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The cave bears from Imanay Cave (Southern Urals, Russia)

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ABSTRACT

In the rich vertebrate fauna of Imanay Cave the abundant material of the small-sized cave bears was originally assigned to the taxon Ursus savini. Teeth and metapodials of statistical amounts were compared with other cave bear faunas and the taxonomic position was determined through morphological and metric analyses. The size of teeth and metapodial bones is significantly smaller in Imanay Cave bears compared to the typical U. deningeri from Mosbach and Hundsheim. Although the teeth are smaller, they reached higher evolutionary level than those from Mosbach or Hundsheim.The bear remains from Imanay Cave show great similarities to the fossils from Kizel Cave in the Ural Mountains described as Ursus rossicus Borissiak, 1930 but also to the remains of small-bodied cave bears of the Alps described as Ursus deningeroides Mottl, 1964. Remarkable are the differences in size of the front dentition: the incisors from Imanay Cave are on average >10% longer and wider than the corresponding teeth from U. deningeroides but also wider than the classic U. deningeri. Preliminary carbon and nitrogen stable isotope analyses suggest that the small cave bears from Imanay Cave were herbivorous.

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Imanay cave; cave bear; *ursus deningeroides*; *ursus savini*; *ursus rossicus*; pleistocene; isotopic analysis; morphometric analysis

Introduction

The Imanay Cave is located in the Southern Ural (Russia, Bashkortostan Republic, Meleuz Region, coordinates 53°02' N, 56° 26' E), 7 km northeast of Nugush village (Figure 1, A), 420 m above sea level, length of cave: about 130 m. The cave has been excavated by Dmitry Gimranov and Pavel Kosintsev (Institute of Plant and Animal Ecology, Ural Branch RAS), Vyacheslav Kotov and Michael Rumyantsev (Institute of History, Language and Literature, UFRC RAS) from 2010 to 2016.

All bone remains of the cave bear from the Imanay Cave were originally assigned to the taxon *Ursus savini* Andrews (1922) (Gimranov and Kosintsev 2020). *U. savini* was chosen because there is no consensus among researchers about the taxonomic position of the small cave bear and the relationship with the *U. deningeri* group, in particular, with *U. deningeroides* (Mottl 1964). Currently, based on morphological and molecular data, many evolutionary lineages or even separate species are recognised (Knapp et al. 2009; Dabney et al. 2013; Stiller et al. 2014; Knapp 2018; Gretzinger et al. 2019; Barlow et al. 2021). Four main groups have been defined, that is, the *U. deningeri* group including *U. deningeri* von Reichenau 1904 and *U. deningeroides* Mottl (1964) and separately the Caucasian cave bear *U. kudarensis* Baryshnikov 1985, the small cave bear group with *U. savini* Andrews (1922) and *U. rossicus* Borissiak (1930), and the cave bear group with *U. spelaeus* Rosenmüller 1794 and *U. kanivetz* Vereshchagin 1973. The most recent studies of ancient mtDNA show the independence of the *ingressus* lineage (Barlow et al. 2021).

The taxonomy status and relationship among the bears from U. deningeri group and the small cave bear group is still poorly understood today because of limited molecular data and the absence of taxonomic revisions. There is evidence that the Urals and the surrounding area were inhabited by *U. rossicus* (Vereschagin and Baryshnikov 2000; Baryshnikov and Foronova 2001; Baryshnikov 2007; Sher et al. 2011; Gretzinger et al. 2019; Barlow et al. 2021). Based on the study of morphological and ancient DNA, it was established that in the Kizel Cave, which is located approximately 700 km north (in a straight line) from the Imanay Cave, the cave bears found there belong to the *rossicus* lineage (Baryshnikov and Puzachenko 2017, 2019, 2020; Barlow et al. 2021). But right the differences in measurements and morphology do not allow an assignment of the Imanay material to this species. *U. eremus* and *U. ingressus* were found in the same caves (Herdengelhöhle); both belonging to the same time span. The presence of two different species of bears with the same adaptations is beyond doubt.

The study of cave bears from Imanay Cave based on morphological and morphometric of teeth and metapodials will make it possible to shed light on the taxonomic position of the small cave bear group and the *U. deningeri* group, establishing the relationship, both within the group and with other cave bears. Moreover, the analysis of carbon and nitrogen stable isotopes of bone collagen will provide an opportunity to better understand the ecology of the studied groups of cave bears, as it has been already performed on numerous cave bear assemblages in Europe (e.g., Bocherens et al. 1994, 1999, 2006, 2011, 2014; Fernandez-Mosquera 1998; Krajcarz et al. 2016; García-Vázquez et al. 2018; Bocherens 2019; Terlato et al. 2019).

