General Palaeontology, Systematics, and Evolution (Vertebrate Palaeontology)

Variability of the upper incisors in the cave bears (Carnivora, Ursidae) from the Caucasus and Urals

Variabilité des incisives supérieures chez les ours des cavernes (Carnivora, Ursidae) du Caucase et de l'Oural

Gennady Baryshnikov [a], Dmitry Gimranov [b,*], Pavel Kosintsev [b]

[a] Zoological Institute of the Russian Academy of Sciences, Universitetskaya Emb. 1, 199034 Saint Petersburg, Russia
[b] Institute of Plant and Animal Ecology, Ural Branch, Russian Academy of Sciences, 202, 8th March Street, 620008 Yekaterinburg, Russia

A B S T R A C T

Morphometric and morphotypic variability of the cave bear upper incisors from two different geographic regions (Caucasus and Urals), different stratigraphic periods (middle and late Pleistocene), and bearing different mitochondrial haplogroups (*kudarensis* and *ingressus*) was studied. The specific diet of the cave bears, i.e. hard vegetables, led to noticeable differences between their incisors and the incisors of the brown bear (*Ursus arctos*). It was found that the upper incisors of the Caucasian cave bears from different stratigraphic periods demonstrate consistent development of their morphology. The late Pleistocene cave bears from the Urals show a greater similarity to the Caucasian cave bears from earlier periods than with the cave bears from later periods. Our results suggest that the incisor morphology has evolved independently in the Caucasian and Ural cave bears as they belong to different phylogenetic lineages and display different ways of adaptation to local environmental conditions.

© 2018 Published by Elsevier Masson SAS on behalf of Académie des sciences.

R É S U M É

La variabilité morphométrique et morphotypique des incisives supérieures d'ours des cavernes de deux régions géographiques différentes (Caucase et Oural), de différentes périodes stratigraphiques (Pléistocène moyen et supérieur) et portant différents haplogroupes mitochondriaux (*kudarensis* et *ingressus*) ont été étudiées. Le régime spécifique des ours des cavernes, c'est-à-dire des végétaux durs, a conduit à des différences notables entre leurs incisives et les incisives de l'ours brun (*Ursus arctos*). Il a été constaté que les incisives supérieures des ours des cavernes du Caucase de différentes périodes stratigraphiques démontrent un développement cohérent de leur morphologie. Les ours des cavernes du Pléistocène supérieur de l'Oural présentent une plus grande similitude avec les ours des

*   Corresponding author.
    E-mail address: djulfa250@rambler.ru (D. Gimranov).

cavernes caucasiens des périodes antérieures qu'avec ceux des périodes postérieures. Nos résultats suggèrent que la morphologie des incisives a évolué indépendamment chez les ours des cavernes du Caucase et de l'Oural, car elles appartiennent à différentes lignées phylogénétiques et présentent différentes manières d'adaptation aux conditions environnementales locales.

© 2018 Publié par Elsevier Masson SAS au nom de Académie des sciences.

1. Introduction

The cave bear is one of the best studied European Pleistocene faunal forms. Thousands of its bone remains have been found and described in a considerable body of literature (Kurtén, 1976; Musil, 1980). The cheek teeth, skulls, mandibles and post-cranial elements are usually described (Baryshnikov, 2007; Erdbrindk, 1953; Rabeder, 1999). However, the incisors are also of great interest since these teeth play an important role in foraging. The cave bears are believed to be highly herbivorous animals, eating mainly hard vegetable food (Bocherens et al., 1994). Therefore, the cave bear incisors are larger and have a more complex morphology compared to the incisors of modern brown bear (*Ursus arctos* L., 1758) (Rabeder, 1999).

Recent studies of the cave bear mitochondrial phylogeny revealed several lineages of this species (Baca et al., 2012; Knapp et al., 2009; Stiller et al., 2014) that can be considered separate species (Rabeder et al., 2004). The incisors of the individuals belonging to those lineages have not yet been subjected to a comparative analysis. The Caucasian cave bear, *U. kudarensis* Baryshnikov, 1985 is of particular interest. It became isolated earlier than the Middle Pleistocene bear *U. deningeri* von Reichenau, 1904, which is considered to be the ancestor of the European species *U. spelaeus* Rosenmüller, 1794 and *U. kanivetz* Vereshchagin, 1973 (= *ingressus* Rabeder et al., 2004).

We have studied a collection of the *U. kudarensis* incisors from two localities in the southern Caucasus (the Kudaro 1 Cave and Kudaro 3 Cave) and the *U. kanivetz* incisors from three localities in the Urals (the Secrets Cave = Tain Cave), the Ignatievskaya Cave and the Zapovednaya Cave) (Fig. 1). The Ural cave bears belong to the *ingressus* haplogroup described for the first time from in central and eastern Europe (Baca et al., 2012; Rabeder et al., 2004; Stiller et al., 2014). However, denomination *kanivetz* has a priority, thus we use it when refer to the Ural bears (Baryshnikov and Puzachenko, 2017).

In our previous work (Baryshnikov, 1998), two subspecies of *U. kudarensis*, namely *U. k. praekudarensis* from the middle Pleistocene and *U. k. kudarensis* from the late Pleistocene were identified. The teeth from the middle Pleistocene layers of the Kudaro 3 Cave (layers 5–8), occupying an intermediate stratigraphic position, were classified as transitional between the two subspecies (Baryshnikov, 1998).

The aim of this paper is to perform a comparative study of the evolution of the cave bear incisors from different stratigraphic levels of the Kudaro caves. Another aim is to trace changes in the morphology of the teeth of the bears from different genetic lineages and geographically remote
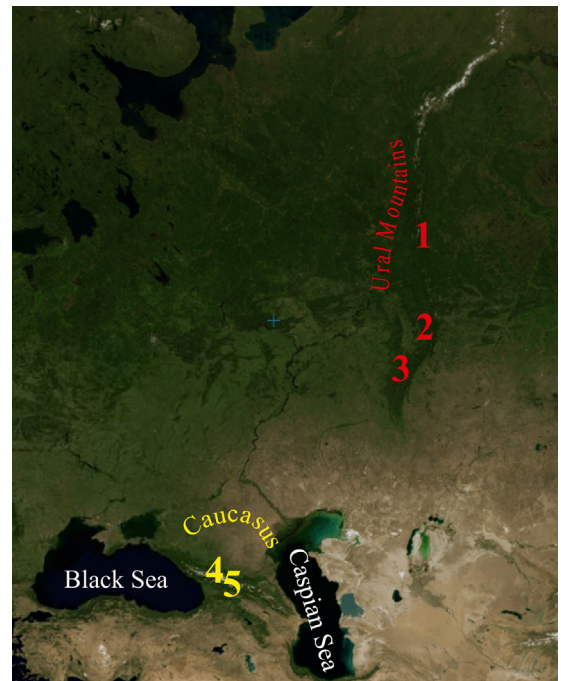
Fig. 1. Map of the cave bear localities. *Ursus kanivetz*: 1–Secrets Cave, 2–Ignatievskaya Cave, 3–Zapovednaya Cave; *U. kudarensis*: 4–Kudaro 1 Cave, 5–Kudaro 3 Cave.

Fig. 1. Carte des localités de l'ours des cavernes. *Ursus kanivetz* : 1–grotte de Secrets, 2–grotte de Ignatievskaya, 3–grotte de Zapovednaya; *U. kudarensis* : 4–grotte de Kudaro 1, 5–grotte de Kudaro 3.

areas: Caucasus vs. Urals. The large sample sizes employed in this study permit the upper and the lower incisors to be described separately.

2. Material and methods

The Kudaro 1 Cave and the Kudaro 3 Cave are located on the southern slope of the Caucasus (southern Ossetia, 42°31′N, 43°38′E), at height nearly 1600 m a. s. l. Both caves are located closely to each other and contain Early Paleolithic archaeological sites (Lioubine, 1998).

In the Kudaro 1 Cave, five cultural levels of the middle Pleistocene (Acheulean layer 5) and the late Pleistocene (Mousterian layers 3–4) age are distinguished. Layers 1 and 2 do not contain the teeth of cave bears. The cave deposits in their basal portion were dated by the radio-thermoluminescent method to $360,000 \pm 90,000$ years BP (RTL-379) for sublayer 5c and to $350,000 \pm 70,000$ BP (RTL-373) for sublayer 5b. The Mousterian sublayer 3a was dated

Table 1
Sample of the cave bear incisors employed in this study.
Tableau 1
Échantillon d'incisives des ours des cavernes utilisées dans cette étude.

Taxa	Locality	Tooth			Total
		I1	I2	I3	
U. k. praekudarensis	Kudaro 1 (layer 5)	55	234	80	369
U. kudarensis	Kudaro 3 (layers 5–8)	16	78	154	248
U. k. kudarensis	Kudaro 1 & 3 (layers 3–4)	112	99	151	362
U. kudarensis	All layers	183	411	385	979
U. kanivetz	Zapovednaya Cave	22	26	69	117
	Ignatievskaya Cave	37	52	59	148
	Secrets Cave	12	22	29	63
	All sites	71	100	157	328
Total		254	511	542	1307

by radiocarbon to 44,150 ± 2400/1,850 BP (Gr-6079) BP (Lioubine, 1998).

