imanay Cave site

There are a few localities providing large deposits of bones of a single species (*Mammuthus primigenius* , *Equus ferus* or *Ursus spelaeus* sensu lato). Localities containing mass bone assemblages of a single species accumulated not due to human activity are commonly referred to as "graveyards". Such graveyards of *Mammuthus primigenius* are known in Europe (Kuzmina, 1971; Maschenko et al., 2006) and Asia (Chlachula et al., 2003; Chlachula and Serikov, 2011; Derevianko et al., 2003; Leshchinskiy, 2006, 2018; Nikolskiy et al., 2010; Pitulko et al., 2016). Mass assemblages of the bison (Krotova and Belan, 1993; Baygusheva et al., 2014) or horse (Sycheva et al., 2016) have been described as well. Pleistocene graveyards of carnivorous mammals are much less common, and most of them contain remains of *U. spelaeus*. The largest graveyards of the cave bear were found in Western and Central Europe (Musil, 1980; Döppes and Rabeder, 1997). In addition, large graveyards of the large cave bear are known in the south of Eastern Europe (Nopdman, 1858; Pidoplychko, 1956; Nagel et al., 2005) and in the Urals (Kuzmina, 1971; Smirnov et al., 1990; Kosintsev and Vorob'ev, 2001). Cave bears, as well as brown bears, used caves for winter dens. There are some rare evidences of mass graveyards of the brown bear (Kosintsev and Bachura, 2015) and cave lion (Vereshchagin, 1971; Diedrich, 2011b). But the lions, unlike the bears, did not use caves as dens and only inhabited the entrance lighted part of the cave. The biggest large feline locality in the world is Rancho La Brea in California (Merriam and Stock, 1932). At that locality, the animals got trapped in natural pitfalls – asphalt puddles. Until now there were no known cave sites containing "cemeteries" of two species of large predatory mammals. The Imanay Cave from the South Urals is unique in this sense since numerous bone remains of both cave bear and cave lion were excavated there. Thus, the cave represents a mass bone

**Table 4**
Skeletal elements of the cave bear from different caves from the Urals.

| Locality | Layer | Depth | Head* | Teeth | Milk teeth | Trunk | Foot proximal parts | Foot distal parts | Total NISP |
|---|---|---|---|---|---|---|---|---|---|
| Imanay | 1 | 0–0.1 m | 46** | 483 | 31 | 128 | 57 | 420 | 1165 |
| Cave | 2 | 0.1–0.2 m | 57 | 877 | 66 | 235 | 78 | 830 | 2143 |
| | 3 | 0.2–0.3 m | 48 | 429 | 18 | 103 | 31 | 346 | 975 |
| | | 0.3–0.4 m | 54 | 562 | 23 | 127 | 58 | 564 | 1388 |
| | 4 | 0.4–0.5 m | 37 | 716 | 2 | 209 | 126 | 700 | 1790 |
| | | 0.5–0.6 m | 80 | 705 | 0 | 244 | 129 | 795 | 1953 |
| | NISP | | 322 | 3772 | 140 | 1046 | 479 | 3655 | 9414 |
| | % | | 3.4 | 40.1 | 1.5 | 11.1 | 5.1 | 38.8 | |
| Kizel | NISP | | 150 | 215 | – | 528 | 281 | 626 | 1800 |
| Cave | % | | 8 | 12 | – | 29 | 16 | 35 | |
| Secrets | NISP | | 1031 | 136 | – | 2922 | 1651 | 1116 | 6856 |
| Cave | % | | 15 | 2 | – | 43 | 24 | 16 | |
| Ignatievskaya | NISP | | 238 | 644 | 2714 | 48 | 88 | 267 | 3999 |
| Cave | % | | 6 | 16 | 68 | 1 | 2 | 7 | |

Legend: *Skeletal elements: head: *cranium, mandibula* and *hyoideum*; teeth; trunk: *vertebra, costa, sternum* and *os penis*; foot proximal elements: *scapula, humerus, ulna, radius, pelvis, femur, tibia, fibula*; foot distal elements: *os sesamoideum, calcaneus, talus, metapodium, phalanx 1, phalanx 2, phalanx 3*. ** total number of specimens.

**Table 5**
Age composition of the cave bear sample from different site from the Urals (based on the tubular bones).

| Locality | Layer | Depth | Group under 1 year | Group from 1 to 5 years | Group over 5 years old | Total NISP |
|---|---|---|---|---|---|---|
| Imanay | 1 | 0–0.1 m | 2* | 54 | 282 | 339 |
| Cave | 2 | 0.1–0.2 m | 4 | 66 | 561 | 633 |
| | 3 | 0.2–0.3 m | 2 | 30 | 247 | 282 |
| | | 0.3–0.4 m | 3 | 62 | 358 | 427 |
| | 4 | 0.4–0.5 m | 9 | 100 | 456 | 570 |
| | | 0.5–0.6 m | 2 | 115 | 488 | 611 |
| | NISP | | 22 | 427 | 2392 | 2862 |
| | % | | 0.8 | 14.9 | 83.6 | 100.0 |
| Kizel | NISP | | 3 | 14 | 26 | 43 |
| Cave | % | | 7.0 | 32.6 | 60.5 | 100.0 |
| Secrets | NISP | | 65 | 498 | 122 | 685 |
| Cave | % | | 9.5 | 72.7 | 17.8 | 100.0 |

Legend: * number of specimens.