Geology, age and fauna of the Imanay Cave

The Imanay Cave was formed in grey dolomite limestone of the Kungurian stage of the Lower Permian (Gimranov and Kosintsev 2020). The Imanay Cave is located on the slope of a low mountain covered with forest and has a narrow entrance (0.7 × 1.0 m) and continues as an 80 m corridor (Figure 1, B). The cave has a grotto (cave chamber) of 5 m in height and 8 m in width at the end of the corridor. A six square metre excavation unit was placed in the

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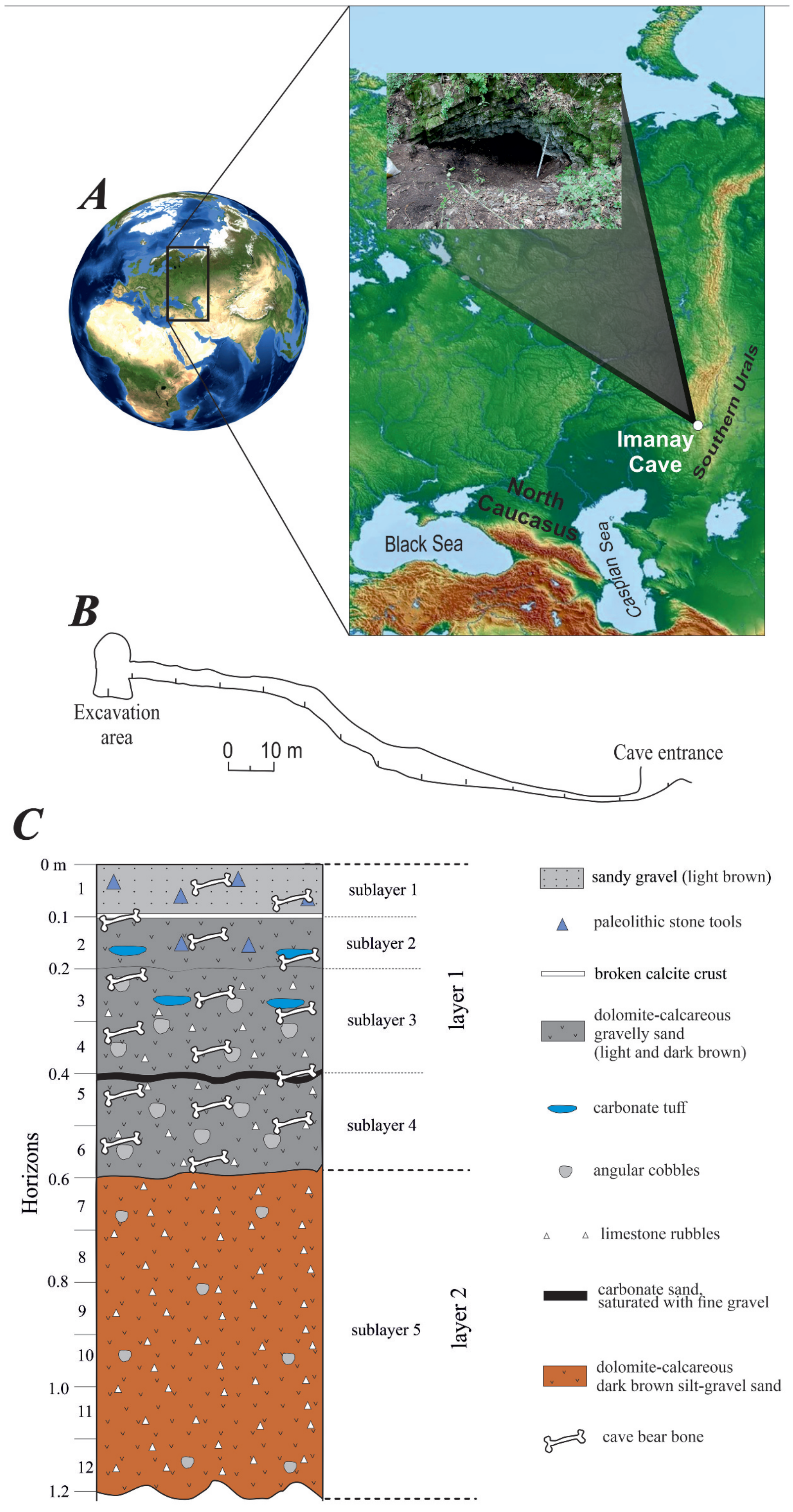

Figure 1. Location of the Imanay Cave. A: map of Eastern Europe showing the position of the Imanay Cave; B: vertical view of the Imanay Cave; C: stratigraphic section of the Imanay Cave.

grotto in the inner part of the cave (see Figure 1). More than 20,000 specimens were excavated from 24 m^3 deposits. Abundant remains of the fauna were unequally distributed within the sediments: 98% of the bones were obtained from the first 0.6 m of sediments (Figure 1, C). The deposits were being excavated in sections of 10 cm. In total, five lithological sublayers and two lithological layers were detected during the excavation (Figure 1, C). About four sublayers were mentioned in a previous publication. Note that sublayer 5 is sufficiently homogeneous (depth 0.6–1.2 m) and consists of dolomite-calcareous dark brown silt-gravel sand with angular cobbles of 20–30 cm in size. Fifth sublayer fully corresponds to the second layer (Figure 1, C). The sedimentology of sublayer 5 (=layer 2) is very different to the first layer (Figure 1, C).