In the Kudaro 3 Cave, eight layers were recognized, of which the Acheulean layers 5–8 are dated to the middle Pleistocene, whereas the Mousterian layers 3–4 were formed in the late Pleistocene (Lioubine, 1998). The geomorphologic data suggest that the Kudaro 3 Cave was first opened for occupation by erosion which occurred approximately 50,000–100,000 BP after the opening of the Kudaro 1 Cave (Nesmeyanov, 1999). The contact zone of the Acheulian and Mousterian layers is dated by two RTL-dates to 252,000 ± 51,000 BP and 245,000 ± 49,000 BP (Lioubine, 1998), which suggests a considerable time gap between their depositions in the cave. For the ursid bones from layer 3, there are three AMS radiocarbon dates: > 41,600 BP (OxA-19611), 47,900 ± 2,500 BP (OxA-19612) and 47,700 ± 1,800 BP (OxA-19613) (Baryshnikov, 2011).

The Secrets Cave (= Tain Cave) is situated in the Middle Urals (59°25′N, 57°46′E), the Ignatievskaya Cave (54°54′N, 57°47′E) and the Zapovednaya Cave (54°33′N, 57°16′E) are located in the Southern Urals. In the Secrets Cave, one square was excavated and two layers were recognized. The depth of layer 2 is up to 0.3 m and it yielded only a few bone remains. A bone of *U. savini uralensis* Vereshchagin, 1973 from this layer is dated by radiocarbon beyond the method limit to > 37,890 BP (SOAN-4528). The depth of layer 1 is up to 0.9 m. Layer 2 yielded 13,369 bones of *U. kanivetz*, comprising 99.4% of all bone remains (Kosintsev and Vorob'ev, 2001). The bones belonging to *U. kanivetz* from this layer gave 6 radiocarbon dates: 37,190 ± 680 BP (VERA-1651), 39,190 ± 3,600 BP (OxA-16961), 39,580 ± 360 BP (OxA-16965), 39,630 ± 360 BP (OxA-16962) 40,340 ± 370 BP (OxA-16963), 47,600 ± 900 BP (OxA-16958) (Baryshnikov, 2007; Pacher and Stuart, 2009).

In the Ignatievskaya Cave, five sites were studied with 6 to 10 layers recognized (Smirnov et al., 1990). Layers 2–9 were formed in the late Pleistocene. These layers yielded 8768 bones of *U. kanivetz*, comprising 67–95% of all bone fragments (Kosintsev and Vorob'ev, 2001). A bone of *Panthera spelaea* from layer 3 (site V) was dated by radiocarbon to 41,900 ± 1,200 BP (OxA-10887), whereas bones of small mammals from the same layer revealed dates of > 27,620

BP (IPAE-59). The bones belonging to *U. kanivetz* from layer 8 (site V) and layer 5 (site II) revealed the following radiocarbon dates beyond the method limit: > 27,500 BP (IEMEG-723) and > 27,500 BP (IPAE-21).

In the Zapovednaya Cave, one site was studied with five layers recognized and dated to the Late Pleistocene. These layers yielded 9,496 bones belonging to *U. kanivetz*, comprising 99.8% of all bone remains. The bones of *U. kanivetz* revealed 5 radiocarbon dates: 28,700 ± 1,050 BP (LU-3715), > 37,250 BP (LU-3876), > 46,600 BP (LU-5135), > 50,200 BP (LU-5134), > 62,400 BP (OxA-19670) (Kosintsev and Bachura, 2013).

We examined the *U. kudarensis* collection from the Zoological Institute of Russian Academy of Sciences in St. Petersburg (ZIN) and the *U. kanivetz* collection from the Institute of Plant and Animals Ecology of the Russian Academy of Sciences in Ekaterinburg (IPAE). The studied specimens were assigned to 6 samples: *U. k. praekudarensis* (the Kudaro 1 Cave, layer 5), *U. k. kudarensis* (the Kudaro 1 Cave and Kudaro 3 Cave, layers 3–4), *U. kudarensis* (the Kudaro 3, layers 5–8), and three samples of *U. kanivetz* from the Urals (the Secrets Cave, the Zapovednaya Cave and the Ignatievskaya Cave). Hereinafter the sample *U. kudarensis* (the Kudaro 3, layers 5–8) is referred to as *U. kud.* (K3, 5–8). Description of the total sample studied is provided in Table 1.

Isolated upper incisors I1 and I2 are difficult to distinguish if we have a few specimens. When studying a large sample, I1 and I2 differ greatly in morphology (namely, the I2 is more complex) and also in size (I2 is larger). When we doubted the correctness of determining the position of a tooth, the samples were excluded from the analysis.

Dental measurements (L — greatest length, W — greatest width) were taken using a digital calliper, to the nearest 0.1 mm. Dental size differences between the groups were assessed using two-dimensional plots. Morphotypic differences were explored via a principal component analysis (PCA) and a correspondence analysis (CA). All statistical analyses were performed using Statistica 8.0. We follow Rabeder (1999) and his terms for the elements of the tooth crown. The morphodynamic index (MI) (Rabeder, 1999) was calculated on the basis of the identified morphotypes.
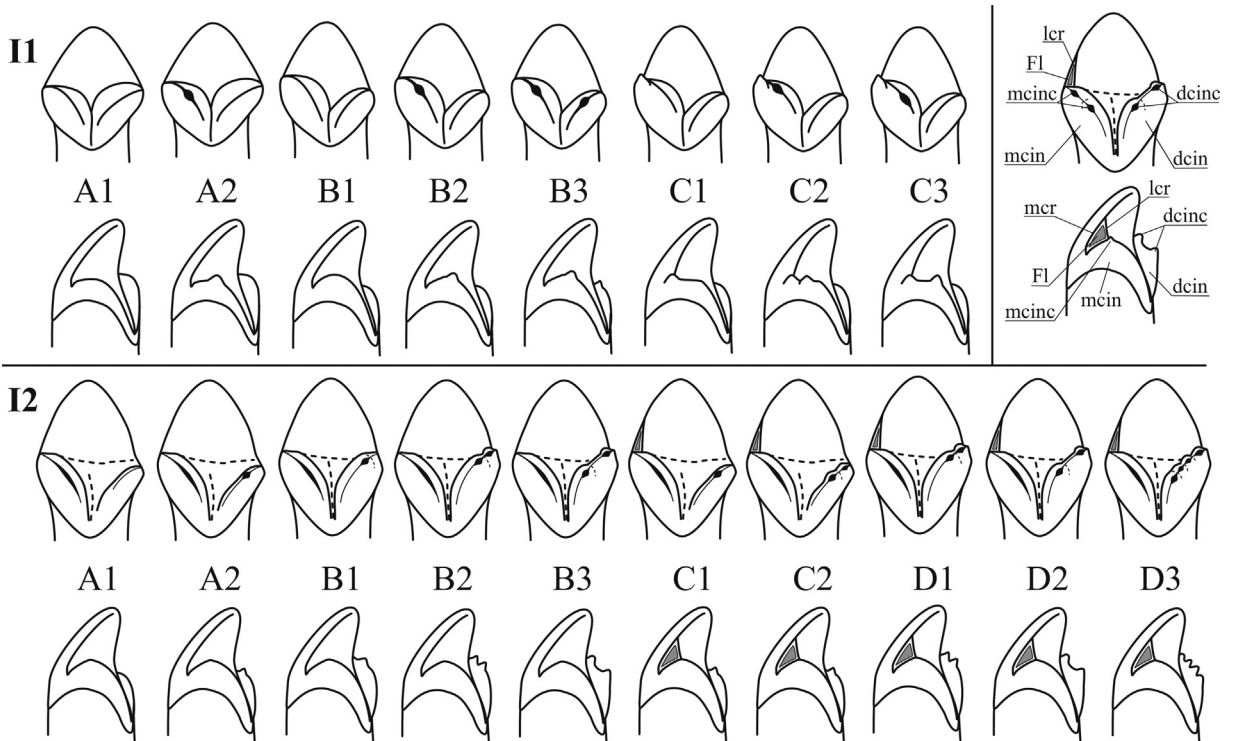
Fig. 2. The I1 and I2 morphotypes of the cave bears; lingual and mesial views. To identify the elements of the tooth crown we follow Rabeder (1999) and his terms with some modifications. Fl: fossa lunaris, lcr: lingual crista, mcr: mesial crista, mcin: mesial cingulum, dcin: distal cingulum, mcinc: mesial cingulum cusp, dcinc: distal cingulum cusp.

Fig. 2. Les morphotypes I1 et I2 des ours des cavernes ; vues linguale et mésiale. Pour identifier les éléments de la couronne dentaire, nous suivons Rabeder (1999) et ses termes, avec quelques modifications. Fl : fossa lunaris, lcr : lingual crista, mcr : mesial crista, mcin : mesial cingulum, dcin : distal cingulum, mcinc : mesial cingulum cusp, dcinc : distal cingulum cusp.

2.1. Description of tooth morphotypes

The **I1** morphotypes are characterized by the degree of development of the cingulum and the number of cusps (Fig. 2):

- *A1*–mesial (mcin) and distal (dcin) cingula of the same size.
- *A2*–mesial and distal cingula of the same size; a cusp in the middle part of the mesial cingulum (mcinc).

B

- *1*–distal cingulum is smaller than mesial.

B

- *2*–distal cingulum is smaller than mesial; a cusp in the middle part of the mesial cingulum.