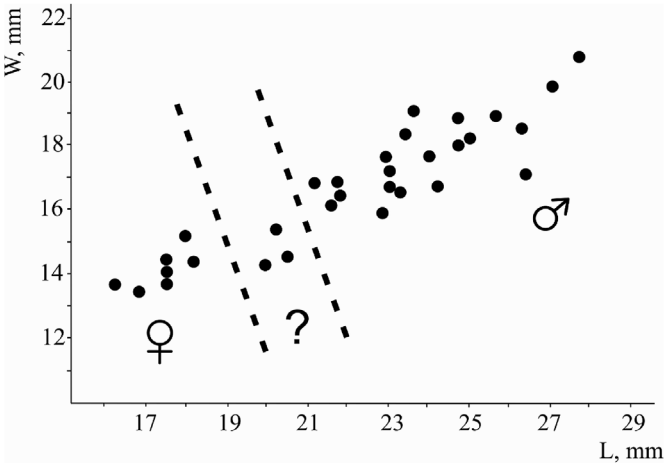


**Fig. 3.** Distribution of length and width of the canines of *U. "savini"* from the Imanay Cave.

assemblage of two species of large carnivorous mammals not directly related to each other in the trophic chain.

### 5.2. Cave bear

The cave bear (*U. "savini"*) is the most prevalent taxon in the Imanay Cave fossil sample. This species comprises 93% of the sample of large mammals from the cave and is represented by at least 110 individuals. Mass bone assemblages of the large cave bear, *U. spelaeus*, are known in the Urals (Kosintsev and Vorob'ev, 2001) and Western Europe (Kurten, 1958). A mass assemblage of *U. kudarensis* was excavated in the Caucasus (Baryshnikov, 1998, 2007). A graveyard of the small cave bear was found in the Urals as well, in the Kizel Cave (Vereshchagin, 1982; Vereshchagin and Baryshnikov, 2000). The taxonomic position of the cave bear from the Kizel Cave is disputed at the moment (Vereshchagin, 1982; Vereshchagin and Baryshnikov, 2000; Baryshnikov, 2007; Baryshnikov and Puzachenko, 2017). Some authors think that *U. savini* is a younger synonym to *U. deningeri* (Rabeder et al., 2010). The size of teeth and the metapodia is quite similar in cave bears from the Kizel and Imanay Caves (Vereschagin and Baryshnikov, 2000).

In deposits of the Imanay Cave, all types of bones of *U. "savini"* are present. All those bones are of similar color ranging from light to deep yellow. Teeth, the phalanges and *os sesamoideus* are prevalent in the

**Table 6**
Stratigraphical distribution of skeletal elements of the cave lion in the Imanay Cave.

| Bones | Layer 1 | Layer 2 | Layer 3 | | Layer 4 | | Total |
|---|---|---|---|---|---|---|---|
| | depth* 0–0.1 | depth 0.1-0.2 | depth 0.2-0.3 | depth 0.3-0.4 | depth 0.4-0.5 | depth 0.5-0.6 | |
| *Calcaneus* | 1** | 1 | | 2 | | | 4 |
| *Costa* | 19 | 33 | 7 | 2 | 2 | 3 | 66 |
| *Cranium* | 1 | 3 | 1 | 1 | | 2 | 8 |
| *Dentes* | 27 | 32 | 15 | 7 | 5 | 4 | 90 |
| *Femur* | 1 | 1 | | 2 | 1 | | 5 |
| *Fibula* | | 4 | | | | | 4 |
| *Humerus* | 2 | | | 1 | | | 3 |
| *Mandibula* | 1 | | | 1 | 1 | 1 | 4 |
| *Metapodium* | 9 | 23 | 1 | 4 | 1 | 2 | 40 |
| *Os sesamoideus* | 33 | 47 | 17 | 7 | 12 | 4 | 120 |
| *Pelvis* | | 3 | 1 | | 1 | | 5 |
| *Phalanx 1* | 10 | 27 | 8 | 6 | 1 | | 52 |
| *Phalanx 2* | 15 | 25 | 1 | 2 | 1 | 5 | 49 |
| *Phalanx 3* | 7 | 18 | 1 | | | 1 | 27 |
| *Radius* | 3 | 2 | 2 | 1 | 2 | | 10 |
| *Scapula* | | | 3 | 4 | 1 | 1 | 9 |
| *Talus* | 1 | 3 | | | 1 | 1 | 6 |
| *Tibia* | 1 | | 1 | | 1 | | 3 |
| *Ulna* | 1 | 1 | 2 | | | | 4 |
| *Vertebra* | 3 | 13 | 5 | 3 | 1 | 2 | 27 |
| Total | 135 | 236 | 65 | 43 | 31 | 26 | 536 |

Legend: * Depth in meters. ** (total) number of specimens.