Five radiocarbon dates for the cave bear remains were obtained from layer 1 (Table 1). From the sublayer 1 (depth 0.0–0.1 m): 26,320 ± 1.790 BP (GIN-14244); from sublayer 2 (depth 0.1–0.2 m): 34,250 ± 120 BP (IGAN-8464), 38,210 ± 200 BP (IGAN-8466), 46,260 ± 350 BP (IGAN-8465); from sublayer 3 (depth 0.2–0.3 m): 31,150 ± 110 BP (IGAN-8462).

Most of the fossil specimens excavated in the Imanay Cave are of a darker colour, ranging from light-brown to black. Almost all such samples displayed the Pleistocene state of preservation. Fragmentation of these bones was high (Gimranov and Kosintsev 2020). The Pleistocene fossils are quite evenly distributed across the whole layer 1. The number of the small and large bones sharply decreases in layer 2. Presently, the taphocoenosis of the Imanay Cave contains about 20,000 specimens of mammal remains. They mostly belong to *Ursus rossicus* or *U.* cf. *deningeroides* and the cave lion (*Panthera leo* ex gr. *fossilis-spelaea*). Rare findings stem from *Castor fibre, Canis* sp., *Cuon* sp., *Vulpes vulpes, V. corsac, Meles* sp., *Gulo gulo, Martes* sp., *Mustela* sp., *U. arctos, U. thibetanus, Mammuthus* sp., *Equus* sp., *Coelodonta antiquitatis, Alces alces, Bison priscus, Saiga tatarica, Ovis ammon*. The only exception are *Lepus* sp. and *Marmota bobak*, which are numerous (Gimranov et al. 2018; Gimranov 2019; Gimranov and Kosintsev 2020). In the bone layer (sublayer 1, 2), Middle Palaeolithic stone artefacts were found, including several bifacial points. These tools show analogies with the Middle Palaeolithic sites of the Caucasus region and Crimea (Kotov et al. 2020). Despite the presence of a rich stone inventory of the Middle Palaeolithic, there is no indication of hunting activities (e.g., cutting marks) so we assume a natural accumulation of the material.

The cave bear comprises 93% (NISP) of the sample of large mammals from the Imanay Cave and is represented by about 120 individuals (MNI). All bones of the skeleton were found, but teeth, phalanges and ossa sesamoidea are prevalent. Such a dominance of small and compact bones suggests that the fossil-bearing sediments were redeposited and sorted at least once or even several times. Most compact bones of the skeleton were preserved in a complete form. The assemblage of the cave is dominated by adult animals (over 5 years old). The distribution of age groups is almost the same over all the sublayer (1–4) within the first layer (Gimranov and Kosintsev 2020).

Materials and methods

Cave bear material present in this study were collected during the excavation of 2015–2016. All cave bear remains are stored in the Museum of the Institute of Plant and Animal Ecology, Ural Branch of Russian Academy of Sciences (Yekaterinburg). Only the remains of cave bears from the first layer (depth 0.0–0.6 m) of the Imanay Cave are included in present study. In the second layer (depth 0.6–1.2 m), the number of fossil bear bones is much lower, with only very few teeth and metapodials.

Morphometry

All the permanent dentition (except for the canines) and all metapodials were metrically and morphologically investigated following the methods of Rabeder et al. (2010). Measurements were taken using a digital caliper, to the nearest 0.1 mm. The obtained data was compared with the corresponding mean values of the cave bear faunas from which sufficient data are available: these are mainly the fossil bear faunas of the Alps (Mottl 1964; Rabeder et al. 2016).

Abbreviations: I1 – first upper incisor, I2 – second upper incisor, I3 – third upper incisor, P4 – fourth upper premolar, M1 – first upper molar, M2 – second upper molar, i1 – first lower incisor, i2 – second lower incisor, i3 – third lower incisor, p4 – fourth lower premolar, m1 – first lower molar, m2 – second lower molar, m3 – third lower molar. Dew . . . distal epiphyseal width, Mc1-5 . . . metacarpal bones of, md index . . . morphodynamic index, Mt1-5 . . . metatarsal bones, PI . . . plumpness index, stand. . . . standardised (the mean values of *U. ingressus* from the Gamssulzen cave serve as standards, according to Rabeder 1995, 1999 and Withalm 2001).

Stable isotopes

Thirty bone fragments of cave bears but also predators (cave lion *Panthera* ex gr. *fossilis-spelaea*) and herbivores (horse *Equus* sp., mammoth *Mammuthus* sp., rhinocerotid, wild ship *Ovis ammon*, saiga antelope *Saiga tatarica* and undetermined cervid) were sampled for determination of nitrogen content (%N) in whole bones to evaluate the quantity of collagen preserved before attempting a collagen extraction. Fossil bones with less than 0.4% nitrogen do not usually contain collagen with reliable isotopic compositions (Bocherens et al. 2005). Sample preparation was performed as follows. Small pieces of bone were cut from identified remains, sonicated in acetone and then rinsed three times in distilled water. After crushing and sieving to obtain a powder of 0.7 mm grain size, an aliquot of around 5 mg was used to measure the nitrogen and carbon content (%N, %C) of the whole bone, in order to screen out samples with excessive collagen (Bocherens et al. 2005). The measurements were performed using a Vario EL III elemental analyser using sulfanilic acid from Merck as an internal standard. The mean standard errors were better than of 0.02% and 0.05%, for %C and %N, respectively.