B

- *3*–distal cingulum is smaller than mesial; cusps in the middle part of both cingula.
- C*1*–distal cingulum is smaller than mesial; a cusp on the mesial cingulum in the contact area with the mesial crista (mcr).
- C*2*–distal cingulum is smaller than mesial; cusps on the mesial cingulum located close to each other.
- C*3*–distal cingulum is smaller than mesial; cusps on the mesial cingulum located far from each other.

The **I2** morphotypes are characterized by the presence of the mesial angle, by the degree of the distal cingulum development and the number of its cusps (Fig. 2):

- *A1*–distal cingulum is smaller than mesial.
- *A2*–distal cingulum is smaller than mesial; a cusp on the distal cingulum (dcinc).

B

- *1*–mesial and distal cingula of the same size; a cusp on the distal cingulum.

B

- *2*–mesial and distal cingula of the same size; two cusps on the distal cingulum located close to each other.

B

- *3*–mesial and distal cingula of the same size; two cusps on the distal cingulum located far from each other.
- C*1*–distal cingulum is smaller than mesial; a cusp on the distal cingulum; an angle formed by the mesial (mcr) and lingual (lcr) cristas with a fossa lunaris (Fl).
- C*2*–distal cingulum is smaller than mesial; two cusps on the distal cingulum located close to each other; fossa lunaris.
- D*1*–mesial and distal cingula of the same size; two cusps on the distal cingulum located close to each other; fossa lunaris.
- D*2*–mesial and distal cingula of the same size; two cusps on the distal cingulum located far from each other; fossa lunaris.
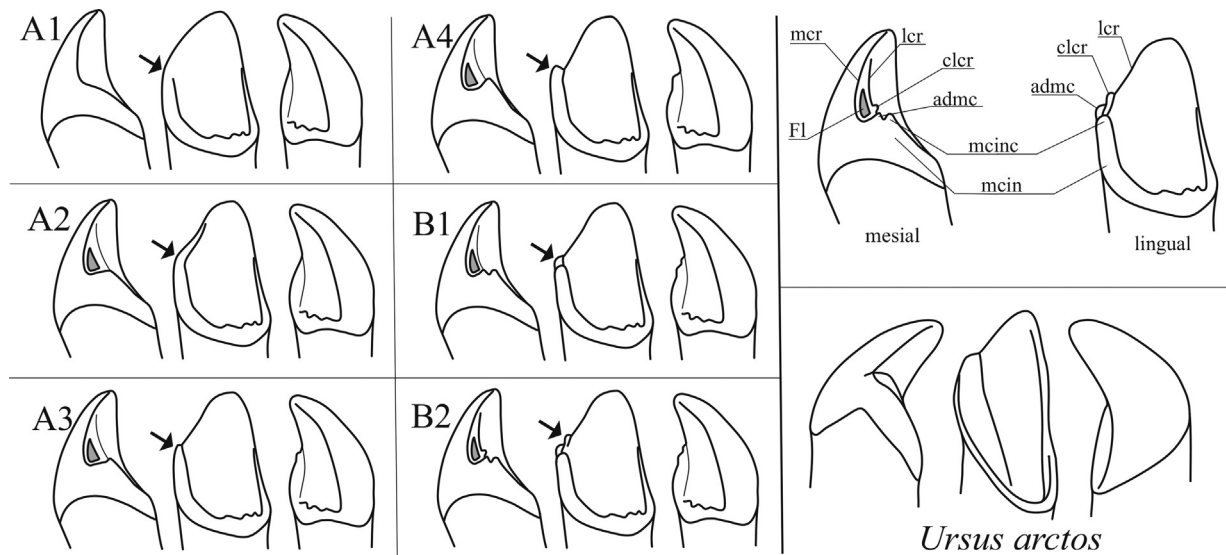
Fig. 3. The I3 morphotypes of the cave bears and the brown bear; lingual, distal and mesial views. To identify the elements of the tooth crown we follow Rabeder (1999) and his terms with some modifications. Fl: fossa lunaris, lcr: lingual crista, mcr: mesial crista, mcin: mesial cingulum, mcinc: mesial cingulum cusp, admc: additional mesial cusp, clcr: cusp lingual crista.

Fig. 3. Les morphotypes I3 des ours des cavernes et de l'ours brun ; vues linguale, distale et mésiale. Pour identifier les éléments de la couronne dentaire, nous suivons Rabeder (1999) et ses termes avec quelques modifications. Fl : fossa lunaris, lcr : lingual crista, mcr : mesial crista, mcin : mesial cingulum, mcinc : mesial cingulum cusp, admc : additional mesial cusp, clcr : cusp lingual crista.

Table 2
Frequency of the I1 morphotypes for the Caucasian and Ural cave bears.
Tableau 2
Fréquence des morphotypes I1 pour les ours des cavernes du Caucase et de l'Oural.

Taxa		A1	A2	B1	B2	B3	C1	C2	C3	Total
U. kanivetz	n	8	12	11	10	21	2	0	0	64
	%	12.5	18.8	17.2	15.6	32.8	3.1	0.0	0.0	100
U. k. kudarensis	n	3	0	5	9	7	4	37	15	80
	%	3.8	0.0	6.3	11.3	8.8	5.0	46.3	18.8	100
U. k. praekudarensis	n	7	0	22	31	7	0	12	2	81
	%	8.6	0.0	27.2	38.3	8.6	0.0	14.8	2.5	100
U. kud. (K3, 5–8)	n	2	0	0	6	0	0	4	0	12

- *D3*–mesial and distal cingula of the same size; 3–4 cusps on the distal cingulum located close to each other; fossa lunaris.

The mesial cingulum may have a cusp, however it is difficult to distinguish it due to its early abrasion, therefore we did not take into account the variability of this pattern.

The **I3** morphotypes differ in the morphology of the crown mesial part (Fig. 3):

- *A1*–no additional elements on the tooth crown.
- *A2*–an angle formed by the mesial and lingual cristas with a fossa lunaris.
- *A3*–fossa lunaris; a small mesial cusp in the contact zone between the mesial cingulum and lingual crista.
- *A4*–fossa lunaris; a massive mesial cusp.

B
- *1*–mesial cusp and an additional mesial cusp (admc) in the contact zone between the mesial cingulum and lingual crista; fossa lunaris.

B
- *2*–fossa lunaris; two mesial cusps and an additional cusp (cldr) at the base of the lingual crista.

3. Results

3.1. Morphotypic analysis

The **I1** morphotype frequencies for the cave bears are given in Table 2. The *U. kanivetz* sample is dominated by group B (65.6%), followed by quite numerous group A (31.3%). The *U. kudarensis* sample is also dominated by group B (50.2%), but group A is quite rare (6.2%). As for the Caucasian cave bears, nearly half of the examined specimens demonstrate morphotypes of group C (43.6%). *U. k. kudarensis* differs from *U. k. praekudarensis* in the following aspects: morphotypes of group B (26.3%) are rather rare, while morphotypes of group C (70.0%) predominate. The values of morphodynamic index (MI) are high in *U. k. kudarensis* and are the lowest in *U. k. praekudarensis* (Table 3).

Table 3
Morphodynamic index in the cave bears groups.
Tableau 3
Indice morphodynamique dans les groupes d'ours des cavernes.

Incisors	Morphotypes	Factor	Taxa			
			1[a]	2[b]	3[c]	4[d]
I1	A1	2	25.0	7.6	17.2	33.3
	A2	3	56.4	0.0	0.0	0.0
	B_1	1.5	25.8	9.5	40.8	0.0
	B_2	2.5	39.0	28.0	95.8	125.0
	B_3	3.5	114.8	30.8	30.1	0.0
	C1	2.5	7.8	12.5	0.0	0.0
	C2	3.5	0.0	161.7	51.8	116.7
	C3	3.5	0.0	65.5	8.8	0.0
	Total		268.8	315.5	244.4	275.0
I2	A1	1.5	15.2	9.8	51.2	0.0
	A2	2.5	19.8	16.3	1.5	0.0
	B_1	3	13.5	0.0	0.0	0.0
	B_2	4	31.6	0.0	0.0	0.0
	B_3	4	8.8	6.4	0.0	0.0
	C1	3.5	35.4	56.4	97.0	63.7
	C2	4.5	101.3	203.4	122.4	302.9
	D1	5	62.0	8.0	3.0	9.0
	D2	5	101.0	88.5	43.5	54.5
	D3	6	13.2	28.8	7.2	10.8
	Total		401.6	417.5	325.7	440.9
I3	A1	1	13.4	5.3	0.0	1.7
	A2	1.5	81.9	33.2	112.5	45.0
	A3	2	55.4	120.4	71.4	113.4
	A4	2.5	4.3	24.3	4.5	8.3
	B_1	3	5.1	8.1	5.4	20.1
	B_2	4	3.2	0.0	0.0	6.8
	Total		163.3	191.2	193.8	195.3
I1–I3	Total		833.6	924.2	763.9	911.1

[a] 1: *U. kanivetz*.
[b] 2: *U. k. kudarensis*.
[c] 3: *U. k. praekudarensis*.
[d] 4: *U. kud.* (K3, 5–8).

Table 4
Frequency of the I2 morphotypes for the Caucasian and Ural cave bears.
Tableau 4
Fréquence des morphotypes I2 pour les ours des cavernes du Caucase et de l'Oural.