**Table 7**
Skeletal elements of the cave lion from different European sites.

| Locality | Layer | Depth | Head* | Teeth | Trunk | Foot proximal parts | Foot distal parts | Total NISP |
|---|---|---|---|---|---|---|---|---|
| Imanay Cave | 1 | 0–0.1 m | 2** | 27 | 22 | 8 | 76 | 135 |
| | 2 | 0.1–0.2 m | 3 | 32 | 46 | 11 | 144 | 236 |
| | 3 | 0.2–0.3 m | 1 | 15 | 12 | 9 | 28 | 65 |
| | | 0.3–0.4 m | 2 | 7 | 5 | 8 | 21 | 43 |
| | 4 | 0.4–0.5 m | 1 | 5 | 3 | 6 | 16 | 31 |
| | | 0.5–0.6 m | 3 | 4 | 5 | 1 | 13 | 26 |
| | NISP | | 12 | 90 | 93 | 43 | 298 | 536 |
| | % | | 2.2 | 16.8 | 17.4 | 8.0 | 55.6 | |
| Binagadi asphalt lake | NISP | | 12 | – | – | 16 | 11 | 39 |
| | % | | 31 | – | – | 41 | 28 | |
| Zoolithen Cave | NISP | | 32 | 26 | 45 | 53 | 83 | 239 |
| | % | | 13.4 | 10.9 | 18.8 | 22.2 | 34.7 | |

Legend: *Skeleton sections(skeletal elements): head: *cranium* and *mandibula*; teeth; trunk: *vertebra, costa, sternum* and *os penis*; foot proximal parts (elements): *scapula, humerus, ulna, radius, pelvis, femur, tibia, fibula*; foot distal parts (elements): *os sesamoideus, calcaneus, talus, metapodium, phalanx 1, phalanx 2, phalanx 3*. ** total number of specimens.

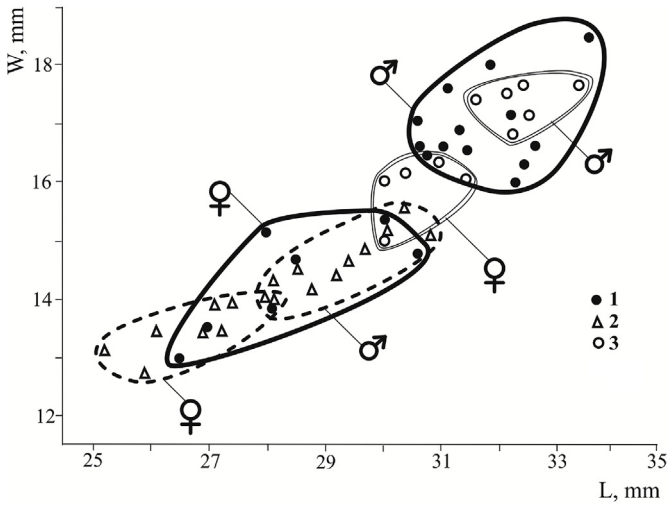


**Fig. 4.** Distribution of length and width of the carnassial (m1) of the cave and modern lion. 1 – cave lion from Weirzchowska Gorna Cave (Poland), 2 – modern African lion, 3– cave lion from Imanay Cave.

sample. Such a prevalence shows that the fossils in general are strongly fragmented and only the most compact and stiff bones of the skeleton could preserve in a complete form. The bones are quite evenly distributed across all excavation horizons. The prevalent age cohort is adults (over 5 years old) and, again, their distribution among the horizons seems to be fairly even. The similar state of preservation (degree of fossilization and fragmentation, color), similar amount of bones in all horizons and the prevalence of adult individuals in all the horizons point towards a gradual accumulation of bear remains in the cave, without long time breaks.

We compared our results for the Imanay Cave with published data on the skeletal sample composition in the Kizel, Secrets and Ignatievskaya Caves (Vereschagin, 1982; Smirnov et al., 1990; Vereschagin and Baryshnikov, 2000; Kosintsev and Vorob'ev, 2001). Those caves were selected since all of them are located in the Urals and contain numerous cave bear remains. In the Kizel Cave, there are less cave bear fossils compared to the other caves but a comparison with this cave was necessary because of the close taxonomic similarity observed between bears of this cave and that from the Imanay Cave. The cave bear remains from the Secrets and Ignatievskaya Caves are classified as *U. spelaeus* sensu lato (Smirnov et al., 1990; Kosintsev and Vorob'ev, 2001; Kosintsev et al., 2016).

While the bones of the distal parts of the foot and teeth are predominant in the Imanay Cave (Table 4), while in the Kizel Cave the vertebrae, trunk ribs and bones of the distal parts of the limbs are prevalent. A similar distribution is observed in the Secrets Cave as well, but there the foot proximal parts are prevalent. In the Ignatievskaya Cave, as well as in the Imanay Cave, teeth are prevalent, but in contrast to Imanay there was only a small amount of the distal parts of the limbs excavated at Ignaievskaya. Importantly, only the samples from the Imanay and Ignatievskaya Caves can be compared directly as in the Kizel and Secrets Caves fossils were collected without rinsing the sediments and thus small bones and teeth might be just left in the cave. Also, due to the chemical composition of soil in the Ignatievskaya Cave, bones are particularly poorly preserved in its sediments and thus the main part of the sample from this cave is comprised of teeth.