For samples with sufficient nitrogen content, collagen extraction was performed following Bocherens et al. (1997). The elemental and isotopic measurements were performed at SUERC (Glasgow, UK) and at the Geography working group in Tübingen. The elemental ratios C/N were calculated as atomic ratios. The isotopic ratios are expressed using the(delta) value as follows: $\delta^{13}C = [^{13}C/^{12}C_{sample}$

Table 1. Radiocarbon dates for the cave bear remains from the Imanay Cave.

Number	Material	Horizon	Radiocarbon age	Error	Calibrated 2-sigma age range (95.4%)	References
IGAN-8464	Left I1–2	2	34,250	120	39,177–39,703	This paper
IGAN-8465	Right I1-2	2	46,260	350	47,674–49,807	This paper
IGAN-8462	Right I1-2	3	31,150	110	35,247–35,930	This paper
IGAN-8466	Right I1-2	2	38,210	200	42,161–42,511	This paper
GIN-14,244	*Thoracic vertebra №3-4*	1-2	26,320	1790	-	Gimranov and Kosintsev 2020

$/^{13}C/^{12}C_{reference} - 1] \times 1000$ (‰), $\delta^{15}N = [^{15}N/^{14}N_{sample}/^{15}N/^{14}N_{reference} - 1] \times 1000$ (‰), with the international reference being V-PDB for $\delta^{13}C$ values and atmospheric nitrogen (AIR) for $\delta^{15}N$ values. The reproducibility was ±0.1‰ for $\delta^{13}C$ measurements, ±0.2‰ for $\delta^{15}N$ measurements, based on multiple analysis of purified collagen from modern bones.

Results

Morphometry

The bear remains from Imanay Cave stem from a small cave bear sensu lato. The main characteristics of the Imanay bears are the following:

1. The dimensions of the teeth (Table 2) and metapodials (Table 3) are as small as we know them only from high alpine cave bears of the Late Pleistocene or from *U. deningeri* of the Middle Pleistocene. But not as small as those of the *U. rossicus* from Kizel Cave (Vereschagin and Baryshnikov 2000).

2. The extremities are very short and plump. In relation (LDH diagram) of means of metapodial lengths and means of cheek tooth length, the beas from the Imanay Cave has the low value of all European cave bears used for comparison (Figure 2) and resembles in this feature of Alpine taxon described as '*Ursus deningeroides*' (Rabeder et al. 2016). However, the smallest size of the cheek teeth and metapodials is found in the bears from the Kizel Cave (Vereschagin and Baryshnikov 2000).

3. The evolutionary level of the 4th premolars (P4/p4 index, Table 2) of the Imanay bears is very low compared to typical cave bear faunas (*U. s. ladinicus, U. eremus* or *U. ingressus*), but higher than that of the classical faunas of *U. deningeri* from Mosbach and Hundsheim (Rabeder et al. 2010).

4. The highest morphological differences between the fauna of the *U. deningeri* group and the typical cave bear faunas of the Late Pleistocene (*U. spelaeus, U. ingressus, U. eremus* etc.) can be found in the incisors – especially on the first and second upper incisors (I1-2). In the fauna of the *deningeri* group, the morphotypes 'd' (*deningeri*) and 'd/p' (*deningeri/spelaeus*) intermediate form (sensu Rabeder 1999) dominate among the I1-2, while these morphotypes occur very rarely in the typical cave bears. The bear of Imanay is clearly separated from the other ones in the cluster of *U. deningeroides* (Figure 3). Unfortunately, we have no data on *U. rossicus* incisors from Kizel Cave.

Table 2. Dimensions and morphodynamic indices teeth of the cave bear from the Imanay Cave

Teeth		Length	Width	MD index
I1-2	mean	10.67	12.12	107.55
	n	106	104	106
I3	mean	–	14.54	–
	n	–	35	–
P4	mean	18.75	12.99	60.34
	n	42	42	30
M1	mean	25.58	18.11	
	n	39	39	
M2	mean	41.85	20.74	
	n	36	36	
i1	mean	6.98	9.88	116.67
	n	30	30	30
i2	mean	10.14	11.50	51.47
	n	36	36	34
i3	mean	13.64	12.65	96.97
	n	33	33	33
p4	mean	14.52	9.75	128.75
	n	40	40	40
P4/p4 index	index			88.14
m1	mean	26.67	13.08	
	n	43	43	
m2	mean	27.91	16.96	110.00
	n	40	40	30
m3	mean	24.60	18.36	
	n	40	40	

Table 3. Dimensions and morphodynamic indices metapodial bones of the cave bear from the Imanay Cave.