Taxa		A1	A2	B_1	B_2	B_3	C1	C2	D1	D2	D3	Total
U. kanivetz	n	9	7	4	7	2	9	20	11	18	2	89
	%	10.1	7.9	4.5	7.9	2.2	10.1	22.5	12.4	20.2	2.2	100.0
U. k. kudarensis	n	4	4	0	0	1	10	28	1	11	3	62
	%	6.5	6.5	0.0	0.0	1.6	16.1	45.2	1.6	17.7	4.8	100.0
U. k. praekudarensis	n	59	1	0	0	0	48	47	1	15	2	114
	%	34.1	0.6	0.0	0.0	0.0	27.7	27.2	0.6	8.7	1.2	100.0
U. kud. (K3, 5–8)	n	0	0	0	0	0	10	37	1	6	1	55
	%	0.0	0.0	0.0	0.0	0.0	18.2	67.3	1.8	10.9	1.8	100.0

The **I2** morphotype frequencies are given in Table 4. The *U. kanivetz* sample is dominated by groups C and D (32.6 and 34.8%, respectively), whereas morphotypes A and B are observed the lowest often (18.0 and 14.6%, respectively). The *U. kudarensis* sample is dominated by group C (67.2%) with morphotypes A and D represented practically in equal numbers (18.0 and 14.6%, respectively); morphotype B was identified in only one case. *U. k. kudarensis* differs from *U. k. praekudarensis* in the following aspects: morphotype A is less frequent (12.9 against 34.7%), group D is more pronounced (24.2 against 10.4%), morphotype B3 (1.6%) is present. The morphotype frequencies observed in *U. kud.* (K3, 5–8) are similar to other subspecies of the Kudaro's

bears. The MI values are high in *U. kud.* (K3, 5–8) and are the lowest in *U. k. praekudarensis* (Table 3).

The **I3** morphotype frequencies are given in Table 5. Morphotypes A2 and A3 in all samples are dominant. Morphotype A2 prevails considerably in *U. kanivetz* and *U. k. praekudarensis* (54.6 and 65.6%, respectively), while morphotype A3 is peripheral (27.7 and 31.3%, respectively). Morphotypes A4 and B2 are rare for these taxa. Morphotype A1 (16.0%) is found in *U. kanivetz*. The third incisors of the *U. k. kudarensis* from layers 3–4 of the Kudaro 1 cave and Kudaro 3 cave and *U. kud.* (K3, 5–8) are similar to each other with regard to morphotype frequencies. All subspecies of the Kudaro's bear display

Table 5
Frequency of the I3 morphotypes for the Caucasian and Ural cave bears.
Tableau 5
Fréquence des morphotypes I3 pour les ours des cavernes du Caucase et de l'Oural.
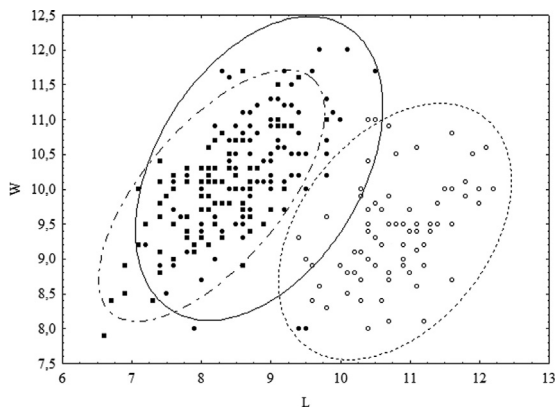
Taxa		A1	A2	A3	A4	B1	B2	Total
U. kanivetz	n	16	65	33	2	2	1	119
	%	13.4	54.6	27.7	1.7	1.7	0.8	100.0
U. k. kudarensis	n	6	25	68	11	3	0	113
	%	5.3	22.1	60.2	9.7	2.7	0.0	100.0
U. k. praekudarensis	n	0	84	40	2	2	0	128
	%	0	65.6	31.3	1.6	1.6	0.0	100.0
U. kud. (K3, 5–8)	n	1	18	34	2	4	1	60
	%	1.7	30.0	56.7	3.3	6.7	1.7	100.0

similar MI values, with the lowest index observed in *U. kanivetz* (Table 3).
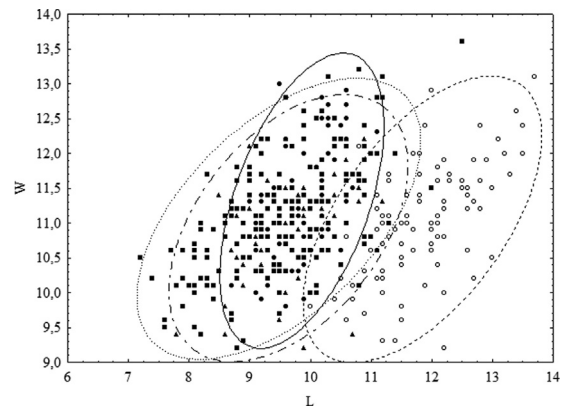
3.2. Morphometric analysis

When describing the size variability of the incisors, we cannot ignore the sexual dimorphism typical of the cave bears which is best manifested in the size of the cranium, canines and sometimes the third upper incisor (Baryshnikov, 2007; Kurtén, 1955, 1976; Rabeder and Withalm, 2014). As the plots show (Figs. 4–6), none of the cave bear incisor samples is divided into clear subgroups. Therefore, we believe that the sexual dimorphism of the upper incisors is not pronounced in the examined groups of the cave bears.

The dimensions of the cave bear incisors are given in Table 6 and Figs. 4–6. As the plots show (Figs. 4–6), size of the incisors in *U. kanivetz* differs from that in *U. kudarensis*. The scatters of the I1 are the least overlapping, whereas the largest overlap is observed in the I2 dimensions. The Caucasian bears form rather compact plots in the morphospace in terms of size of the I1, I2, and, particularly, I3. The incisors of *U. kanivetz* are larger compared to the teeth of *U. kudarensis*. The interspecific differences are primarily observed in the tooth length (L), whereas the crown width (B) is of a lesser importance (Table 6).
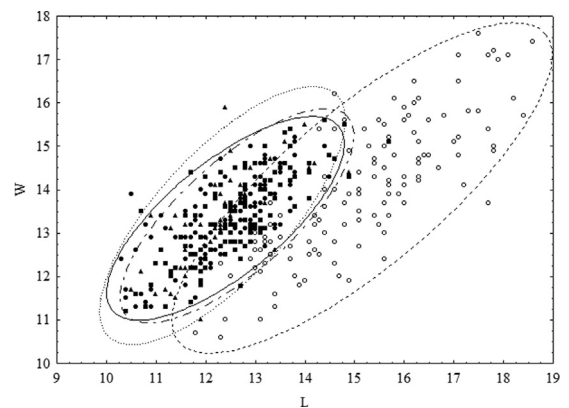
Fig. 5. Length (L) and width (W) of the I2 in the cave bears. White circles: *U. kanivetz*, black circles: *U. k. kudarensis*, black square: *U. k. praekudarensis*, black triangle: *U. kud.* (K3, 5–8); ellipses delineate 95% of the empirical range.
Fig. 5. Longueur (L) et largeur (W) de I2 chez les ours des cavernes. Cercles blancs : *U. kanivetz*, cercles noirs : *U. k. kudarensis*, carrés noirs : *U. k. praekudarensis*, triangle noir : *U. kud.* (K3, 5–8) ; les ellipses délimitent 95 % de la gamme empirique.

Fig. 6. Length (L) and width (W) of the I3 in the cave bears. White circles: *U. kanivetz*, black circles: *U. k. kudarensis*, black square: *U. k. praekudarensis*, black triangle: *U. kud.* (K3, 5–8); ellipses delineate 95% of the empirical range.
Fig. 6. Longueur (L) et largeur (W) de I3 chez les ours des cavernes. Cercles blancs : *U. kanivetz*, cercles noirs : *U. k. kudarensis*, carrés noirs : *U. k. praekudarensis*, triangle noir : *U. kud.* (K3, 5–8) ; les ellipses délimitent 95 % de la gamme empirique.

Fig. 4. Length (L) and width (W) of the I1 in the cave bears. White circles: *U. kanivetz*, black circles: *U. k. kudarensis*, black square: *U. k. praekudarensis*; ellipses delineate 95% of the empirical range.
Fig. 4. Longueur (L) et largeur (W) de I1 chez les ours des cavernes. Cercles blancs : *U. kanivetz*, cercles noirs : *U. k. kudarensis*, carrés noirs : *U. k. praekudarensis* ; les ellipses délimitent 95 % de la gamme empirique.

Table 6
Measurements of the upper incisors in the cave bears from the Caucasus and the Urals (mm).
Tableau 6
Mesures des incisives supérieures chez les ours des cavernes du Caucase et de l'Oural (mm).