The age distributions in the samples from the Imanay, Kizel and Secrets Caves were compared (Table 5). There are no comparable data for the Ignatievskaya Cave though it was previously shown that mostly young and adult animals with an absent or a weak dental attrition got buried in the cave (Smirnov et al., 1990). The prevalent age cohort at Imanay as well as at Kizel is adults (over 5 years old) while in the Secrets Cave young animals (group from 1 to 5 years) were prevalent. Clearly, the age composition of the latter sample was different from that in the Imanay and Kizel Caves.

The sexual composition of the sample from Imanay appears to be strongly biased: males are prevalent (75%) which means a sex ratio of 3:1. This is in a sharp contrast with the caves from the Urals with mass assemblages of bear bones where females are prevalent (Kosintsev and Vorob'ev, 2001; Smirnov et al., 1990). The same is true for the Kizel Cave in which there are two times more female than male individuals (Vereschagin and Baryshnikov, 2000). The prevalence of males in the Imanay sample was confirmed by an analysis of other bones (and it still needs to be tested using other teeth and skeletal elements). Length (L) and width (W) of the distal epiphysis of the metacarpus were measured in 23 individuals (Fig. 5). As sexual dimorphism is much less pronounced in *U. "savini"* compared to *U. spelaeus*, it is difficult to clearly discriminate two sexes based on the size of the metapodial bones. But in general, our results confirm that the proportion of males is much higher in the sample (Fig. 5).

### 5.3. Cave lion

The number of bone remains of the cave lion at Imanay Cave is 536 specimens belonging to not less than 11 individuals. This location yielded the largest mass assemblage of cave lion bones in Eurasia. At Rancho La Brea in California, the world's biggest assemblage of large Pleistocene felids, bones of more than 40 individuals of *P. atrox* were found (Merriam and Stock, 1932). At the Binagadi asphalt location in the Caucasus, 64 bones of 11 individuals were excavated

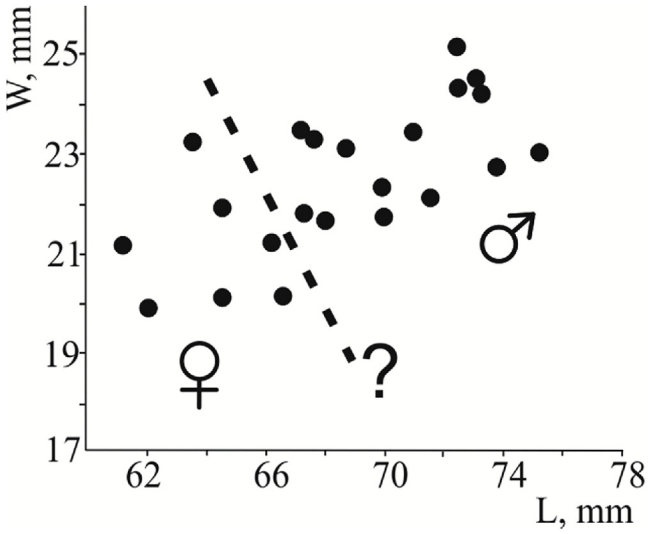


**Fig. 5.** Distribution of length and width of *metacarpus 4* in *U. "savini"* from the Imanay Cave.

(Vereshchagin, 1971). The only cave assemblage of cave lion bones known so far was the Zoolithen Cave in Germany where 239 bones belonging to at least 8 animals were found (Diedrich, 2011b). Those remains were excavated far apart from the entrance of the cave and their accumulation is mostly related to the predatory activity of the cave hyena (Diedrich, 2011a). All the European cave lion skeletal samples listed above were assigned to *P. spelaea*. But large size of bones and teeth of the cave lions from Imanay made us to assign it to the *fossilis-spelaea* group without providing a precise taxonomic diagnosis (see Material and Methods for details).

All bones of the skeleton of *P.* ex gr. *fossilis-spelaea* are present in the Imanay Cave and all these bones display a similar coloring – from light to deep yellow. The *P.* ex gr. *fossilis-spelaea* remains are mostly concentrated in the upper two horizons of the excavation unit (70%). The *phalanx 1–3* and *os sesamoideus* are highly prevalent in the sample; the distal parts of the hindlimb are predominant in general. The fossils are strongly fragmented and only the most compact and stiff bones of the skeleton could preserve in a complete form. At Binagadi asphalt lake, bones of the head and limbs are prevalent (Table 7) which can be explained by the method using which the fossils were collected (Vereshchagin, 1971), i.e. without rinsing the sediments. Probably, due to the very same reason the limb bones are prevalent in the sample from the Zoolithen Cave (Diedrich, 2011b).

Bones with non-fused epiphyses were not detected in the sample; deciduous teeth, jaws with changing teeth generations or permanent teeth with a high degree of attrition were not observed as well. As such, we suggest that all the remains in the sample of *P.* ex gr. *fossilis-spelaea* belong to mature and adult but not senile animals. The absence of juvenile individuals is an interesting feature of the sample from Imanay which is typical neither for the Rancho La Brea nor for the Bingada samples (Merriam and Stock, 1932; Vereshchagin, 1971; Diedrich, 2011b).