Metapodia		Length	Dew.	PI	Length stand.	Dew. stand.	PI stand.
Mc1	mean	49.20	15.08	30.70	77.48	78.12	101.01
	n	13	13	13			
Mc2	mean	63.03	20.43	32.55	85.53	80.76	94.83
	n	12	12	12			
Mc3	mean	66.10	20.85	31.61	82.83	78.67	95.19
	n	15	15	15			
Mc4	mean	68.64	22.35	32.59	82.10	79.82	97.31
	n	24	24	24			
Mc5	mean	69.04	25.16	36.53	83.69	86.17	103.22
	n	18	18	18			
mt1	mean	55.39	16.39	29.64	104.32	92.62	88.93
	n	17	17	17			
mt2	mean	55.73	17.01	30.53	82.80	79.85	96.47
	n	11	11	11			
mt3	mean	63.65	17.66	27.75	82.34	75.48	91.69
	n	13	13	13			
mt4	mean	68.33	19.01	27.85	81.06	77.58	95.82
	n	16	16	16			
mt5	mean	72.78	20.21	27.75	84.93	82.81	97.47
	n	17	17	17			
all	mean				84.92	81.50	96.33
	n	156	156	156			

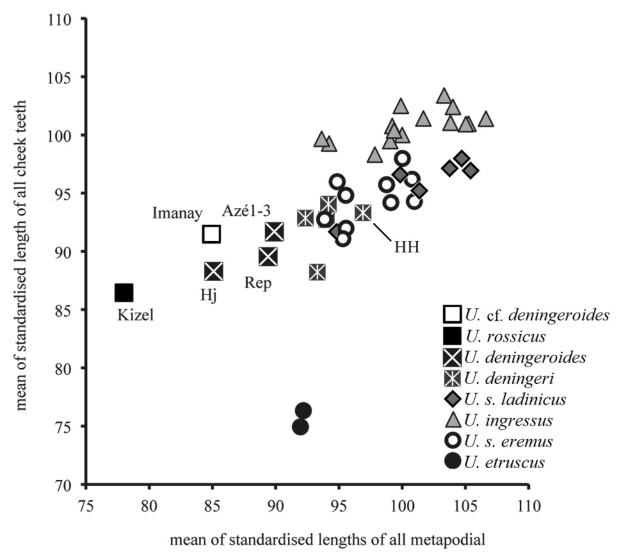

Figure 2. LDH diagram (Locomotion vs. Dietary Habits diagram) of European cave bear faunas. The values of Imanay bears lie in the cluster of *Ursus deningeroides*. Azé1-3 ... Grotte d'Azé 1, unit 1–3 (Burgundy, France), HH ... fissure filling of Hundsheim (Lower Austria), Hj ... Herkova jama (Slovenia), Rep ... Repolust Cave (Styria, Austria), Kizel ... Kizel Cave (Ural, Russia).

Stable isotopes

Among the 30 bones tested for collagen conservation using elemental analysis, 16 of them yielded very low nitrogen percentages (from 0.02 to 0.34%), including all the tested wild sheeps and saiga specimens. Only 14 specimens yielded nitrogen amounts above 0.4%, the threshold value for possible

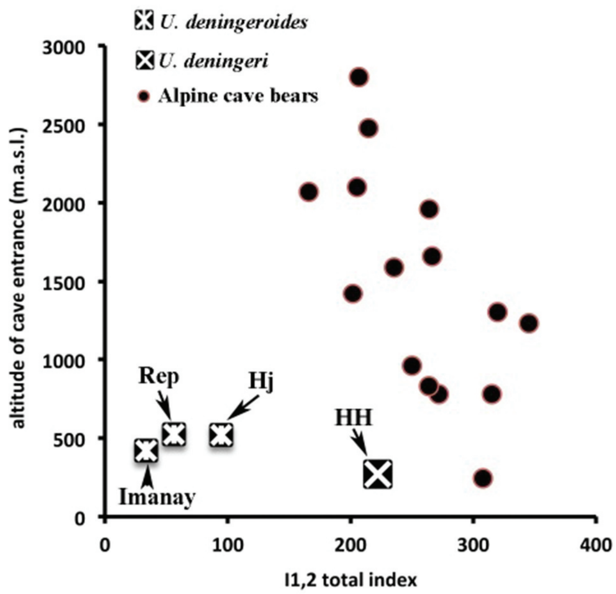

Figure 3. The morphodynamic index (I1-2 index, sensu Rabeder 1999) of the first two upper incisors of the bears in relation to the altitude of the cave entrances. Comparing the values from the Imanay Cave and the alpine faunas, the fauna of Imanay is closest to the *Ursus deningeroides* from Herkova jama and Repolust Cave. HH ... fissure filling of Hundsheim (Lower Austria), Hj ... Herkova jama (Slovenia), Im ... Imanay Cave, Rep ... Repolust Cave (Styria, Austria).

collagen preservation. Among those for which collagen extraction was attempted, five cave bear bones, three cave lion bones and five herbivore bones (one mammoth, one rhinoceros, two horses and one cervid) yielded well-preserved collagen, based on their %C, %N and C/N values (Table 4), the extract from one cave bear bone (IMN-13) exhibited chemical composition outside the accepted range for well-preserved collagen (Table 4). The isotopic results are presented in Table 4 and Figure 4. The δ^{13}C values of the cave bears ranged from −21.8 to −20.8‰, lower than those of most herbivores (−20.4 to −19.5‰), except for mammoth (−22.4‰), and lower than for the cave lion (−19.4 to −18.2‰). The δ^{15}N values of the cave bears are also the lowest measured on the faunal remains, ranging from 3.1 to 5.1 ‰, while most herbivores have δ^{15}N values ranging from 7.1 to 8.3‰ and the cave lion have δ^{15}N values ranging from 9.9 to 11.4‰ (Table 4), one exception are both analysed horses with δ^{15}N values surprisingly high (12.5 and 13.2 ‰). Horses were excluded from the analyses, see details below.