Taxa	Locality	Measurements	I1		I2		I3	
			Lim (min–max)	Mean	Lim (min–max)	Mean	Lim -(min–max)	Mean
U. kanivetz	Zapovednaya	L	9.7–12.1	11.1	10.6–13.7	12.0	13.0–18.6	15.5
		W	8.6–11.0	9.7	9.2–13.1	11.1	11.3–17.6	14.2
	Secrets Cave	L	9.4–11.1	10.4	10.6–13.2	11.7	11.8–17.7	14.7
		W	8.4–10.9	9.5	9.6–12.9	11.2	10.6–15.8	13.4
	Ignatievskaya	L	9.5–12.2	10.7	10.0–13.5	11.8	12.3–18.2	14.9
		W	8.0–11.0	9.2	9.3–12.4	11.0	11.0–17.2	14.3
	All sites	L	9.4–12.2	10.8	10.0–13.7	11.8	11.8–18.6	15.2
		W	8.0–11.0	9.4	9.2–13.1	11.1	10.6–17.6	14.0
U. k. kudarensis	Kudaro 1 & 3	L	7.2–10.8	8.8	8.7–11.1	9.9	10.3–14.5	12.4
	(layers 3–4)	W	8.0–12.0	10.3	9.8–13.0	11.3	11.3–15.2	13.3
U. k. praekudarensis	Kudaro 1 (layer 5)	L	6.6–9.8	8.1	7.2–12.5	9.5	10.4–15.7	12.6
		W	7.9–11.7	9.9	9.2–13.6	11.1	11.2–15.6	13.4
U. kud.	Kudaro 3 (layers 5–8)	L	7.7–9.6	8.3	7.8–11.2	9.6	10.5–14.9	12.3
		W	9.0–11.0	9.9	8.4–12.2	10.9	11.0–15.9	13.4
All layers		L	6.6–12.2	8.6	7.2–12.5	9.6	10.3–15.7	12.5
		W	7.9–12.0	10.1	8.4–13.6	11.1	11.0–15.9	13.4

4. Discussion

4.1. Morphotypic analysis

Morphotypic differences between the taxa were explored using principal component analysis. The plots for each incisor describing the relationships between the cave bear samples can be found in Fig. 7.

All examined groups clearly differ from each other in terms of the **I1** morphotype frequency. The PC1 experience the highest loadings from morphotypes C and A1, whereas for the PC2 - from morphotypes B2 and B3 (Table 7A). Groups C2 and C3 predominate in *U. k. kudarensis*. These groups are absent in *U. kanivetz*. The *U. k. praekudarensis* sample is clearly separated from all other samples due to a low frequency of morphotypes C2 and C3, and high values of morphotype B2. The position of the I1 sample in *U. kud.* (K3, 5–8) is not clear because of its low sample size (only 12 teeth were analyzed).

All groups are quite isolated from each other with regard to the **I2** morphology (Fig. 7, B). The position of *U. kud.* (K3, 5–8) is an exception: this sample is plotted closer to *U. k. kudarensis*. High loadings to the PC1 come from morphotypes A2, B1–B3, C1, D1, D2 (Table 7). The Ural cave bear is quite peculiar due to uniform frequencies of virtually all the morphotypes. *U. k. kudarensis* differs from *U. k. praekudarensis* by the dominance of morphotype C2 (*U. k. kudarensis*) and of morphotype A1 (*U. k. praekudarensis*). Almost total absence of morphotypes B distinguishes the Caucasian cave bear from the Ural bear.

U. kanivetz and *U. kudarensis praekudarensis* are quite isolated from other groups on and close to each other with regard to the **I3** morphology (Fig. 7, C). In terms of the values of the PC1, *U. kud.* (K3, 5–8) is similar to *U. k. kudarensis*, and differs from it only on the PC2 which describes 30% of total variance. The main differences between the samples are observed in the ratio between the percentages of dominant morphotypes A2 and A3 displaying the highest loadings for the first component (Table 7).

Table 7
PC loadings of the morphotypic variables (percentage of morphotypes).
Tableau 7
Chargements PC des variables morphotypiques (pourcentage de morphotypes).

	Variable	PC1	PC2
I1	A1	−0.800906	0.320449
	A2	−0.435430	−0.832050
	B_1	−0.356573	−0.452789
	B_2	−0.551113	0.831079
	B_3	−0.278404	−0.952145
	C1	0.734549	−0.622367
	C2	0.795405	0.582147
	C3	0.993858	−0.080543
	Variance	43.74%	41.62%
I2	A1	0.352323	−0.808497
	A2	−0.929630	0.124358
	B_1	−0.884947	−0.390711
	B_2	−0.884947	−0.390711
	B_3	−0.960492	0.112898
	C1	0.896379	−0.353216
	C2	0.460189	0.764552
	D1	−0.905676	−0.307075
	D2	−0.957029	0.246376
	D3	−0.349282	0.744851
	Variance	63.50%	24.06%
I3	A1	−0.356322	−0.073764
	A2	−0.900900	0.173145
	A3	0.964161	−0.217465
	A4	0.647422	−0.752771
	B_1	0.790725	0.605501
	B_2	0.399408	0.871163
	Variance	51.20%	29.58%

As the PCA results show, no common patterns between the three incisors are observed in terms of the distribution of their morphotypes dimensions in the examined groups of the cave bears. The plot for the first incisor morphotype frequencies does not provide a clear picture of the relationships between the sample centroids. It is difficult to evaluate the similarity between the examined groups using the I2 morphotypes as well, with the exception of an apparent similarity between the *U. kud.* (K3, 5–8) and *U. k. kudarensis* samples. The situation is different for the

I3 morphology. As our analysis demonstrates, this tooth's morphotype frequencies are similar between *U. kanivetz* and *U. kudarensis praekudarensis*.

The PCA results show that *U. k. praekudarensis* and *U. k. kudarensis* are consistently plotted remotely from each other. The position of *U. kud.* (K3, 5–8) varies among different analyses. The morphotype ratio for the I1 brings the *U. kud.* centroid closer to *U. k. praekudarensis*, while based on the I2 morphology it is closer to *U. k. kudarensis*, while the I3 plot places it at an equal distance from both
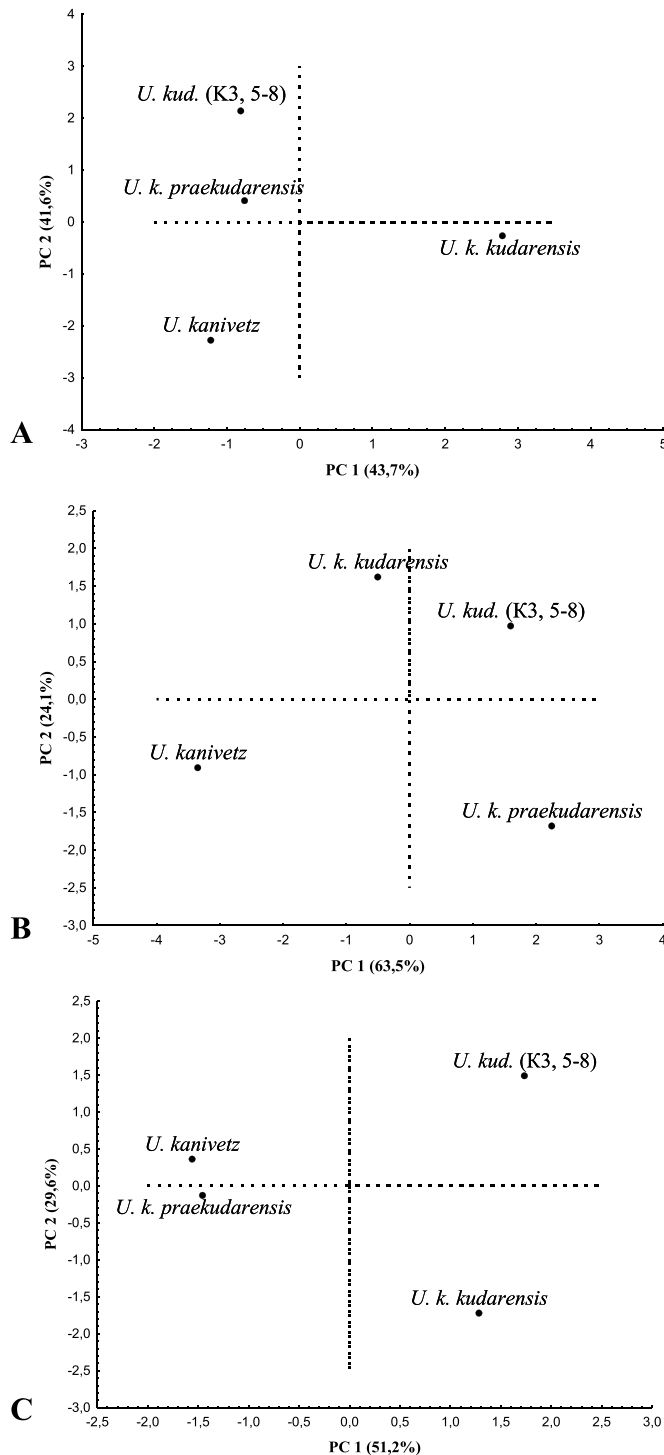
Fig. 7. Principal component analysis based on the I1 (A), I2 (B), and I3 (C) morphotype frequencies.
Fig. 7. Analyse en composantes principales, basée sur les fréquences des morphotypes I1 (A), I2 (B) et I3 (C).
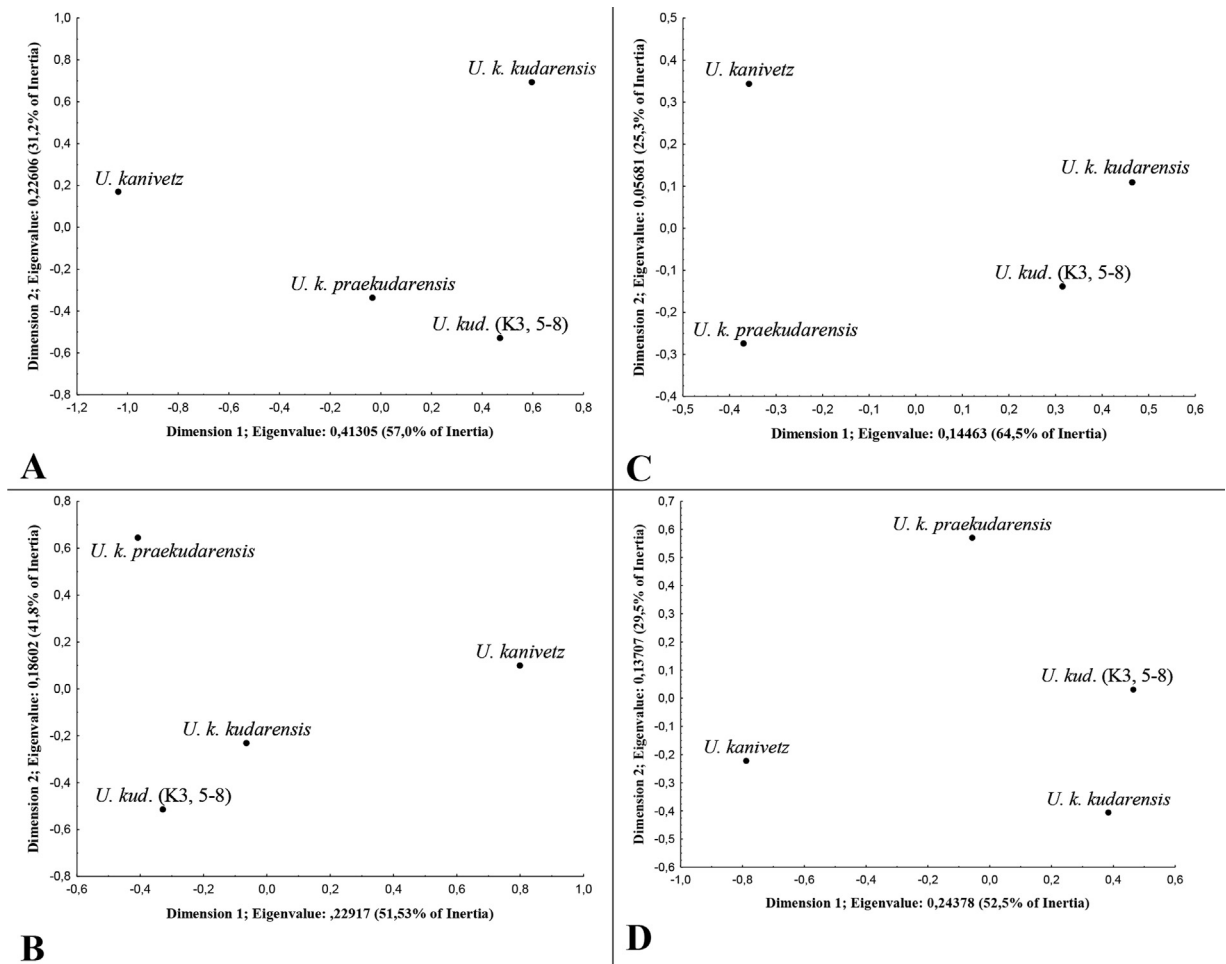
Fig. 8. Correspondence analysis two-dimensional row plot, based on symmetrical normalization, illustrating the relationships among the four cave bears groups based on the I1 (A), I2 (B), I3 (C), I1–I3 (D) morphology.