Sexual composition of the sample was assessed based on the size of the lower carnassial (m1) (Fig. 4). Of 11 specimens analyzed, 6 can be assigned to males and 5 – to females. So the sex ratio is close to 1:1, as it was observed at Zoolithen as well (Diedrich, 2011a).

### 5.4. Geological age of the pleistocene fauna

Most of the species whose remains display the Pleistocene state of preservation have inhabited the Southern Urals throughout the Late Neo-Pleistocene and Holocene (Kosintsev and Bachura, 2013). The Himalayan bear (*U. thibetanus*) was a member of the fauna of the Mikulinsky interglacial (MIS5e) (Gimranov, 2019; Kuzmin et al., 2017). The aesculapian snake (*Zamenis* cf. *longissimus*) (Ratnikov, 2009) was a part of the same fauna as well (Gimranov et al., 2018). The red wolf (*Cuon* sp.), small cave bear (*U. "savini"*) and argali (*O. ammon*) represent the fauna of the first half to middle Late Neo-Pleistocene (MIS5–3). The mammoth (*M. primigenius*) was present throughout the Late Pleistocene (MIS5–2) (Kosintsev and Bachura, 2013). The combination of remains of species of chronologically different faunas is explained by mechanical mixing of bone remains.

Stone tools were found in the upper horizons of the excavation unit alongside with fossil bones. The stone tool inventory is analogous to the collection of bifacial stone tools from the third cultural level of the Ilskaya Mousterian site in the Northern Caucasus (Gimranov et al., 2017). The artifacts from Ilskaya are dated to the beginning-first half of the Late Pleistocene (Shchelinskii and Kulakov, 2005). Today we do not have convincing evidences that the accumulation of cave bear and lion fossils in the Imanay Cave was related to human activity. The absence of any signs of human or other predator's activity on the bones suggests that the mass assemblage of cave bear and lion bones emerged as a result of natural mortality of the animals. Two radiocarbon dates for the cave bear remains were obtained: 26320 ± 1790 (GIN-14244) and 34940 ± 140 (IGAN-5652). One radiocarbon date for the cave lion remains was obtained: 42410 ± 260 (IGAN-5652). These dates comply with the second half of MIS3 or the Bryansk (Denekamp) Interstadial. The results of complex mineralogical and geochemical studies carried out at the Institute of Geology, Komi Research Center, Ural Branch of the RAS, have shown that the bones of the cave lion and that of the cave bear differ substantially: the latter are more fossilized. This might suggest that fossils of the two species were accumulated during different time periods (Silaev et al., 2018). The same suggestion is indirectly confirmed by the differences in distribution of bones of the two species observed across different horizons of the excavation. Cave bear bones are found in all the horizons at an almost equal amount while cave lion bones are mostly concentrated in the upper horizons. The time of accumulation of the species of the mammoth faunistic complex can be dated by the Late Pleistocene (MIS5–2).

### 5.5. Geological age of the holocene fauna

Most of the Holocene species whose remains were found at Imanay have inhabited the Southern Urals during the whole Holocene and inhabit it at present (Kosintsev and Bachura, 2013). Most of the Holocene remains belong to the hare (*Lepus* sp.) and marmot (*M. bobak*). It is difficult to define the time of accumulation of the remains precisely – likely most of those bones fell into the cave during the late Holocene. Most of badger bones got accumulated in recent times.

## 6. Conclusions

The Imanay Cave is a unique palaeontological object: it is the only site in the world containing mass bone assemblages of both cave bears and cave lions. Accumulation of the bones was not related to human or other large terrestrial carnivores activity, thus it emerged as a result of natural mortality of the animals. Remains of the two species were accumulated during different periods of the Late Pleistocene. The cave bear, as well as the brown bear, might use the cave as a shelter during the cold period of the year and produce offspring in the cave. The cave lion might use the cave as a shelter as well, but in the absence of subadult lion remains in the Imanay Cave it is difficult to come to a definite conclusion regarding the reasons of the accumulation of their remains in the cave.

Our analysis of the species composition of vertebrate fauna, archaeological data and radiocarbon dates suggests that the bone remains in the Imanay Cave have been accumulated throughout the whole Late Pleistocene and Holocene (MIS5-1). The time of accumulation of the cave lion and cave bear fossils can be broadly determined as the first

half to the middle of the Late Pleistocene (MIS5–3). Further research of the Imanay Cave will open up the possibility of understanding the causes of emergence of these mass graveyards of those large terrestrial vertebrates.

## Data availability

The skeletal collection from the Imanay Cave is housed at the Museum of the Institute of Plant and Animal Ecology UB RAS (Yekaterinburg) and can be accessed by any interested researcher.

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## References

Marciszak, A., Schouwenburg, C., Darga, R., 2014. Decreasing size process in the cave (Pleistocene) lion *Panthera spelaea* (Goldfuss, 1810) evolution – a review. Quat. Int. 339–340, 245–257.