Discussion

The so-called '*deningeri* group' includes cave bears, with relatively small dimensions and archaic features, which mainly concerns cheek teeth (Wagner and Čermák 2012). The variability in the dimensions and in the morphology of the dentition is at least as great as in the 'true' cave bears ("*U. spelaeus* group"). Numerous taxa (species and subspecies) have been established whose phylogenetic relationships to each other are still completely unknown. Beside the name-giving species *U. deningeri*, others have been described: *U. savini, U. rossicus* and *U. deningeroides, U. uralensis* (see Spassov et al. 2017). We consider the group of small cave bears (*U. savini* and *U. rossicus*) separately from the *U. deningeri* group. In this small morphological study, we can initially only consider the relationships to *U. rossicus, U. deningeroides* and to the classic *U. deningeri*, because sufficient morphological data are only available from these taxa.

The cave bears from the Imanay Cave belong to the smallest cave bears in Europe according to the standardised mean values of the teeth and metapodials (Figure 1, Tables 2 and 3). Unfortunately, there are no data on the incisors of *U. rossicus*, but the dimensions of the metapodials are in close range with the metapodials *U. rossicus* from the Kizel Cave (Vereschagin and Baryshnikov 2000; Baryshnikov and Puzachenko 2017). Unfortunately, this is why we cannot display the position of the bear from the Kizel Cave (Middle Ural) on the graph. We assume that the bears from the Kizel Cave will be similar in size of incisors to the bears from Imanay Cave and bears of the *U. deningeri* group. At the moment the Imanay bear is also morphologically close to the bears that are referred to as *U. 'deningeroides'*. A large number of teeth and metapodials in the faunal assemblage of the Repolust Cave (Döppes and Rabeder 1997) and Herkova jama (Frischauf et al. 2013) allows a comparison of these two faunas. The morphological matches concern both the P4/p4 index and the index of the first two maxillary incisors (I1-2 index). The values of the Imanay bears are in the clusters of *U. 'deningeroides'* (Figures 2 and 3).

However, there is a clear difference in the dimensions of the incisors. The incisors from the Imanay Cave are on average more than 10% larger than the teeth from other sites of the *deningeri* group. This peculiarity remains to be explained. Therefore, on the basis of this, the fossil record of cave bears from the investigated cave is determined as much as *Ursus* cf. *deningeroides*.

Ursus deningeroides Mottl (1964) from other caves

This taxon was originally described from the Repolust Cave in the Graz Mountains (Styria, Austria, Mottl 1964; Döppes and Rabeder 1997) and later also from Herkova jama in Slovenia, in

Table 4. List of isotopic values of carbon and nitrogen of bones animals from Imanay Cave.

Lab. number	N samples	Species	Bone	%Nbone	%C	%N	C/N	d^{13}C	d^{15}N
IMN-2	227	Cave lion	Left mandibula	0.56	19.3	6.5	3.4	−19.4	11.4
IMN-4	11,909	Cave lion	Left mandibula	0.51	38.3	14.0	3.2	−18.2	9.9
IMN-6	11,908	Cave lion	Left mandibula	0.56	36.2	12.9	3.3	−18.3	11.4
IMN-11	888	Cave bear	Left mandibula	1.03	21.3	7.2	3.4	−21.0	3.1
IMN-12	887	Cave bear	Right mandibula	0.50	14.5	5.0	3.4	−21.8	4.0
IMN-14	48	Cave bear	Right mandibula	0.52	7.3	2.6	3.2	−21.8	8.8
IMN-15	2079	Cave bear	Right mandibula	0.71	17.9	5.9	3.5	−21.3	3.4
IMN-18	947	Cave bear	Left mandibula	0.55	16.5	6.1	3.2	−20.8	5.1
IMN-20	12,154	Horse	Tooth	0.35	21.0	7.6	3.2	−19.5	13.2
IMN-21	12,155	Horse	Tooth	0.33	25.4	8.9	3.3	−20.4	12.5
IMN-22	12,156	Rhinoceros	Radius	0.61	22.7	8.2	3.2	−20.0	8.3
IMN-23	12,157	Mammoth	Tooth	0.37	28.6	10.4	3.2	−22.4	7.2
IMN-30	12,164	Deer	Horn	0.45	14.5	5.8	2.9	−20.0	7.1