Fig. 8. Analyse par correspondance de lignes bidimensionnelles, basée sur une normalisation symétrique, illustrant les relations entre les quatre groupes d'ours des cavernes, basées sur la morphologie I1 (A), I2 (B), I3 (C), I1–I3 (D).

subspecies (Fig. 7). This result can reflect the transitional nature of this form (transition from *U. k. praekudarensis* to *U. k. kudarensis*).

The position of *U. kanivetz* relative to *U. kudarensis* is more certain. In terms of the I1 and I2 morphology, it occupies an isolated position, though in terms of the I3 morphology it is close to *U. k. praekudarensis* (Fig. 7). Generally, *U. kanivetz* is more distinct from *U. kudarensis* in terms of the incisor morphology, than are the forms of the latter species from each other.

While the PCA is commonly used for the analysis of metric variables, the CA is typically used when analyzing the frequencies of qualitative features. Thus, our next step was to perform a CA of the morphotype frequencies in the examined groups of the cave bears (Fig. 8, A–D). In all cases, *U. k. praekudarensis* and *U. k. kudarensis* are the most remote points on the plots. The position of *U. kud.* (K3, 5–8) is less certain. In terms of the frequencies of the I2, I3 morphotypes, it is closer to *U. k. kudarensis* (Fig. 8B–C), while in terms of the frequencies of the I1 morphotypes, it is closer to *U. k. praekudarensis* (Fig. 8, A). This reflects a transitional

position of *U. kud.* (K3, 5–8). However, in general, *U. kud.* (K3, 5–8) plots close *U. k. kudarensis* more often. This gives us a reason to assume that the *U. kud.* (K3, 5–8) sample belongs to the later subspecies of the Caucasian cave bear (*U. k. kudarensis*). *U. kanivetz* is clearly distinguished from the *U. kudarensis* subspecies by the morphotypes of the upper incisors (Fig. 8, A–D).

The MI values vary to some extent in the samples. Inside the samples, the incisors demonstrate common to all three teeth trends to either amplification or simplification (Table 3, Fig. 9).

High MI values are typical of *U. k. kudarensis* and *U. kud.* (K3, 5–8). This proves again the proximity of the *U. kud.* (K3, 5–8) sample to *U. k. kudarensis*, rather than to *U. k. praekudarensis*. *U. kanivetz* and *U. k. praekudarensis* both display a high proportion of simple morphotypes. The MI values of *U. k. praekudarensis* are also the lowest. The *U. k. praekudarensis* sample is the most ancient of all and is dated to the Late Middle Pleistocene.

A morphotypic study of the cave bears incisors was previously carried out on large samples from some Austrian
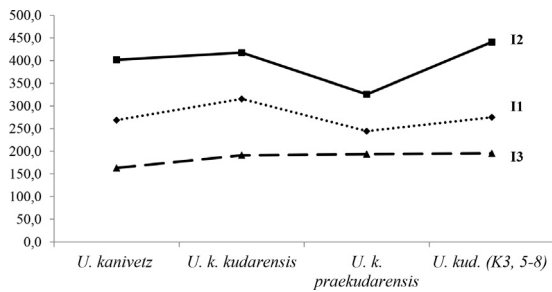
Fig. 9. Ratio diagrams of the morphodynamic index (MI) of the upper incisors of the cave bears groups (according to (total) Table 3).
Fig. 9. Diagrammes de *ratio* de l'index morphodynamique (MI) des incisives supérieures chez les groupes d'ours des cavernes (selon Tableau (total) 3).

caves (Rabeder, 1999). As G. Rabeder pooled the I1 and I2 data, it is rather difficult to compare the frequencies of morphotypes obtained in the present study to those published by Rabeder (1999). It is also impossible to compare the frequencies of the I3 morphotypes, as Rabeder (1999) did not analyze variability of the mesial part of the tooth. We also did not find any tooth with Kalyx distalis (denoted Kd by Rabeder, 1999) on the distal part. Despite this fact, the results published by Rabeder can be used to describe the morphologic changes of the incisors in different cave bear phyla. The lowest MI values are shown by the sample from the Repolust Cave deposits. This cave is dated to the late middle Pleistocene. The remains of the cave bears from this cave belong to *U. deningeri*, though its affiliation to the *deningeri*-group is doubted (Rabeder, 1999; Rabeder and Withalm, 2014; Rabeder et al., 2009). The *U. deningeri*incisors are often characterized by the dominance of simply built morphotypes without additional elements, they are very simple in morphology and similar to morphotypes B1 and B2 (I1), A1 (I2), A1 (I3). The I1 and I2 in *U. kanivetz ingressus* (Rabeder et al., 2004) from Gamssulzenhöhle and *U. spelaeus* ssp. from Herdengelhöhle have similar MI values. These cave bears have fairly developed incisors with a fossa lunaris, a pronounced lingual crista (Linqualkante) and cusps on the cingula. The incisors in *U. spelaeus ladinicus* Rabeder et al., 2004 and

U. s. eremus Rabeder et al., 2004 from Conturines Cave and Schwabenreith-Höhle are not very developed.

Thus, we can come to the conclusion that *U. k. praekudarensis* had a simple morphology of the incisors that resembles the incisors of *U. deningeri*; both samples are dated to the middle Pleistocene. The incisors of *U. k. kudarensis* and *U. kud.* (K3, 5–8) are much more developed. The incisors of *U. kanivetz ingressus* are the most developed of all the Austrian samples. The incisors of *U. spelaeus ladinicus* and *U. s. eremus* are less developed. It seems that the morphology of the incisors between these species is barely distinguished. A medium degree of the development is typical of *U. kanivetz* from the Urals.

The morphology of the cave bear incisors typical for the basal taxa of this phylum is characterized by the absence of any additional elements on the tooth crown, while the derived morphology shows the development of certain additional elements. Morphotypes A1 and B1 are primitive for the I1, whereas morphotype A1 is primitive for the I2, and morphotypes A1 and A2 – for the I3. This gives us an evidence to suggest that *U. k. praekudarensis* retains a lot of archaic features that were also typical of the Deninger's bear (Tchernov and Tsoukala, 1997). *U. k. kudarensis* has some derived adaptive features that developed in parallel with other late Pleistocene bear species (*U. kanivetz* and *U. spelaeus*).