Baryshnikov, G.F., 1998. Cave bears from the paleolithic of the greater Caucasus. In: In: Saunders, J.J., Styles, B.W., Baryshnikov, G.F. (Eds.), Quaternary Paleozoology in the Northern Hemisphere. Illinois State Museum Scientific Papers, vol 27. pp. 69–118.

Baryshnikov, G., 2001. The Pleistocene black bear (*Ursus thibetanus*) from the Urals (Russia). Lynx 32, 33–43.

Baryshnikov, G., 2007. Morphological variability of cheek teeth in cave bears. Scientific Annals, School Geol. 98, 81–102.

Baryshnikov, G.F., Boeskorov, G.G., 2001. The Pleistocene cave lion, *Panthera spelaea* (Carnivora, Felidae) from Yakutia, Russia. Cranium 18, l–18.

Baryshnikov, G.F., Puzachenko, A.Y., 2017. Morphometrical analysis of metacarpal and metatarsal bones of cave bears (Carnivora, Ursidae). Fossil Imprint 73, 7–47.

Baygusheva, V.S., Titov, V.V., Timonina, G.I., Simakova, A.N., Tesakov, A.S., Plicht, J., 2014. Mass burial of late Pleistocene bisons in the northeastern part of the sea of Azov area (port Katon, Rostov region). Dokl. Earth Sci. 454, 140–142.

Boeskorov, G.G., Baryshnikov, G.F., 2013. Pozdnechetvertichnyye Khishchnyye Mlekopitayushchiye Yakutii [Late Quaternary Carnivora of Yakutia]. Nauka Press, Saint-Petersburg, pp. 199 (in Russian).

Borissiak, A.A., 1932. Novaya rasa peshchernogo medvedya iz chetvertichnykh otlozheniy Sev. Kavkaza [New race of cave bear from Quaternary of the Northern Caucasus]. Trudy Paleozoologicheskogo instituta AN SSSR 1, 137–202 (In Russian, with German summary).

Chlachula, J., Serikov, Y.B., 2011. Last glacial ecology and geoarchaeology of the central Trans-Ural area: the Sosva river upper palaeolithic complex, western Siberia. Boreas 40, 146–160.

Chlachula, J., Drozdov, N.I., Ovodov, N.D., 2003. Last interglacial peopling of Siberia: the middle palaeolithic site Ust'-Izhul', the upper Yenisei area. Boreas 32, 506–520.

Derevianko, A.P., Molodin, V.I., Zenin, V.N., Leshchinskiy, S.V., Mashchenko, E.N., 2003. Pozdnepaleoliticheskoye mestonakhozhdeniye shestakovo [the late paleolithic shestakovo site]. In: Petrin, V.T. (Ed.), The Late Paleolithic Shestakovo Site. Institute of Archeology and Ethnography of the Siberian Branch of the RAS, Novosibirsk, pp. 168 (in Russian).

Diedrich, C.G., 2011a. Late Pleistocene steppe lion Panthera leo spelaea (Goldfuss, 1810) footprints and bone records from open air sites in northern Germany e Evidence of hyena-lion antagonism and scavenging in Europe. Quat. Sci. Rev. 30, 1883–1906.

Diedrich, C.G., 2011b. The largest European lion *Panthera leo spelaea* (Goldfuss 1810) population from the Zoolithen Cave, Germany: specialised cave bear predators of Europe. Hist. Biol. 23, 271–311.

Döppes, D., Rabeder, G., 1997. Pliozäne und pleistozäne Faunen Österreichs. Ein Katalog der wichtigsten Fossilfundstellen und ihrer Faunen. Mitt. Komm. Quartärforsch. Österr. Akad. Wiss. V. 10, 411.

Erokhin, N.G., Bachura, O.P., 2011. Novyy Podkhod K Komp'yuternoy Formalizatsii Razdroblennosti Kostnykh Ostatkov Mlekopitayushchikh V Arkheologicheskikh Issledovaniyakh [A New Approach to Computerized Formalization of Fragmentation of Bone Remains of Mammals in Archaeological Research]. Methodology of Interdisciplinary Archaeological Research: Sat. Scientific Art. And Method. Recommendations. Nauka Press, Omsk, pp. 62–69 (in Russian).

Gimranov, D., 2019. In: New data on *Ursus* (Euarctos) *thibetanus* G. Cuvier 1823 (Carnivora, Ursidae) of the Pleistocene Urals. 98. Zoological Journal, pp. 1168–1176.

Gimranov, D.O., Kotov, V.G., Rumyantsev, M.M., 2017. Rezul'taty Kompleksnykh Issledovaniy Mnogosloynoy Must'yerskoy Stoyanki V Peshchere Imanay-1 Na Yuzhnom Urale [The Results of Comprehensive Studies of the Multi-Layer Mousterian Site in the Cave of Imanay-1 in the Southern Urals]. V (XXI) Russian Archaeological Congress. "Altayskiy gosudarstvennyy universitet" Press, Barnaul, pp. 251–252 (in Russian).