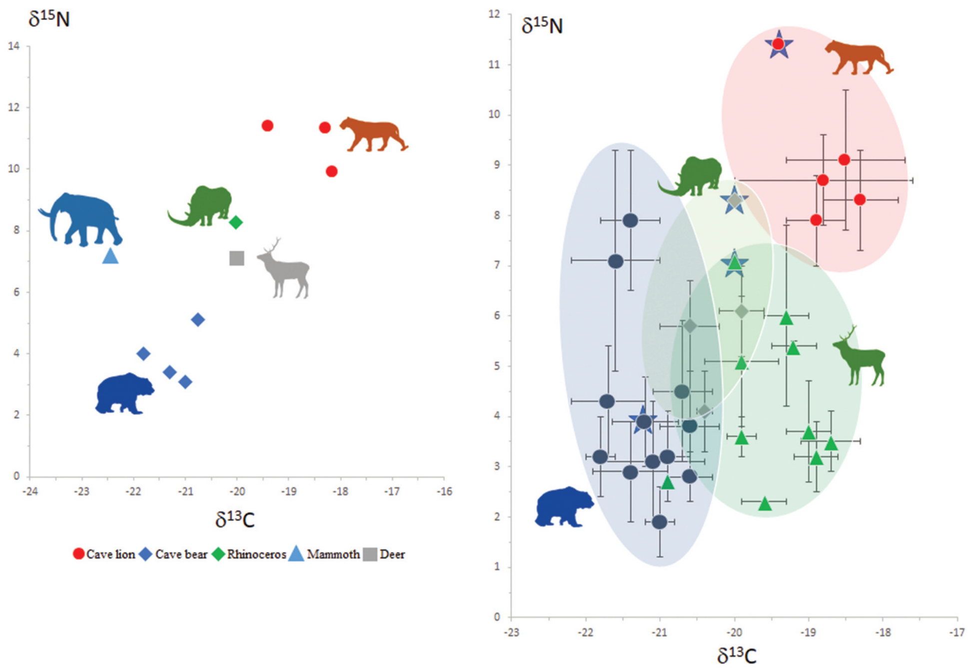

Figure 4. Left: δ^{13}C-δ^{15}N scatter plot of cave bear and coeval herbivorous and carnivorous from Imanay Cave (data in Table 4). Right: Comparison of δ^{13}C and δ^{15}N values of Imanay specimens with other sites in Europe (data from Bocherens 2019). The stars indicate the results obtained on specimens from Imanay Cave for the different species.

the cave of Flatz in Lower Austria and perhaps in the Grotte d'Azé (Burgundy, France) (Argant 1991, Frischauf al. 2013; Pacher and Rabeder 2018). The accompanying fauna of some of these bear sites contains elements such as *Equus* cf. *mosbachensis, Hystrix* cf. *'vinogradovi'* and primitive voles, which suggest a somewhat older geological age than is often documented for the Late Pleistocene alpine cave bears.

Small cave bear group from other sites

C.W. Andrews was the first to describe the *U. savini* in 1922 from the Bacton Forest Bed locality (Middle Pleistocene) in England (Andrews 1922). Baryshnikov (2007) integrates *U. savini* with *U. rossicus*, whereas Spassov et al. (2017) suggested the distinction between *U. savini* (including *U. rossicus*) and *U. uralensis* (from Kizel Cave). Unfortunately, there are almost no data on the incisors and metapodial of the bear from the Bacton Forest Bed, and the age of the locality is interpreted ambiguously (Wagner and Čermák 2012). Therefore, we do not consider the size of the teeth and metapodials of *U. savini* in our analysis.

U. rossicus lived in the Middle and Late Pleistocene territory of Eastern Europe, Urals and Western Siberia (Vereshchagin and Baryshnikov 2000; Spassov et al. 2017). *U. rossicus* was first described from the outskirts of the city of Krasnodar in 1930 by the Russian palaeontologist A.A. Borissiak (1930). Unfortunately, it is difficult to determine the geological age of these finds, so we do not include the size of the teeth and metapodial of the bear from Krasnodar in the analysis. But we note that *U. rossicus* from Krasnodar has very small incisors and metapodials and is similar to the *U. deningeri* group.

According to Gretzinger et al. (2019: suppl. Figure 3) based on mtDNA evidence *U. rossicus* from Denisova Cave and Strashnaya Cave (Altai Mountains, Russia) form a sister clade to all other cave bears of *spelaeus*-group. According to nuclear and mitochondrial evidence, it occupies the basal position in relation to *U. spelaeus* sensu lato (Barlow et al. 2021).

Chronology of cave bear remains

Radiocarbon dates of cave bear remains from the Imanay Cave yield calibrated ages from approximately 41,000 to 26,000 years calBP (Gimranov and Kosintsev 2020). These dates would provide the geologically youngest ages of the *deningeri* group bears and support the very contradictory hypothesis that *U. deningeri* sensu lato lived contemporaneously with the highly evolved cave bears of the Late Pleistocene in the Urals and perhaps also in the Alps. Attempts to date the remains from Repolust Cave and Herkova Jama have so far been unsuccessful, only producing 'older than' dates. In both caves, the fossil-bearing sedimentary beds are partially disturbed by marmot and fox burrows. In the Repolust Cave, the main fossiliferous layers of the ursid remains are called 'grey sand', 'rusty brown phosphate soil' and 'shaft fill' (Mottl 1964). These layers contained remains of *U. deningeroides* as well as of a large-sized cave bear (probably of *U. ingressus*) but also remains of subtropical steppe dwellers (*Hystrix, Ochotona and Bison*), alpine elements (*Marmota, Capra ibex*) and clearly Middle Pleistocene elements, such as *Equus mosbachensis, Canis mosbachensis* and *Arvicola 'hunasensis'*. No clear stratigraphy is preserved there any more (Döppes and Rabeder 1997). In the Herkova jama, the situation is similar, in that here also a juxtaposition of remains of the small '*U. deningeroides*' and a large cave bear can be observed. The sediments are strongly disturbed by burrowing animals (*Marmota, Vulpes*) as well. The placement of the *U. deningeroides* remnant in the Middle Pleistocene is based on the low evolutionary level of these bears and the co-occurrence with Middle Pleistocene taxa (Mottl 1964).