4.2. Morphometric analysis

The incisors in *U. kanivetz* are bigger compared to *U. kudarensis*, (Figs. 4–6 and Table 6). The *U. kudarensis* sample groups demonstrate a substantial overlap in the incisor length and width. The work by Rabeder (1999) provides data on width and height of the I3 belonging to the *Austrian*cave bears. No data is given for the length. To compare our results with those of Rabeder, we combined the data for the I1 and I2 dimensions (Table 8) and added the width of the I3. The results of the comparison are presented as a three-dimensional plot (Fig. 10) based on the mean values of the length (x), width (y) for the I1 + I2, and width of the I3 (z).

Position of the sample centroids in Fig. 10 primarily shows that *U. kanivetz kanivetz* differs from other taxa by
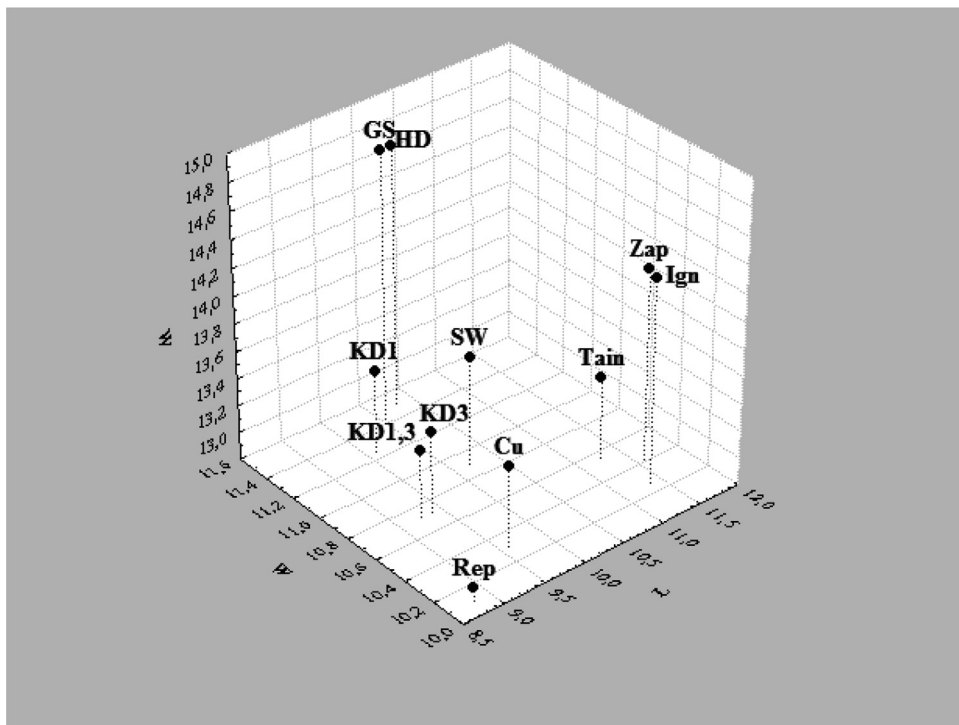
Table 8
Sample means of the upper incisors measurements of the cave bears of western Europe, the Caucasus and the Urals.
Tableau 8
Moyenne des mesures des incisives supérieures chez les ours des cavernes de l'Europe occidentale, du Caucase et de l'Oural.

Taxa	Locality	I1, I2			I3	
		n	L	W	n	W
U. kanivetz ingressus[a]	Gamssulzenhöhle	30	10.0	11.4	59	14.8
U. spelaeus sp.	Herdengelhöhle	24	10.3	11.5	39	14.7
U. spelaeus ladinicus	Conturuneshöhle	40	9.6	10.3	37	13.4
U. spelaeus eremus	Schwabenreith-Höhle	20	10.2	10.9	80	13.6
U. deningeri	Repolust	20	8.8	10.1	74	12.9
U. kanivetz kanivetz	Zapovednaya Cave	48	11.6	10.4	69	14.2
U. k. kanivetz	Secrets Cave	33	11.3	10.6	18	13.4
U. k. kanivetz	Ignatievskaya Cave	87	11.4	10.3	43	14.3
U. kudarensis kudarensis	Kudaro 1 & 3 (layers 3–4)	166	9.3	10.7	58	13.3
U. k. praekudarensis	Kudaro 1 (layer 5)	273	9.6	11.3	119	13.4
U. kud.	Kudaro 3 (layers 5–8)	68	9.4	10.7	50	13.4

[a]Data for the cave bears from the Western Europe are quoted from Rabeder (1999).

Fig. 10. Three-dimensional plot of dimensions of the upper incisors of the cave bears of western Europe, the Caucasus and the Urals. GS: Gamssulzenhöhle, HD: Herdengelhöhle, Cu: Conturines Cave, SW: Schwabenreith-Höhle, Rep: Repolust Cave, Zap: Zapovednaya Cave, Tain: Secrets Cave, Ign: Ignatievskaya Cave, KD1,3: Kudaro 1 & 3 (layers 3–4), KD1: Kudaro 1 (layer 5), KD3: Kudaro 3 (layers 5–8).

Fig. 10. Diagramme tridimensionnel des dimensions des incisives supérieures des ours des cavernes d'Europe occidentale, du Caucase et de l'Oural. GS : Gamssulzenhöhle, HD : Herdengelhöhle, Cu : Grotte des Conturines, SW : Schwabenreith–Höhle, Rep : Grotte Repolust, Grotte Zap : Zapovednaya, Grotte Tain : Secrets, Ign : Grotte Ignatievskaya, KD1,3 : Kudaro 1 & 3 (couches 3–4), KD1 : Kudaro 1 (couche 5), KD3 : Kudaro 3 (couches 5–8).

the incisor size. Species differentiation is primarily based on the tooth length (L) of the I1 and I2. *U. k. kanivetz* shows a faint resemblance to *U. k. ingressus* in terms of the width of the I3. All the measurements of *U. k. ingressus* are very similar to *U. spelaeus* ssp. from Herdengelhöhle. The *U. deningeri* sample from Repolust Cave deposits occupies an isolated position. The Caucasian cave bears are plotted close to *U. spelaeus ladinicus* and *U. s. eremus* from Conturines Cave and Schwabenreith-Höhle. They are similar in the length of the I1 and the width of the I3. Within this group, the width of the I2 is the largest in *U. k. praekudarensis* and smallest in *U. s. ladinicus*. It is worthy of note that *U. k. praekudarensis* displays an isolated position compared to *U. k. kudarensis* and *U. kud.* (K3, 5–8) that are plotted quite close to each other.

As it comes from the comparison of the incisor size, all the *U. kanivetz* samples are quite distinct, though subspecies of *U. k. kanivetz* and *U. k. ingressus* occupy different positions in the plot. The *U. deningeri* sample with the smallest incisors holds a unique position. *U. kudarensis* differs from *U. spelaeus* by some dimensions, though within this group we can distinguish *U. k. praekudarensis* with quite large I2 and *U. s. ladinicus* with small I2.

4.3. Comparison with other species of the genus Ursus

The morphology of the I1 and I2 is quite similar between *U. arctos* and *U. maritimus* (Gimranov and Kosintsev, 2017).

The identified morphotypes in both species do not have any exact analogies among the cave bear incisors. The morphology features of the I3 of the brown bear are described in Fig. 3. It has no additional elements on the mesial cingulum and the mesial crista. The mesial cingulum has quite a developed morphology with a surface without a tip at the base of the mesial crista; there is no lingual crista as well. The form of the I3 in *U. arctos* is apparently more stabbing than that of the cave bears, and finds no analogies among the latter (Erdbrindk, 1953).

The data on morphology of the upper incisors of extinct *U. minimus* Devèze de Chabriol et Bouillet, 1827 and *U. etruscus* Cuvier, 1823, that are believed to be the ancestors of the cave and brown bears, is very scarce. The I3 in *U. minimus* has a poorly pronounced mesial cingulum with a small surface (Qiu et al., 2009). The upper incisors in *U. etruscus* also have a primitive morphology (Baryshnikov, 2007; Koufos et al., 2017; Teilhard de Chardin, 1940). It should be noted that the incisors of *U. arctos* are very similar to the incisors of *U. etruscus*.

The upper incisors of the cave bears including those of *U. deningeri*, the basal representative of the European cave bears, display a more complex morphology. Teeth of *U. deningeri* are characterized by a massive cingula, sometimes with pronounced tips and additional cusps (Gimranov and Kosintsev, 2017; Rabeder, 1999, Rabeder et al., 2009; Tchernov and Tsoukala, 1997). Another Late Middle Pleistocene species, *U. savini* Andrews, 1922, had

a more developed morphology of the upper incisors (Borissiak, 1932) than *U. deningeri*, *U. spelaeus*, *U. kudarensis* and *U. kanivetz*. Thus, the upper incisors, like other teeth of the cave bears, are quite specific. Their crowns have a lot of additional elements. Such morphology is undoubtedly related to an adaptation to a specific diet, i.e. hard vegetables.