Gimranov, D.O., Kotov, V.G., Rumyantsev, M.M., Silaev, V.I., Yakovlev, A.G., Yakovleva, T.I., Zelenkov, N.V., Sotnikova, M.V., Devyashin, M.M., Plasteeva, N.A., Zaretskaya, N.E., Nurmukhametov, I.M., Smirnov, N.G., Kosintsev, P.A., 2018. A mass burial of fossil lions (Carnivora, Felidae, *Panthera* (leo) ex gr. *fossilis-spelaea*) from Eurasia. Dokl. Biol. Sci. 482, 191–193.

Gorchakovsky, P.L., 1975. Vegetation World of the Highland Urals. Nauka, Moscow, pp. 283 (in Russian).

Igoshina, K.N., 1964. Vegetation of the Urals. In: Vegetation of the USSR and Foreign Countries. Nauka, Moscow-Leningrad, pp. 83–230 (In Russian).

Kosintsev, P.A., Bachura, O.P., 2013. Late Pleistocene and Holocene mammal fauna of the southern Urals. Quat. Int. 284, 161–170.

Kosintsev, P.A., Bachura, O.P., 2015. A mass burial of Brown bears (*Ursus arctos* L., 1758) from the upper Pleistocene of the northern Urals. Dokl. Biol. Sci. 462, 128–130.

Kosintsev, P.A., Vorob'ev, A.A., 2001. Biologiya bol'shogo peshchernogo medvedya (*Ursus spelaeus* Ros. et Hein.) na Urale [Biology of Large Cave Bear (*Ursus spelaeus* Ros. et Hein.) in the Ural Mountains]. In: Rozanov, A. Yu (Ed.), Mamont I Yego Okruzheniye: 200 Let Izucheniya [Mammoth and its Environment: 200 Years of Investigations]. GEOS Press, Moscow, pp. 266–278 (in Russian).

Kosintsev, P.A., Gasilin, V.V., Gimranov, D.O., Bachura, O.P., 2016. Carnivores (Mammalia, Carnivora) of the Urals in the late Pleistocene. Quat. Int. 420, 145–155.

Krotova, A.A., Belan, N.G., 1993. Amvrosievka. A Unique Upper Paleolithic Site in Eastern Europe. From Kostenki to Clovis: Upper Paleolithic – Paleo-Indian Adaptations. Plenum Press, New York, pp. 125–142.

Kurten, B., 1958. Leaf and death of the Pleistocene cave bear, a study in paleoecology. Acta Zool. Fenn. 90, 1–59.

Kuzmin, Y.V., Kosintsev, P.A., Vasiliev, S.K., Fadeeva, T.V., Hodgins, G.W.L., 2017. The northernmost and latest occurrence of the fossil porcupine (*Hystrix brachyura vinogradovi* Argyropulo, 1941) in the Altai Mountains in the Late Pleistocene (ca. 32,000 - 41,000 cal BP). Quat. Sci. Rev. 161, 117–122.

Kuzmina, I.E., 1971. Formirovaniye teriofauny Severnogo Urala v pozdnem antropogene [Formation of theriofauna of Northern Urals in late anthropogenic period]. Tr. Zool. Inst. AN SSSR 1, 44–122 (in Russian).

Leshchinskiy, S.V., 2006. Paleoecological investigations, taphonomy and genesis of the Lugovskoe Site. Archaeol. Ethnol. Anthropol. Eurasia 1, 33–40.

Leshchinskiy, S.V., 2018. Results of latest paleontological, stratigraphic and geoarchaeological research of the Volchia Griva mammoth fauna site. Proceedings of the Zoological Institute 322, 315–332 (in Russian with abstract in English).

Maschenko, E.N., Gablina, S.S., Tesakov, A.S., Simakova, A.N., 2006. The Sevsk woolly mammoth (Mammuthus primigenius) site in Russia: taphonomic, biological and behavioral interpretations. Quat. Int. 142–143, 147–165.

Merriam, J.C., Stock, C., 1932. The Felidae of Rancho La Brea. DC: Carnegie Institution of Washington, Washington, pp. 231.

Musil, R., 1980. Ursus spelaeus – Der Höhlenbär. I. Museum für Ur-und Frühgeschichte Thüringens [Ursus spelaeus - The cave bear. I. Museum of Prehistory and Early History of Thuringia]. Weimar, Germany, pp. 94.

Nagel, D., Pronin, K., Rabeder, G., Michael Hofreiter, M., Huijer, W., Kavcik, N., Urbanek, C., Withalm, G., Orlov, N., 2005. Nerubajskoe a new cave bear site in the old nordmann territory \ Mitt. Komm. Quartärforsch. Österr. Akad. Wiss. 14, 123–134.

Nikolskiy, P.A., Basilyan, A.E., Sulerzhitsky, L.D., Pitulko, V.V., 2010. Prelude to the extinctinction: revision of the Achchagyi-Allaikha and Berelyokh mass accumulations of mammoth. Quat. Int. 219, 16–25.

Nopdman, A., 1858. Paleontlogie Suedrusslands. I. *Ursus Spelaeus* (Odessanus).