Therefore, remains are a surmise until absolute age data allow clarification of this question. There is the possibility that the fossil-bearing strata in Imany Cave are redeposited in a similar way as known from the Repolust and the Herkova Caves. The available radiocarbon dates should be viewed as critically as those from Repolust Cave (Döppes and Rabeder 1997). The co-occurrence of two ursids of very different evolutionary stages might indicate a Middle Pleistocene small species (*U. rossicus* or *U.* cf. *deningeroides*) and a Late Pleistocene larger species (*U. ingressus* or *U. kanivetz*). This can only be clarified by new C14 dating or molecular dating. It should also be for the Imanay material that only unambiguously determinable elements (e.g., teeth and metapodials) are used for dating to resolve this question. However, there are radiocarbon dates for the bears from Kizel Cave (*U. rossicus*). Nine dates fit into the range from 31,870 to 46,250 BP (Barlow et al. 2021). This once again suggests that small cave bears in the Urals could survive until the Late Pleistocene.

Palaeoecology of the cave bears

The isotopic results of the cave bears from Imanay Cave compared to those of coeval herbivores and predator are in a similar position in the scatter plot of $\delta^{13}C$ and $\delta^{15}N$ values than other European cave bears (Figure 4), with lower $\delta^{13}C$ and $\delta^{15}N$ values than all other taxa. Such low isotopic composition indicates a vegetarian diet, even if the rest of the analysed species in Imanay Cave do not follow completely the isotopic pattern seen in the rest of northern Europe during the same period of time (e.g., Bocherens 2015).

Especially outliers are the horses, with very high $\delta^{15}N$ values and high $\delta^{13}C$ values, while they typically have $\delta^{13}C$ values as low as those of mammoths and $\delta^{15}N$ values lower or similar to those of mammoths (e.g., Drucker et al. 2015). This pattern could be linked to foraging in more open and arid areas, possible in the southern lowland, as high $\delta^{15}N$ values were measured in saiga antelope around the Black Sea (Drucker et al. 2017). However, since the analysed specimens are deciduous teeth, it is more likely that these unusual isotopic abundances are due to a suckling signal (Bocherens et al. 1994). Therefore, these specimens will not be considered further for palaeoecological implications.

Also, the analysed mammoth exhibits one of the lowest $\delta^{15}N$ value among ungulates, which is unusual for this species that exhibits, typically, the highest $\delta^{15}N$ values among Late Pleistocene herbivores (e.g., Bocherens 2015; Ma et al. 2021). A similar pattern has been documented at the southern edge of mammoth distribution in Ukraine and southern Siberia (Drucker et al. 2018; Arppe et al. 2019) for late glacial periods, shortly before the extinction of the species in the respective areas. Additional isotopic investigations of ancient mammals in the Urals during the Late Pleistocene will help understanding the possible reasons for these patterns.

Interestingly, the three analysed cave lion specimens exhibit $\delta^{13}C$ and $\delta^{15}N$ values indicating the consumption of meat from ungulates, such as woolly rhinoceros and deer, although other ungulates not analysed in this study could also have been part of the diet. In any case, these isotopic values rule out cave bear as the main prey of these cave lions, in contrast with what has been found in caves from Germany and Belgium for some cave lions (Bocherens et al. 2011).

Despite these uncertainties on some ungulates and the limited amount of isotopic data, the cave bears clearly yielded isotopic values indicative of a herbivorous diet. Future isotopic analyses on the other types of cave bears from the Urals will allow us to establish if some niche partitioning occurred among the cave bears in this region, as it was the case in Austria (Bocherens et al. 2011) and as it is suggested by tooth microwear patterns (Ramirez Pedrasa et al. 2021).

Conclusions

The small-sized cave bears from the Imanay Cave are, on the one hand, metrically and morphologically very close to the small-sized bears of the Alps described as *U. deningeroides* Mottl (1964). On the other hand, metrically there is also a large agreement with the bears described as *U. rossicus* Borissiak (1930) from Krasnodar and from the Kizel Cave, of which the morphological data still have to be collected. It can be suggested already that there is a close relationship between these two groups. Genetic analyses are in progress and hopefully can verify or reject this assumption. The isotopic investigations demonstrated that these small cave bears were clearly herbivores, as all other cave bears analysed so far.

Our study is mainly concerned with the relationships of the small bears from Imanay Cave to the small cave bears in the Alps, as described in Herkova- der Repolust- und der Flatzer Tropfsteinhöhle. We want to study the relations to the type fauna of Krasnodar or to the fauna of Kizel Cave or to other small cave bears in Europe and Asia (Baryshnikov 2001; Spassov et al. 2017) in more detail only when DNA data and chronological data as well as data from the incisors is available.

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