The cave bears (subgenus *Spelearctos*) form an independent evolutionary lineage in the phylogenetic tree of the genus *Ursus* (Baryshnikov, 2007; Rabeder et al., 2009), developing a hypocarnivorous trend. The main line of the genus (*U. minimus–U. etruscus–U. arctos*) is characterized by the retention of plesiomorphic patterns in the morphology of the incisors and cheek teeth.

Morphology of the incisors of the Caucasian and Ural cave bears is in line with the general evolutionary trend in cave bear-like ursids, characterized by the development of the tooth morphology and the emergence of additional elements on the crown. However, their phylogenetic isolation means that the advanced patterns in the Caucasian cave bears developed in parallel with other cave bears. The most ancient studied subspecies, *U. k. praekudarensis*, exhibits many primitive characters of the incisor morphology. Compared to *U. k. praekudarensis*, the incisor form in *U. deningeri* suggests that this subspecies is more advanced (that the latter), which complies with the evolutionary position of the Caucasian cave bears.

5. Conclusion

The main conclusion of this study is that the incisor morphology is not any less important and informative in terms of studying the cave bear phylogeny than more commonly used skeletal elements and check teeth.

The PCA and CA results show that *U. k. praekudarensis* and *U. k. kudarensis* are very specific compared to other taxa in terms of the incisor morphology and, in the same time, differ substantially from each other. *U. kud.* (K3, 5–8) occupies a transitional position between these subspecies, but more often exhibits similarities to *U. k. kudarensis*. This allows us to assume that the *U. kud.* (K3, 5–8) sample belongs to the latter subspecies, i.e. *U. k. kudarensis*, which is also proved by high MI values in *U. k. kudarensis* and *U. kud.* (K3, 5–8). With regard to the incisor morphology, *U. kanivetz* is clearly distinct from *U. kudarensis*. This difference is more pronounced compared to the difference between the subspecies of *U. kudarensis*, though both *U. kanivetz* and *U. k. praekudarensis* display high frequencies of simple morphotypes.

Sexual dimorphism of the upper incisors is not pronounced in the examined groups of the cave bears. *U. deningeri* had the smallest incisors. The incisors in *U. kanivetz* are larger than in *U. kudarensis*. Subspecies *U. kanivetz kanivetz* and *U. k. ingressus* occupy distant positions on the plots. Generally, the Ural cave bears have longer and narrower I1 and I2 than other studied taxa. We can distinguish *U. k. praekudarensis* with quite large I2 and *U. s. ladinicus* with small I2. The *U. kudarensis* subspecies demonstrate a substantial overlap in the incisor length and width.

Morphology of the incisors of the Caucasian and Ural cave bears are clearly different from that of modern *U. arctos* and *U. maritimus*, as well as from that of ancient taxa *U. minimus* and *U. etruscus*. The incisors in *U. deningeri*, *U. spelaeus*, *U. savini*, *U. kudarensis* and *U. kanivetz* are similar to each other which is in line with the general evolutionary direction of the cave bear lineage towards the development of the tooth morphology and hypocarnivorous adaptation. The tendency to develop additional elements on the occlusal surface is explained (evolutionary speaking) by the adaptation of the cave bears to a specific diet based on relatively hard vegetables.

References

Baca, M., Stankovic, A., Stefaniak, K., Marciszak, A., Hofreiter, M., Nadachowski, A., Weglenski, P., Mackiewicz, P., 2012. Genetic analysis of cave bear specimens from Niedzwiedzia Cave, Sudetes, Poland. Palaeontol. Electron. 15 (2), 1–16.

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

Baryshnikov, G., 2007. (Bears Family (Carnivora, Ursidae)) Semeystvo Medvezh'i (Carnivora, Ursidae). Fauna Rossii i sopredel'nykh stran (in Russian). Nauka, St. Petersburg (541 p.).

Baryshnikov, G.F., 2011. Pleistocene Felidae (Mammalia, Carnivora) from Paleolithic site in Kudaro caves in the Caucasus. Proc. Zool. Inst. RAS 315 (3), 197–226.

Baryshnikov, G.F., Puzachenko, A.Y., 2017. Morphometric analysis of metacarpal and metatarsal bones of cave bears (Carnivora, Ursidae). Fossil Imprint 73 (1–2), 7–47.

Bocherens, H., Fizet, M., Mariotti, A., 1994. Diet, physiology and ecology of fossil mammals as inferred from stable carbon and nitrogen isotope biogeochemistry: implications for Pleistocene bears. Palaeogeogr. Palaeoclimatol. Palaeoecol. 107 (3–4), 213–225.

Borissiak, A., 1932. (New race of cave bear from the Quaternary deposits of Northern Caucasus). Novaya rasa peshchernogo medvedya iz chetvertichnykh otlozheniy Sev. Kavkaza (in Russian). Trudy Paleozoolog. Inst. 1, 137–201.

Erdbrink, P., 1953. A review of fossil and recent bears of the Old World with remarks on their phylogeny based on their dentition. Jan de Lange, Deventer, Netherlands (597 p.).

Gimranov, D.O., Kosintsev, P.A., 2017. Morphotypic variability of the incisors of the brown (*Ursus arctos*) and polar (*Ursus maritimus*) bears (Carnivora, Ursidae) (in Russian). Zool. J. 96 (5), 547–562.

Knapp, M., Rohland, N., Weinstock, J., Baryshnikov, G., Sher, A., Doris, N., Rabeder, G., Pinhasi, R., Schmitt, H., Hoffreiter, M., 2009. Fist DNA sequences of Asian cave bear fossils reveal deep divergences and complex phylogeographic patterns. Mol. Ecol. 18 (6), 1225–1238.

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., Vorob'ev, A.A., 2001. Biology of Large Cave Bear (*Ursus spelaeus* Ros. et Hein.) in the Ural Mountains (in Russian). In: Mammoth and its Environment: 200 Years of Investigations. GEOS Press, Moscow, pp. 266–278.

Koufos, G.D., Konidaris, G.E., Harvati, K., 2017. Revisiting Ursus etruscus (Carnivora, Mammalia) from the Early Pleistocene of Greece with description of new material. Quat. Int. (in press).

Kurtén, B., 1955. Sex dimorphism and size trends in the cave bear, *Ursus spelaeus* Rosenmüller and Heinroth. Acta Zool. Fennica 90, 1–48.

Kurtén, B., 1976. The cave bear story. Life and death of a vanished animal. Columbia University Press, New York (163 p.).

Lioubine, V.P., 1998. The Acheulian epoch of in the Caucasus. (in Russian). Peterburgskoe Vostokovedenie, St. Petersburg (192 p.).

Musil, R., 1980. *Ursus spelaeus*–Der Höhlenbar. Weimar: Weimarer Monographien zur Ur- und Friihgeschichte. Teil I (94 p.).

Nesmeyanov, S.A., 1999. (Geomorphological aspects of Paleolithic palaeoecology of the Westwrn Caucasus). Geomorphologicheskie aspekty paleoecologii gornogo paleolita na primere Zapadnogo Kavkaza (In Russian). Nauchnyi Mir, Moscow (392 p.).

Pacher, M., Stuart, A.J., 2009. Extinction chronology and palaeobiology of the cave bear (*Ursus spelaeus*). Boreas 38, 189–206.

Qiu, Z.X., Deng, T., Wang, B.Y., 2009. First ursine bear material from Dongxiang, Gansu: addition to the Longdan mammalian fauna. Vertebr. PalAsiat. 47, 245–264.

Rabeder, G., 1999. Die Evolution des Höhlenbärengebisses. Mitt. Komm. Quartärkomm. Österr. Akad. Wiss. 11, 1–102.

Rabeder, G., Withalm, G., 2014. Sexual Dimorphism and Sex-Ratio of Cave Bears from Križna jama (Slovenia). Mitt. Komm. Quartärforsch. Österr. Akad. Wiss. 21, 109–116.

Rabeder, G., Pacher, M., Withalm, G., 2009. Early Pleistocene bear remains from Deutsch-Altenburg (Lower Austria). Mitt. Komm. Quartärforsch. Österr. Akad. Wiss. 17, 1–135.

Rabeder, G., Hofreiter, M., Nagel, D., Withalm, G., 2004. New taxa of Alpine Cave Bears (Ursidae, Carnivora). Cah. Sci. 2, 49–67.

Smirnov, N.G., Bolshakov, V.N., Kosintsev, P.A., Panova, N.K., Korobeynikov, Yu.I., Olshvang, V.N., Erokhin, N.G., Bikova, G.V., 1990. Historical Ecology of Animals of the South Urals Mountains (in Russian). Uralskoe Otd. Akademyi Nauk SSSR Press, Sverdlovsk (245 p.).

Stiller, M., Molak, M., Prost, S., Pacher, M., Rabeder, G., Baryshnikov, G., Rosendahl, W., Muenzel, S., Bocherens, H., Grandal-d'Anglade, A., Hilpert, B., Germonpré, M., Stasyk, O., Pinhasi, R., Ho, S., Hofreiter, M., Knapp, M., 2014. Mitochondrial DNA diversity and evolution of the Pleistocene cave bear complex. Quat. Int. 339 (34), 224–231.

Tchernov, E., Tsoukala, E., 1997. Middle Pleistocene (Early Toringian) Carnivore Remains from northern Israel. Quat. Res. 48 (1), 122–136.

Teilhard de Chardin, P., 1940. The fossils from Locality 18 near Peking. Palaeontologia Sinica. New Ser C 9, 1–94.