Helsingfors, pp. 110.
Ovodov, N.D., Tarasov, A.Yu, 2009. Bol'shaya koshka (*Panthera* sp.) I malyy peshchernyy medved' (*Ursus rossicus*) v Sibiri [Big cat (*Panthera* sp.) and small cave bear (*Ursus rossicus*) in Siberia]. Yeniseiskaya province 4, 129–135 (In Russian).
Pidoplychko, I.G., 1956. Materialy Do Vyvchennya Mynulykh Faun URSR. [Materials for the Study of the Past Fauna of the USSR]. Kiev. View of the USSR Academy of Sciences, pp. 264 (in Ukrainian).
Pitulko, V.V., Pavlova, E.Y., Basilyan, A.E., 2016. Mass accumulations of mammoth (mammoth 'graveyards') with indications of past human activity in the northern Yana-Indighirka lowland, Arctic Siberia. Quat. Int. 406, 202–217.
Rabeder, G., Pacher, M., Withalm, G., 2010. Early Pleistocene bear remains from Deutsch-Altenburg (lower Austria). Mittl. Komm. für Quartarforsch. Osterreichischen Akad. Wiss. 17, 1–135.
Ratnikov, V.Yu, 2009. Iskopayemyye ostatki sovremennykh vidov zemnovodnykh i cheshuychatykh presmykayushchikhsya kak material dlya izucheniya istorii ikh arealov [Fossils of modern amphibians and scaly reptiles as material for studying the history of their ranges]. Tr. Nauch.-issled. Inst. Geol. Voronezh. 59, 1–91.
Rumyantseva, A.Ya, 1964. Climate. In: The Nature of the Chelyabinsk Region, pp. 60–89 Chelyabinsk, (in Russian).
Sabol, M., 2011. Masters of the lost world: a hypothetical look at the temporal and spatial distribution of lion-like felids. Quaternaire 4, 229–236.
Shchelinskii, V.E., Kulakov, S.A., 2005. Il'skaya Must'erskaya Stoyanka (Raskopki 1920-Kh–1930-Kh Godov [The Il'skaya Mousterian Site: the 1920s to 1930s Excavations]. "Yevropeyskiy dom" Press, Saint-Petersburg, pp. 96 (in Russian).
Silaev, V.I., Simakova, YuS., Parshukova, M.N., Gimranov, D.O., 2018. Kostenosnyye elyuvial'nyye grunty v Imanayskoy peshchere na Yuzhnom Urale [Bone-bearing eluvial soils in the Imanay Cave in the southern Urals]. Problems of mineralogy, petrography and metallogeny 21, 168–184.
Smirnov, N.G., Bolshakov, V.N., Kosintsev, P.A., Panova, N.K., Korobeynikov, YuI., Olshvang, V.N., Erokhin, N.G., Bikova, G.V., 1990. Istoricheskaya Ekologiya Zhivotnykh Gor Yuzhnogo Urala [Historical Ecology of Animals of the South Urals Mountains]. UrO AN SSSR Press, Sverdlovsk, pp. 245 (in Russian).
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. Integr. Zool. 9, 517–530.
Sotnikova, M.V., Gimranov, D.O., 2017. O Nakhodkakh Gigantskikh L'vov V Must'yerskikh Sloyakh (Pozdniy Pleystotsen) Peshchery Imanay (Yuzhnyy Ural) [On the Finds of Giant Lions in the Mousterian Layers (Late Pleistocene) of the Imanay Cave (Southern Urals)]. Materials of the LXIII Session of the Paleontological Society at the RAS. pp. 207–208 St. Petersburg.
Spassov, N., Hristova, L., Ivanova, S., Georgiev, I., 2017. First record of the "small cave bear" in Bulgaria and the taxonomic status of bears of the *Ursus savini* Andrews – *Ursus rossicus* Borissiak group. Fossil Imprint 7, 275–291.
Sycheva, S.A., Bessudnov, A.N., Chepalyga, A.L., Sadchikova, T.A., Sedov, S.N., Simakova, A.N., Bessudnov, A.A., 2016. Divnogorie pedolithocomplex of the Russian Plain: latest Pleistocene deposits and environments based on study of the Divnogorie 9 geoarchaeological site (middle reaches of the Don River). Quat. Int. 418, 49–60.
Turner, A., 1984. Dental sex diInorphislll in European lions (Panthera leo L.) of the Upper Pleistocene: palaeoecological and palaeoethological implications. In: 21. Ann. Zool. Fennici, pp. 1–8.
Vereshchagin, N.K., 1971. Peshchernyy lev i yego istoriya v Golarktike i v predelakh SSSR [The cave lion and its history in the Holarctic and on the territory of the USSR] Tr. Zool. Inst. AN SSSR 69, 123–199.
Vereshchagin, N.K., 1982. Kizelovskaya peshchera - lovushka dlya zhivotnykh na Srednem Urale [Kizel Cave as a trap for animals in the Middle Urals]. Tr. Zool. Inst. AN SSSR 111, 37–44 (in Russian).
Vereshchagin, N.K., Baryshnikov, G.F., 2000. Small cave bear *Ursus* (Spelearctos) *rossicus uralensis* from the Kizel cave in the ural (Russia). Geoloski zbornik 15, 53–66.
Weinstock, J., 2009. Epiphyseal fusion in brown bears: a population study of grizzlies (*Ursus arctos horribilis*) from Montana and Wyoming. Int. J. Osteoarchaeol. 19, 416–423.